Review Article

The buck effect in goats: A review of neuroendocrine mechanisms, modulating factors, and applications in reproductive management

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Abstract

The male effect (buck effect) is a sustainable, hormone-free biostimulation strategy in caprine reproduction, in which introducing sexually active bucks to seasonally anestrous does increases luteinizing hormone (LH) pulse frequency, thereby stimulating folliculogenesis and ovulation. This review provides a comprehensive synthesis of the sensory, neuroendocrine, breed-related, and management factors governing male biostimulation in goats (*Capra hircus*). Olfactory signals, including the identified primer pheromone 4-ethyloctanal, are perceived through the main and accessory olfactory systems and act together with visual, auditory, and tactile cues. These sensory inputs activate the hypothalamic gonadotropin-releasing hormone (GnRH) pulse generator probably through the medial amygdala and the arcuate kisspeptin/neurokinin B/dynorphin (KNDy) neuronal network; the resulting rise in estradiol may subsequently trigger a preovulatory LH surge. The response is strongly modulated by photoperiod and latitude, buck libido, female body condition, breed-specific anestrous depth, and climatic stressors, particularly in tropical production systems. To optimize outcomes, practical management frameworks now integrate artificial photoperiod treatments of bucks, social facilitation protocols, such as the buck-to-buck effect, targeted nutritional supplementation, and fixed-time artificial insemination. Emerging tools such as synthetic buck odor and crude pheromone extracts show potential for non-contact reproductive control but still require validation of their ovulatory efficacy during anestrus. Overall, male biostimulation links sensory biology with practical herd management and represents a promising hormone-free alternative to exogenous hormonal treatments, consistent with growing demands for animal welfare and sustainable livestock production.

Keywords: biostimulation, buck effect, goat, kisspeptin, male effect, reproduction

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Received October 4, 2026
Accepted October 28, 2026
https://doi.org/10.56808/2985-1130.4145

Introduction

Goats (*Capra hircus*) in temperate and subtropical regions are photoperiodic seasonal breeders, exhibiting distinct cycles of ovarian activity alternated with anestrous periods dictated primarily by day length (Delgadillo *et al.*, 2015). During seasonal anestrus, the cessation of ovulation and estrus behavior poses a major constraint on achieving year-round reproductive efficiency and milk/meat production (Sankarganesh *et al.*, 2025). Even in equatorial and tropical regions, where goats often display reduced reproductive seasonality, strategic induction and synchronization of estrus remain pivotal for optimizing herd fertility and production logistics. Consequently, the biological limitations imposed by both seasonal and lactational anestrus continue to represent a major production bottleneck in modern caprine enterprises.

Traditionally, reproductive management in goats has relied heavily on exogenous hormonal protocols. These typically involve progestagen-impregnated intravaginal sponges or controlled internal drug release (CIDR) devices, frequently combined with equine chorionic gonadotropin (eCG) and prostaglandins to induce and synchronize estrus (Abecia *et al.*, 2012; Anakkul *et al.*, 2013; Thiangthientham *et al.*, 2022). Although highly effective, the widespread use of synthetic hormones presents significant drawbacks. Key concerns include pharmaceutical residues in food products, environmental contamination, refractoriness caused by neutralizing antibodies against heterologous gonadotropins, and increasingly stringent regulations regarding animal welfare and organic livestock production (Lopez-Sebastián *et al.*, 2014). Therefore, developing reliable, sustainable, and hormone-free estrus induction protocols has become a key priority to promote clean, green, and ethical caprine reproductive management.

Among non-pharmacological interventions, the male effect, known as the buck effect in goats, is a well-established biostimulatory phenomenon wherein the sudden introduction of sexually active males stimulates the resumption of ovarian cyclicity and ovulation in anestrous females (Gelez and Fabre-Nys, 2004). Although the male effect was initially reported in sheep during the 1940s and later described in swine and cattle (Rekwot *et al.*, 2001; Rosa and Bryant, 2002; Ungerfeld *et al.*, 2004), it remains most pronounced and best characterized in small ruminants. In seasonally anestrous sheep and goats, this phenomenon serves as an effective, hormone-free strategy for estrus induction and synchronization (Delgadillo *et al.*, 2009; Bedos *et al.*, 2010; Delgadillo *et al.*, 2012a). Physiologically, male-derived chemical signals, primarily pheromones, activate the hypothalamic-pituitary-gonadal (HPG) axis in anestrous females, triggering pulsatile secretion of gonadotropin-releasing hormone (GnRH) and luteinizing hormone (LH) (Okamura *et al.*, 2010).

Recent advances in neuroendocrine research have further elucidated the pathways governing this biostimulatory response, spanning from initial olfactory perception to the activation of the GnRH pulse generator via kisspeptin/neurokinin B neuronal networks (Sakamoto *et al.*, 2013). Furthermore, major milestones, such as the identification of 4-ethyloctanal as a key male goat pheromone (Murata *et al.*, 2014) and the discovery of the buck-to-buck effect (Delgadillo *et al.*, 2022), have broadened both the theoretical framework and application potential of biostimulation.

Despite recent neuroendocrine and molecular breakthroughs, field responses to the buck effect remain highly variable due to complex interactions between intrinsic goat physiology and extrinsic management conditions. Therefore, an integrated synthesis linking central neurobiology with farm-level application is needed to minimize response inconsistency. This review provides a comprehensive overview of the buck effect in caprine reproduction. Specifically, it synthesizes knowledge regarding sensory cues, central neuroendocrine mechanisms, key intrinsic and extrinsic modulating factors, and practical implementation strategies in goat farming systems. Key points are summarized at the end of each major section.

Sensory Cues Involved in the Male Effect

The male effect is driven by a multisensory stimulation framework encompassing olfactory, visual, auditory, and tactile signals that converge on the female HPG axis (Walkden-Brown *et al.*, 1999; Gelez and Fabre-Nys, 2004). Although multisensory input enhances the overall reproductive response, distinct sensory modalities contribute via hierarchical roles, with chemical signaling acting as the indispensable primary trigger.

Olfactory cues and pheromonal signaling: The olfactory system represents a major sensory modality mediating the male effect. Although full male exposure provides a combination of visual, auditory, tactile, behavioral, and olfactory stimuli, olfactory cues alone can initiate the central neuroendocrine response (Gelez and Fabre-Nys, 2004; Sankarganesh *et al.*, 2025). Early studies demonstrated that exposure to male wool, hair, or isolated male odor stimulated LH secretion in anestrous females, highlighting the importance of chemical communication (Claus *et al.*, 1990; Walkden-Brown *et al.*, 1993).

Pheromone perception in goats is mediated through a dual olfactory architecture involving both the main olfactory system (MOS) and the vomeronasal system (VNS, or accessory olfactory system, AOS). The MOS detects airborne volatile chemicals during respiration or sniffing, whereas the VNS is particularly involved in detecting low-volatility or liquid-phase semiochemicals. Chemical cues can be transported from the oral cavity to the vomeronasal organ (VNO) via the nasopalatine (incisive) duct, often facilitated by the flehmen response. This functional distinction is not absolute, and both systems may contribute to the detection of reproductive chemosignals.

In goats, the buck-derived volatile 4-ethyloctanal has been identified as a primer pheromone component that activates the GnRH pulse generator (Murata *et al.*, 2014), whereas its oxidized derivative, 4-ethyloctanoic acid, mainly contributes to the characteristic odor (see the subsection on VOCs). Furthermore, the goat V1R

gene (gV1Ra1, a putative pheromone receptor gene) is expressed in both the VNO and the main olfactory epithelium (MOE), providing an anatomical basis for possible contributions of both olfactory pathways to pheromone detection (Wakabayashi *et al.*, 2002, 2007). However, this expression pattern does not establish the ligand specificity of the receptor.

Functional evidence in small ruminants, particularly sheep, indicates that the MOS can mediate the LH response to male odor even when VNO function is disrupted: surgical ablation of the VNO or transection of the vomeronasal nerve does not completely abolish the response (Gelez and Fabre-Nys, 2004). These findings support an important role for the MOS in male biostimulation and indicate that an intact VNS is not essential for the LH response under those experimental conditions.

Neural activation studies provide further refinement to this functional framework. Ohara *et al.* (2014) demonstrated that exposure to male goat hair extract significantly increased c-Fos-immunoreactive cells in the accessory olfactory bulb (AOB) and associated vomeronasal brain regions, whereas activation in the main olfactory bulb (MOB) was less pronounced and did not reach statistical significance. Conversely, Gelez and Fabre-Nys (2006) reported increased c-Fos expression in both the MOB and AOB following exposure to a ram or its fleece, with the MOB being more strongly activated by male than by female odor. Nevertheless, because these stimuli consisted of intact males or complex fleece odors rather than isolated compounds, these findings do not provide evidence of equivalent neural processing for isolated pheromonal compounds.

Collectively, the empirical literature supports a stimulus- and context-dependent involvement of the MOS and VNS in the male effect, rather than an obligatory or experimentally validated synergistic mechanism.

Molecular characterization: volatile organic compounds (VOCs) and buck odor: The characteristic odor of bucks during the breeding season, traditionally described as "goaty," is associated with secretions from specialized cutaneous sebaceous glands. In horned males, prominent scent glands are located caudomedial to the horn bases. However, odor-producing sebaceous structures are not confined to this region. Enlarged sebaceous glands have also been described in the head and neck regions, and scent glands are present in polled breeds, although their anatomical location may differ. Therefore, the absence of horns should not be equated with the absence of odor-producing glands. Testosterone promotes both sebaceous gland development and primer pheromone production, thereby explaining the reduced pheromonal activity of castrated bucks in the absence of androgen supplementation (Iwata *et al.*, 2000; Wakabayashi *et al.*, 2000). These findings support androgen-dependent pheromone production by sebaceous glands in the head region, rather than an exclusive dependence on cornual glands. This dependence on androgens also links pheromone production to reproductive management, because photoperiodic treatments that increase testosterone secretion also enhance buck odor and biostimulatory efficacy (Flores *et al.*, 2000; Delgadillo and Vélez, 2010; Zarazaga *et al.*, 2021; see Photoperiodic treatment of bucks).

Early chemical analyses identified 6-trans-nonenal as a contributor to the characteristic male goat odor and suggested that related nonenals arise through the oxidation of glandular lipids. Sensory evaluations also demonstrated that branched-chain fatty acids (including 4-ethyloctanoic acid, 4-methyloctanoic acid, and 4-ethyloct-2-enoic acid) contribute to this goaty odor, which, however, should not be equated with reproductive bioactivity (Smith *et al.*, 1984). Specifically, although 4-ethyloctanoic acid is a primary constituent of the characteristic male scent, it does not exhibit primer-pheromone activity in bioassays monitoring hypothalamic GnRH pulse-generator activity (Iwata *et al.*, 2003). Therefore, its contribution to odor and reported role in female attraction must be distinguished from the neuroendocrine activity required to trigger the male effect.

A major advance in male-effect research was the identification of a specific volatile compound capable of stimulating the central reproductive axis. Using gas chromatography–mass spectrometry (GC–MS) to analyze male goat headspace volatiles, Murata *et al.* (2014) identified 4-ethyloctanal, a neutral and volatile ethyl-branched aldehyde. Electrophysiological recordings of hypothalamic multiple-unit activity (MUA) demonstrated that exposure to this compound activates the GnRH pulse generator in female goats, supporting its role as a primer-pheromone component. The oxidation of 4-ethyloctanal yields 4-ethyloctanoic acid, a branched-chain carboxylic acid that is less volatile than its aldehyde precursor. This chemical conversion links a neuroendocrine-active aldehyde to an odor-associated fatty acid reported to contribute to female attraction, suggesting a potential transition between primer and releaser pheromonal functions. Differences in volatility and persistence could allow these chemically related signals to operate over distinct spatial and temporal scales; however, this hypothesis requires direct experimental verification under natural conditions. Consequently, distinguishing odor-associated compounds from those with proven primer-pheromone activity is crucial for the development and validation of targeted synthetic biostimulants.

Key points: (i) Primer pheromone production in bucks is androgen-dependent and occurs in sebaceous glands of the head region, not only at the horn base. (ii) 4-Ethyloctanal activates the GnRH pulse generator, whereas 4-ethyloctanoic acid mainly contributes to odor and releaser activity. (iii) Odor intensity should therefore not be equated with primer-pheromone activity.

Facilitatory sensory cues (visual, auditory, and tactile signals): The male effect relies substantially on olfactory stimulation. Nevertheless, non-olfactory sensory modalities supply important facilitatory cues that enhance both behavioral estrus expression and central neuroendocrine responsiveness. Visual and tactile stimuli provided by male courtship behaviors, such as nudging, foreleg kicking, tongue flicking, and

mounting attempts, enhance female receptivity and estrous behavior (Walkden-Brown *et al.*, 1993; Delgadillo *et al.*, 2006). Conversely, anogenital sniffing and the flehmen response represent chemo-investigative behaviors through which the buck samples female urinary and vaginal chemosignals, partially via the vomeronasal organ; these should therefore be categorized as male investigative behaviors rather than visual displays directed at the female. Auditory cues also contribute live buck vocalizations during the breeding season stimulate estrous behavior and LH secretion in anestrous goats. (Delgadillo *et al.*, 2012b). However, these effects were observed exclusively in females with prior male exposure, suggesting that neuroendocrine and behavioral responsiveness to male vocalizations relies on experience, likely through a conditioned association with other male cues. Whether these auditory signals also enhance female spatial orientation toward the male remains to be directly evaluated. Furthermore, direct physical and tactile interactions during unhindered contact amplify female stimulation (Gallego-Calvo *et al.*, 2014).

Despite these contributions, the requirement for somatosensory contact depends on the underlying physiological context. In prepubertal females, preventing physical contact with bucks does not impair the acceleration of puberty onset, indicating that non-contact cues, including chemical signals, are sufficient to drive gonadotropic activation (Chasles *et al.*, 2018). Similarly, exposure to male hair or its extracts, including application via nasal masks, stimulates LH secretion in anestrous goats (Claus *et al.*, 1990) and ewes (Ohara *et al.*, 2014). In goats, 4-ethyloctanal activates GnRH pulse-generator activity, a pathway thought to involve the arcuate kisspeptin/neurokinin B/dynorphin (KNDy) neuronal network (Wakabayashi *et al.*, 2010; Murata *et al.*, 2014). Consequently, visual, auditory, and tactile signals play a facilitatory rather than obligatory role in puberty acceleration and may act synergistically with olfactory inputs to enhance the speed and synchrony of the female response.

However, a critical nuance regarding male courtship intensity must be considered for ovulation induction in anestrous adult females. This distinction can be conceptualized into two components of the neuroendocrine response: an initial pulsatile phase characterized by increased GnRH/LH pulse frequency, and a subsequent surge phase culminating in the preovulatory LH surge and ovulation. Although the initial pulsatile phase can be triggered by male odor alone, the preovulatory surge phase strictly depends on sustained follicular development and estradiol secretion. Exposure of anestrous does to pharmacologically sedated bucks, which still provide olfactory and visual cues but lack active courtship behaviors, fails to induce a preovulatory LH surge or ovulation (Martínez-Alfaro *et al.*, 2014). It should be noted that this study evaluated the occurrence of the preovulatory LH surge and ovulation rather than the characteristics of subsequent luteal phases. Consequently, a non-responsive outcome should be characterized as an absence of the preovulatory LH surge and ovulation, and should be distinguished from silent ovulation, which is a common feature of successful male-induced ovulation (see Endocrine response and ovulatory outcomes).

These findings suggest that while pheromones initiate pulsatile gonadotropic activity, intense male courtship behavior provides the necessary additional stimulation to sustain LH secretion until the surge threshold is achieved. Because sedation suppresses the entire repertoire of male sexual behavior, this experimental approach cannot delineate which specific component (e.g., tactile contact, courtship displays, or vocalizations) is required for the surge response. A "permissive (olfactory) versus threshold-achieving (multisensory)" model therefore offers a compelling conceptual framework.

Regarding the central neuroendocrine circuitry translating this multisensory input into the surge response, species-specific anatomical distinctions must be recognized. Although the preovulatory surge in rodent models is classically attributed to kisspeptin neurons in the anteroventral periventricular nucleus (AVPV), sheep lack a distinct AVPV structure. Instead, kisspeptin populations in small ruminants are distributed within the preoptic area (POA) and the arcuate nucleus (ARC) (Lehman *et al.*, 2010; Merkley *et al.*, 2012). In ewes, both preoptic and arcuate kisspeptin populations have been implicated in driving the preovulatory LH surge (Smith *et al.*, 2009). In goats, however, kisspeptin neurons within the medial POA, rather than the ARC, appear to be specifically involved in estradiol-induced surge-like LH release (Matsuda *et al.*, 2015). Whether male-derived sociosexual cues directly engage this preoptic kisspeptin surge mechanism remains an open and important question in caprine reproductive biology.

Multisensory integration in male biostimulation: Under natural herd conditions, the female brain integrates these multifaceted sensory inputs into a unified neuroendocrine response. In behavioral ecology, multimodal signals may function either through redundancy, ensuring reception when one channel is degraded, or through inter-signal interactions, in which one component modulates the receiver's response to another (Partan and Marler, 1999; Hebets and Papaj, 2005). Applied to the male effect, this framework suggests that visual, auditory, and tactile cues from sexually active bucks may potentiate the neuroendocrine response to chemical primers, possibly through neural summation that facilitates progression from pulsatile LH secretion to the preovulatory surge. This interpretation is consistent with experimental evidence, although it remains to be directly verified at the neural level.

Although isolated pheromonal compounds (such as 4-ethyloctanal) or male hair extracts can partially activate the GnRH pulse generator, full multisensory exposure achieves superior reproductive efficacy. Ovulatory responses are lower when females are separated from bucks by a fence than when full physical contact is permitted (Delgadillo *et al.*, 2006; Gallego-Calvo *et al.*, 2014), and suppression of male sexual behavior abolishes the preovulatory LH surge despite the continued presence of male odor (Martínez-Alfaro *et al.*, 2014). In contrast, intermittent but intense

contact with sexually active males is sufficient to induce ovulation (see Exposure duration and contact intensity).

Understanding this sensory hierarchy allows for the strategic refinement of both natural male introduction protocols and synthetic pheromone applications. Consequently, a practical principle emerges for precision biostimulation: if "clean, green, and ethical" protocols based on isolated volatiles, such as synthetic 4-ethyloctanal, are developed, they are more likely to be effective when combined with intermittent direct contact with sexually active, preferably photostimulated, bucks (Flores *et al.*, 2000; Delgadillo and Vélez, 2010) rather than used as stand-alone stimuli. The field efficacy of such integrated protocols, however, remains to be validated experimentally.

Key points: (i) Chemical signals are the primary trigger of the male effect and can be detected by both the MOS and VNS; the relative contribution of each system is stimulus- and context-dependent. (ii) Male odor alone can increase LH pulsatility, whereas intense courtship and physical contact are required for a reliable preovulatory LH surge and ovulation in anestrous adult does. (iii) Visual, auditory, and tactile cues are facilitatory rather than obligatory, and the response to vocalizations depends on prior experience with males.

Neuroendocrine Mechanisms

Neural pathways from pheromone detection to hypothalamic integration: Following peripheral chemoreception, primary sensory signals are transmitted via the MOB and AOB into the limbic system. The two pathways reach the medial nucleus of the amygdala (MeA) through different routes. AOB mitral cells project directly to the MeA and the bed nucleus of the stria terminalis (BNST), whereas MOB output is relayed predominantly through primary olfactory cortical targets, including the anterior cortical amygdaloid nucleus (ACo) and the posterolateral cortical amygdala (PLCo), before reaching the MeA, with only a sparse direct MOB projection to the MeA (Scalia and Winans, 1975; Baum and Kelliher, 2009; Kang *et al.*, 2009). The MeA can therefore be regarded as a central limbic node in which direct vomeronasal and largely indirect main olfactory inputs converge. Because these connections have been characterized mainly in rodents and other non-ruminant mammals, their detailed organization in small ruminants remains to be confirmed. The MeA projects, either directly or indirectly via the BNST, to key hypothalamic reproductive centers (Gelez and Fabre-Nys, 2004; Sakamoto *et al.*, 2013). Specifically, these limbic projections target the ARC, where kisspeptin neurons regulate GnRH pulse-generator activity, as well as the POA, where GnRH neurons reside.

This neuroanatomical framework is supported by both functional and structural evidence. In seasonally anestrous ewes, exposure to male goat hair extracts significantly increased c-Fos immunoreactivity in the AOB, MeA, and ARC, whereas no significant increase was detected in the MOB (Ohara *et al.*, 2014). Furthermore, neuroanatomical tracing using biotinylated dextran amine (BDA) injected into the MeA of ovariectomized goats has demonstrated that medial amygdaloid efferent fibers project directly to the ARC, where they form close appositions with a subset of kisspeptin/neurokinin B (NKB) neurons. In the same study, an NKB receptor antagonist completely suppressed the pheromone-induced increase in GnRH pulse-generator activity and LH secretion, thereby establishing both a structural and a functional link between olfactory perception and central reproductive control (Sakamoto *et al.*, 2013).

Kisspeptin/neurokinin B/dynorphin (KNDy) neurons as the GnRH pulse generator and the central target of male pheromones: Located within the ARC, a distinct population of neurons co-expresses kisspeptin, NKB, and dynorphin A. Commonly referred to as KNDy neurons, these cells function as the intrinsic pacemaker of the hypothalamic GnRH pulse generator, acting as the core oscillator that generates GnRH pulses, whereas GnRH neurosecretory terminals in the median eminence function as its downstream effector (Okamura *et al.*, 2010; Wakabayashi *et al.*, 2010; 2013; Nestor *et al.*, 2023; Ohkura and Nakamura, 2026). These neurons integrate diverse endogenous and environmental signals, including nutritional status, metabolic state, stress, seasonal photoperiod, and pheromonal cues, to regulate the frequency of GnRH secretion. Within the local KNDy network, NKB acts via neurokinin 3 receptors (NK3R) through autocrine and paracrine stimulation to synchronize neuronal firing across the population, whereas dynorphin provides inhibitory feedback through κ-opioid receptors to terminate each pulse volley.

Male pheromones activate this network primarily through NKB–NK3R signaling (Sakamoto *et al.*, 2013), and 4-ethyloctanal, a component of buck odor, has been shown to activate the GnRH pulse generator in female goats (Murata *et al.*, 2014). Whether pheromonal signals also attenuate dynorphinergic inhibition has not been directly tested and remains a plausible hypothesis. Synchronized activation of the KNDy network induces the episodic release of kisspeptin, which binds to kisspeptin receptors (KISS1R) on GnRH neurons, including their neurosecretory terminals in the median eminence, thereby driving pulsatile GnRH secretion into the hypophyseal portal circulation (Nestor *et al.*, 2023).

The essential role of NKB signaling in this pathway has been confirmed experimentally. In ovariectomized goats, male pheromone exposure rapidly evokes an MUA volley, the electrophysiological signature of GnRH pulse generator activation, within approximately 30 s (Wakabayashi *et al.*, 2013; Sakamoto *et al.*, 2013). In contrast, the corresponding LH pulse appears in peripheral blood only several minutes later, because GnRH must be released into the hypophyseal portal circulation, stimulate gonadotropes, and LH must then enter the systemic circulation (Mori *et al.*, 1991; Tanaka *et al.*, 1997). Consistent with this delay, peripheral LH pulses begin approximately 10 min and peak approximately 16 min after the corresponding portal GnRH pulses in ewes (Skinner *et al.*, 1997), and intravenous administration of the NK3R agonist senktide elicits an MUA volley

within approximately 2–3 min (Wakabayashi *et al.*, 2013) and a peak in LH concentration at 10-20 min in goats (Endo and Tanaka, 2014). Intravenous administration of an NK3R antagonist completely abolishes both pheromone-induced MUA volleys and associated LH pulses, demonstrating that NKB signaling is indispensable for pheromone-induced activation of the GnRH pulse generator (Sakamoto *et al.*, 2013). Continuous pheromone exposure sustains accelerated GnRH pulse frequency throughout a 4-h exposure period (Ichimaru *et al.*, 1999); however, brief exposure studies reveal an intrinsic refractory period within the system. Specifically, a 1-s pheromone stimulus applied during the late inter-volley interval (three-quarters of the mean interval) consistently triggers an MUA volley within 60 s, whereas stimulation applied shortly after a preceding volley fails to do so, even though an instantaneous rise in MUA is observed regardless of timing (Murata *et al.*, 2011). This temporal refractoriness indicates that the timing and pattern of male exposure critically influence the consistency of the central neuroendocrine response.

Endocrine response and ovulatory outcomes: Prior to male introduction, seasonally anestrous females exhibit low-frequency GnRH and LH pulses, maintained largely by an enhanced negative feedback sensitivity to circulating estradiol (Karsch *et al.*, 1984). Exposure to active bucks or their pheromones rapidly overrides this central inhibition, triggering an immediate increase in ARC MUA and a subsequent rise in GnRH pulse frequency; notably, this response also occurs in ovariectomized goats, indicating that the male stimulus activates the GnRH pulse generator independently of ovarian steroid feedback (Okamura *et al.*, 2010; Sakamoto *et al.*, 2013). Increased GnRH stimulation prompts the anterior pituitary gland to accelerate the pulsatile release of LH into the systemic circulation (Okamura *et al.*, 2010). This elevated LH pulse frequency drives rapid ovarian follicular development and increases circulating estradiol concentrations, which eventually exert positive feedback, operating primarily within the mediobasal hypothalamus and at the pituitary gland (Caraty *et al.*, 1998), culminating in the preovulatory GnRH/LH surge and subsequent ovulation (Chemineau *et al.*, 2006; Delgadillo *et al.*, 2006). Depending on buck libido, female body condition, breed sensitivity, and the depth of seasonal anestrus, the first induced ovulation typically occurs 2 to 4 days after male exposure (Chemineau, 1983; Chemineau *et al.*, 2006), with overall ovarian response rates ranging between 50% and 100% (Delgadillo *et al.*, 2006; Zarazaga *et al.*, 2019).

A defining feature of this induced ovulation is its variable association with estrous behavior and its frequently short luteal phase. In ewes, estradiol alone is insufficient to induce overt receptive sexual behavior (standing heat); full behavioral expression requires prior neural exposure to progesterone (progesterone priming), which is thought to act partly by upregulating estrogen receptors in the mediobasal hypothalamus, including the ventromedial hypothalamus (VMH) (Caraty *et al.*, 2002; Fabre-Nys and Gelez, 2007). In rodents, ovarian steroids also upregulate oxytocin receptors in the VMH, where oxytocin facilitates female receptivity (Schumacher *et al.*, 1990). In ewes, however, progesterone priming potentiates mating-related oxytocin release in the mediobasal hypothalamus, yet oxytocin infused into this region reduces, rather than enhances, sexual receptivity, suggesting that hypothalamic oxytocin may contribute to the termination of receptivity after mating in this species (Kendrick *et al.*, 1993). Progesterone priming is also required for the full expression of the estradiol-induced GnRH surge (Caraty and Skinner, 1999). Consequently, in anestrous ewes lacking functional luteal tissue, the first male-induced preovulatory follicle produces sufficient estradiol to trigger the LH surge and ovulation, but this ovulation is not accompanied by estrus (silent ovulation; Chemineau *et al.*, 2006).

Goats appear less reliant on progesterone priming. In Creole goats, for example, approximately two-thirds of first induced ovulations are accompanied by estrus, while the remainder are silent, with the proportion of silent ovulations increasing with the depth of anestrus (Chemineau, 1983; Chemineau *et al.*, 2006). The first ovulation is commonly followed by a short luteal phase lasting approximately 5 to 6 days in about three-quarters of does (Chemineau, 1983). This premature luteal regression has been attributed to poor-quality ovulatory follicles forming corpora lutea with reduced progesterone secretion, combined with estrogen-stimulated uterine prostaglandin F2 alpha (PGF2α) release that induces early luteolysis; the absence of prior luteal progesterone exposure is thought to increase the sensitivity of this uterine mechanism. These mechanisms remain working hypotheses (Chemineau *et al.*, 2006). Because some initial ovulations are silent and followed by short-lived corpora lutea, relying solely on behavioral estrus detection during the early post-introduction days can underestimate the true ovarian response rate of the herd.

Following the regression of this short-lived corpus luteum (CL), a second ovulation occurs approximately 6 to 10 days after male introduction, depending on breed and the length of the short cycle. This second ovulation is accompanied in most does (approximately 89% in Creole goats) by visible behavioral estrus and is generally followed by a normal-length, functional luteal phase (Chemineau, 1983; Chemineau, 1987; Chemineau *et al.*, 2006; Pellicer-Rubio *et al.*, 2016). Recognizing this two-stage ovarian dynamic is critical for practical herd management. Because estrus and conception after the male effect are distributed across two distinct peaks, natural breeding or artificial insemination (AI) should cover both periods, with particular emphasis on the second induced estrus. Alternatively, progesterone or progestagen pretreatment can suppress short luteal phases and concentrate estrus into a single peak (Chemineau *et al.*, 2006; González-Bulnes *et al.*, 2006), thereby improving estrous synchrony, conception rates, and overall reproductive efficiency.

Key points: (i) Male cues reach ARC KNDy neurons through olfactory–amygdala pathways and activate the GnRH pulse generator via NKB–NK3R signaling,

eliciting an MUA volley within seconds and LH pulses within minutes. (ii) The resulting increase in LH pulsatility drives follicular development, estradiol positive feedback, and ovulation 2 to 4 days after male introduction. (iii) In goats, the first induced ovulation is variably accompanied by estrus and frequently followed by a short luteal phase, whereas the second ovulation, approximately 6 to 10 days after introduction, is usually fertile.

The Male Effect Across Climatic Zones: Efficacy and Environmental Modulators

The applicability and efficacy of the male effect in small ruminants vary substantially across geographical regions, primarily dictated by latitudinal variations in photoperiodic amplitude and local environmental dynamics (Table 1).

Temperate regions: In high-latitude temperate regions, small ruminant reproductive activity is strictly seasonal and regulated primarily by annual variations in day length (Rosa and Bryant, 2003). Within these temperate production systems, the male effect is most effective during the transition between seasonal anestrus and the natural breeding season, typically advancing the onset of cyclic ovulatory activity by several weeks (Delgadillo *et al.*, 2009; Gómez-Brunet *et al.*, 2012). At the neuroendocrine level, and as described in the preceding sections, buck-derived biostimulatory signals rapidly activate ARC KNDy neurons, which serve as the central pacemaker of the GnRH pulse generator. This elicits an MUA volley within seconds and drives an increase in LH pulse frequency, reflecting GnRH pulse frequency, within minutes to hours (Okamura *et al.*, 2010; Murata *et al.*, 2011; Sakamoto *et al.*, 2013). During this transitional period, as photoperiodic inhibition and estradiol negative feedback wane (Karsch *et al.*, 1984), accelerated pulsatile LH secretion is readily translated into progressive follicular development and a preovulatory LH surge.

Conversely, during deep anestrus, the response to male introduction is often minimal or entirely absent. This unresponsiveness reflects strong photoperiodic inhibition of the female HPG axis, mediated largely by heightened sensitivity to estradiol negative feedback (Karsch *et al.*, 1984), as well as a concurrent decline in male libido and biostimulatory quality. In bucks, long days are thought to suppress central GnRH drive, as reflected by reduced LH secretion, diminished testicular activity, and a marked drop in circulating testosterone concentrations (Zarazaga *et al.*, 2021). Because primer pheromone synthesis within specialized sebaceous glands of the head region is testosterone-dependent (Iwata *et al.*, 2000; Wakabayashi *et al.*, 2000), this seasonal androgen decline is expected to diminish both male sexual behavior and pheromonal potency.

Upon male introduction during the transitional period, the first induced ovulation typically occurs within 2 to 4 days. In goats, this ovulation is accompanied by estrus in a substantial proportion of does, whereas in ewes it is invariably silent (Chemineau *et al.*, 2006; Pellicer-Rubio *et al.*, 2016). This initial ovulation is frequently followed by a short luteal phase lasting approximately 5 to 6 days (Gelez and Fabre-Nys, 2004; Chemineau *et al.*, 2006). As discussed in the subsection on endocrine response and ovulatory outcomes, the CL formed after the first male-induced ovulation may undergo premature luteolysis mediated by uterine PGF2α. This process is thought to involve a lack of prior luteal progesterone priming, resulting in an inadequate progesterone-mediated suppression of uterine PGF2α synthesis (Chemineau *et al.*, 2006). A second ovulation, associated with normal luteal longevity and overt estrous behavior, occurs approximately 6 to 10 days post-introduction, establishing the first fertile cycle of the season (Chemineau *et al.*, 2006; Delgadillo *et al.*, 2006; Pellicer-Rubio *et al.*, 2016).

To overcome the limited response during deep anestrus in temperate production systems, two complementary reproductive management strategies can be applied. First, bucks can be rendered sexually active and pheromonally potent out of season using artificial photoperiod regimens (e.g., exposure to long days followed by melatonin treatment or natural short days), as detailed in the subsection on photoperiodic treatment of bucks. Under temperate conditions, Alpine bucks subjected to long-day treatment during winter induced ovulation in 86% of anestrous does, compared with only 5% for untreated bucks (Chasles *et al.*, 2016). Second, short-term progesterone or progestagen pretreatment of females (utilizing intravaginal sponges or CIDR devices) prior to buck introduction prevents the short luteal phase, presumably by preconditioning the uterus, so that the first induced ovulation is accompanied by estrus and can be fertile (Chemineau *et al.*, 2006). When artificial long-day regimens for both sexes were combined with an 11-day progestagen treatment prior to male introduction, 92% of lactating Alpine and Saanen goats exhibited an LH surge during deep anestrus and 98% of these ovulated; high fertility was subsequently achieved following one or two fixed-time AI (Pellicer-Rubio *et al.*, 2008). Nevertheless, because exogenous progestagens remove the hormone-free advantage of the male effect, sustainable hormone-free protocols continue to be refined and evaluated (Pellicer-Rubio *et al.*, 2016).

Subtropical regions: Although annual photoperiodic fluctuations are reduced compared to temperate latitudes, they remain sufficient to drive distinct non-breeding seasons in local goat breeds (Delgadillo *et al.*, 2004). However, investigations in subtropical systems have fundamentally altered the understanding of the male effect by demonstrating that male sexual behavior, rather than female photoperiodic inhibition, serves as the primary limiting factor during seasonal anestrus (Flores *et al.*, 2000; Delgadillo *et al.*, 2009). Indeed, when males are rendered sexually active during the non-breeding season via photoperiodic manipulation, they consistently induce estrus behavior and ovulation in 80-100% of anestrous females, whereas untreated, sexually inactive males stimulate responses in only approximately 10% of does (Delgadillo *et al.*, 2001).

Tropical regions: In tropical regions near the equator, minimal annual variation in photoperiod results in a significantly shallower depth of seasonal anestrus and extended natural breeding activity (Chemineau *et al.*, 2004). Consequently, the proportion of females with cyclic ovulatory activity remains high throughout the year, with the minimum monthly ovulation rate never falling below 56% (Chemineau *et al.*, 2004). This reduced photoperiodic constraint allows the male effect to be successfully implemented year-round as a hormone-free tool for estrus induction and synchronization, as validated in Creole, Saanen, and dairy goat herds maintained under tropical conditions (Chemineau, 1983; Freitas *et al.*, 2004). Male introduction in tropical goats rapidly induces ovulation in up to 97% of anovulatory females, with 68% exhibiting overt estrus and 76% demonstrating a transient short luteal phase prior to establishing normal cyclic activity with fertility exceeding 79% (Chemineau, 1983).

Despite the capacity for continuous breeding in tropical latitudes, non-photoperiodic environmental factors (specifically nutritional status, male seasonality, and heat stress) replace day length as the principal regulators of reproductive performance.

Nutritional status and metabolic signaling: In tropical regions, seasonal rainfall patterns and vegetation dynamics dictate feed availability, positioning nutritional status as the primary environmental regulator of small ruminant reproduction (Freitas *et al.*, 2004). Temperate breeds respond predominantly to short-day photoperiods; in contrast, the anestrous state in tropical goats may occur primarily due to energy deficiency rather than photoperiodic inhibition (Chemineau *et al.*, 2004). Alternating wet and dry seasons induce recurrent periods of negative energy balance that suppress reproductive axis activity in both sexes, ultimately dictating the overall efficacy of the male effect (Delgadillo *et al.*, 2009).

In females, nutritional status governs body condition score, live weight, and circulating metabolic signals that directly modulate hypothalamic sensitivity to socio-sexual biostimulation (Gallego-Calvo *et al.*, 2015; Vera-Avila *et al.*, 2017; see Female factors). Chronic or severe energy deficits prolong postpartum anestrus, impair folliculogenesis, lower ovulation rates, and may attenuate the LH response to male introduction (Freitas *et al.*, 2004; Delgadillo *et al.*, 2009). Undernourished females consequently exhibit diminished responsiveness to incoming male socio-sexual signals, resulting in delayed or inconsistent ovulatory synchronization.

In males, energy balance is likely to influence sexual libido, courtship behavior, and overall biostimulatory capacity. Strategic nutritional flushing of does and adequate energy supply to bucks before male exposure are therefore recommended to support metabolic signaling, female responsiveness, and conception rates in tropical goat production systems (Freitas *et al.*, 2004; Gallego-Calvo *et al.*, 2015). Integrating tactical feed supplementation with biostimulation protocols provides a practical, integrated management strategy to mitigate seasonal anestrus during dry periods.

Seasonal variations in male biostimulatory capacity: Female tropical goats display shallower anestrus; nevertheless, male sexual behavior and biostimulatory quality can still exhibit marked seasonal fluctuations. Bucks in tropical environments display significant seasonal variations in body weight, scrotal circumference, odor intensity, and courtship behavior, with sexual activity peaking during cooler or rainier months and declining during hot, dry periods (Ponce-Covarrubias *et al.*, 2023). Male stimulus intensity represents a crucial driver of central neuroendocrine activation in females; therefore, seasonal declines in buck libido can directly compromise the overall efficacy of the male effect (Delgadillo *et al.*, 2006; Ponce-Covarrubias *et al.*, 2023).

Heat stress and thermoregulatory management: In not only tropical but also subtropical, arid, and semi-arid environments, high ambient temperatures combined with intense solar radiation and elevated relative humidity represent formidable environmental stressors that compromise caprine reproductive performance (Danso *et al.*, 2024). Prolonged exposure to elevated thermal conditions, particularly when ambient temperatures exceed 32 to 33 °C, triggers systemic physiological stress that simultaneously suppresses female hypothalamic responsiveness and compromises male biostimulatory capacity.

In females, heat stress activates the hypothalamic-pituitary-adrenal axis, elevating circulating glucocorticoid concentrations that inhibit the secretion of GnRH, LH, and follicle-stimulating hormone (Danso *et al.*, 2024). This endocrine disruption reduces ovarian estrogen synthesis, leading to an increased incidence of silent estrus, impaired oocyte maturation, delayed ovulation, and reduced conception rates. Consequently, heat-stressed females exhibit diminished sensitivity within the HPG axis, attenuating their capacity to process and respond to incoming male socio-sexual signals.

Male sexual libido and active courtship behaviors represent primary determinants of the male effect; therefore, thermal stress directly compromises biostimulatory efficacy through multiple interrelated male pathways (Delgadillo *et al.*, 2009). At the neuroendocrine level, heat stress suppresses Leydig cell steroidogenesis, causing lower circulating testosterone concentrations and significantly prolonged mounting reaction times (Salles *et al.*, 2020). As noted for temperate regions, primer pheromone synthesis within sebaceous glands is androgen-dependent (Iwata *et al.*, 2000); thus, this heat-induced reduction in testosterone production may impair both the concentration and volatile quality of biostimulatory compounds, including 4-ethyloctanal (Murata *et al.*, 2014; Danso *et al.*, 2024), although this has not been measured directly. Concurrently, elevated testicular temperatures disrupt normal spermatogenesis, resulting in progressive testicular degeneration, reduced sperm motility, and a high proportion of morphologically abnormal spermatozoa (Salles *et al.*, 2020; Danso *et al.*, 2024).

Preserving male stimulus strength and overall reproductive outcomes during hot seasons requires

active environmental and management interventions. Implementing targeted heat abatement strategies, such as providing natural or artificial shade, enhancing barn ventilation, and utilizing evaporative cooling systems, effectively mitigates thermal loads on breeding bucks (Salles *et al.*, 2020). Furthermore, scheduling male-female physical exposure during the cooler diurnal hours, particularly early morning or late evening, optimizes courtship intensity while protecting bucks from extreme solar exposure, thereby sustaining the overall efficacy of the male effect in tropical goat production systems.

Key points: (i) Photoperiod is the main constraint on the male effect in temperate regions, male sexual inactivity is a key constraint in subtropical regions, and nutrition and heat stress are the principal modulators in the tropics. (ii) In temperate regions, the male effect is most effective during the transitional period, whereas its use during deep anestrus requires photostimulated bucks and, where acceptable, progestagen pretreatment of females. (iii) Management strategies should therefore be adapted to the climatic zone and production system.

Table 1 Main constraints on the male effect and corresponding management strategies across climatic zones.

Climatic zone	Main constraint	Typical response to male introduction	Main management strategies
Temperate	Strong photoperiodic inhibition in both sexes; enhanced estradiol negative feedback in females and low testosterone in bucks during long days	High responsiveness during the transitional period; weak or absent during deep anestrus when untreated bucks are used	Use of photostimulated bucks out of season; short-term progestagen or progesterone pretreatment of females where acceptable (Pellicer-Rubio *et al.*, 2008; Chasles *et al.*, 2016)
Subtropical	Seasonal sexual inactivity and reduced libido in bucks during out-of-season periods	High ovulation rates when using sexually active bucks vs. minimal response with untreated control bucks (Flores *et al.*, 2000)	Out-of-season photostimulation of bucks; application of the "buck-to-buck effect" to stimulate male libido (Delgadillo *et al.*, 2001, 2022)
Tropical	Nutritional deficits, heat stress, and seasonal variation in buck libido and body condition	Ovulatory response achievable year-round, with ovulation rates reaching up to 97% under optimal conditions (Chemineau, 1983)	Strategic nutritional supplementation (flushing); heat-stress abatement protocols; buck exposure during cooler periods of the day (Gallego-Calvo *et al.*, 2015; Vera-Avila *et al.*, 2017; Salles *et al.*, 2020; Danso *et al.*, 2024)

Factors Affecting the Efficacy of the Male Effect

Male sexual activity and reproductive condition: The sexual activity of the buck is a critical determinant of the success of the male effect. Flores *et al.* (2000) demonstrated that male reproductive condition represents the primary limiting factor influencing male effect efficiency during seasonal anestrus in female goats. Sexually active bucks, characterized by elevated testosterone levels, intense courtship behavior, and strong odor production, are significantly more effective at inducing ovulation in anestrous does than sexually inactive males (Véliz *et al.*, 2002; Delgadillo *et al.*, 2015). Specifically, in seasonally anovulatory lactating goats, induction of the male effect depends mainly on the presence of sexually active bucks rather than the co-presence of estrus females, indicating that the male's reproductive status is a key variable (Véliz *et al.*, 2002).

At the central neuroendocrine level, high male sexual activity is required to induce neural activation within the medial POA and the ARC of anestrous goats (Bedos *et al.*, 2016). However, Zarazaga *et al.* (2022) challenged the view that elevated baseline testosterone concentrations are an absolute prerequisite. At Mediterranean latitudes, introducing bucks after a period of isolation to anestrous females stimulated a rapid rise in buck testosterone levels, indicating that high initial testosterone is not strictly required to elicit an adequate ovulatory response. This finding suggests a reciprocal interaction between sexes during male introduction, wherein interactions with anestrous does can partially drive the sexual activation of the buck.

Photoperiodic treatment of bucks: Manipulating buck sexual activity through photoperiodic management represents one of the most practical strategies to enhance male effect efficacy during seasonal anestrus. Specifically, exposing bucks to artificially long days (16 hours of light per day for 2.5 months), either alone or followed by melatonin treatment, stimulates intense libido and odor production during the natural non-breeding season (Delgadillo *et al.*, 2001; 2002). This biostimulatory enhancement renders treated males highly effective at inducing ovulation in anestrous does across subtropical, Mediterranean, and temperate production systems (Delgadillo *et al.*, 2001; Chasles *et al.*, 2016; Zarazaga *et al.*, 2021).

The necessity and success of photostimulation are further modulated by breed-specific depth of reproductive seasonality (Zarazaga *et al.*, 2021). For instance, in breeds with pronounced seasonality such as the Blanca Andaluza, bucks maintained under natural photoperiod induce estrus in only 50% of does, whereas photostimulated bucks achieve significantly

higher response rates. Conversely, in breeds with shallow seasonality like the Murciano-Granadina, bucks remain effective even without artificial light treatment. These findings underscore the importance of breed selection and provide a practical alternative framework when light-control facilities are unavailable.

Female factors (body condition, age, breed, and reproductive status): The nutritional status and body condition of does significantly influence their response to the male effect. Gallego-Calvo *et al.* (2015) demonstrated that reproductive performance following male introduction improves as body weight and body condition score (BCS) increase. Similarly, Vera-Avila *et al.* (2017) reported that BCS interacts with the depth of seasonal anestrus to dictate ovulatory success in anovulatory Criollo × Nubian goats, with does in superior body condition exhibiting higher ovulation rates. These findings emphasize that adequate nutritional management is a vital prerequisite for maximizing male effect outcomes, particularly in extensive systems where seasonal feed scarcity often compromises body condition.

Female age and maturity also critically influence the biostimulatory response. In young females, exposure to sexually active or photostimulated bucks serves as a potent social cue that activates the gonadotropic axis and accelerates pubertal onset (Chasles *et al*., 2018; Zarazaga *et al*., 2019). Specifically, does exposure to intact bucks from weaning result in puberty attained approximately 1.5 months earlier than in those exposed to castrated males or kept in isolation (Chasles *et al*., 2018). These early-pubertal females subsequently exhibited regular ovarian cycles with normal luteal function, suggesting that male-induced early puberty does not impair subsequent ovarian cyclicity.

Male-to-female ratio, prior separation, and exposure dynamics: Optimizing the male effect in practice requires careful consideration of three primary operational variables: the male-to-female ratio, the necessity of prior sex separation, and the duration or intensity of male exposure.

Male-to-female ratio: For optimal reproductive synchronization, a ratio of approximately one photostimulated buck per 20 does has been recommended (Zarazaga *et al*., 2018). During mid-anestrus, highly active bucks can effectively stimulate larger groups, with ratios up to 1:39 demonstrating satisfactory estrus induction (Zarazaga *et al*., 2018; Espinoza-Flores *et al.*, 2024). In field conditions, this ratio should be adjusted based on individual serving capacity, male age, breed, and physical housing constraints.

Re-evaluating prior male separation: Traditionally, complete spatial and sensory isolation between bucks and does for at least 3 to 4 weeks prior to biostimulation was considered mandatory to prevent sensory habituation and maximize the novelty of male reintroduction (Walkden-Brown *et al*., 1999). However, recent management protocols demonstrate that prolonged total isolation is not strictly required when intensely active bucks are deployed. Anestrous does kept in continuous contact with sexually inactive bucks still exhibit high ovulatory and estrus responses upon the sudden introduction of photostimulated, sexually active males (Véliz *et al*., 2002; Delgadillo *et al*., 2006; Zarazaga *et al*., 2017). Similarly, introducing a novel active buck can trigger rapid neuroendocrine responses without prior isolation, particularly when direct physical contact is permitted (Gallego-Calvo *et al*., 2014). Nevertheless, temporary separation remains a practical management strategy to enhance stimulus novelty, facilitate controlled mating, and simplify estrus monitoring.

Exposure duration and contact intensity: Continuous male exposure traditionally yields the most consistent ovulatory responses (Walkden-Brown *et al*., 1993); however, the critical determinant of biostimulatory success is the quality, intensity, and nature of socio-sexual interactions rather than contact duration alone (Delgadillo *et al*., 2006). When highly active, photostimulated bucks are deployed, continuous daily cohabitation until ovulation is not strictly required. Restricted direct exposure for as little as 4 hours daily is sufficient to trigger fertile ovulation, provided the stimulus is intense, direct, and repeated predictably over several days (Bedos *et al*., 2010).

Partial socio-sexual stimulation may also be insufficient to sustain ovulatory activity. Under tropical photoperiod and adequate nutrition, Nubian, Alpine, and Nubian × Criollo goats exposed only to visual, olfactory, and auditory male cues still displayed a restricted ovulatory season averaging 4.3 months (Rivera Lozano *et al*., 2011). Together with the evidence summarized above, this finding supports the importance of direct physical contact for full neuroendocrine activation and uniform estrus synchronization across the herd.

Key points: (1) The sexual activity of the buck is the most influential determinant of the male effect, and photoperiodic treatment is the most practical way to enhance it, particularly in strongly seasonal breeds. (2) Female body condition, age, and depth of anestrus modulate the response. (3) Prolonged prior isolation is not essential when sexually active bucks are used, whereas intense, direct physical contact is more important than exposure duration alone.

Practical Applications in Goat Reproductive Management

Hormone-free reproductive management: The male effect offers a sustainable hormone-free alternative to exogenous hormonal treatments for estrus induction and synchronization in goats. This approach directly aligns with increasing consumer demand for natural livestock products and addresses public health concerns regarding synthetic hormone residues in food products (Lopez-Sebastián *et al*., 2014; Pellicer-Rubio *et al*., 2016). To optimize performance without exogenous hormones, Delgadillo *et al.* (2012a) proposed an integrated management strategy combining buck photoperiodic treatment, the male effect, and strategic

nutrition. This multi-factorial framework targets the reproductive axis at key physiological tiers: photoperiodic treatment enhances buck libido and odor intensity, the male effect triggers the female HPG axis, and targeted nutritional management optimizes body condition to maximize ovulatory response.

When applied to AI schemes during seasonal anestrus, these non-hormonal protocols effectively induce and synchronize estrus in lactating does, supporting their potential for timed AI programs (Lopez-Sebastián *et al.*, 2014; Pellicer-Rubio *et al.*, 2016). Nevertheless, hormone-free induction inherently yields greater variability in the timing of estrus onset and ovulation compared to traditional progestagen-based protocols. Consequently, precise estrus detection and tight operational management remain critical prerequisites for achieving acceptable fertility rates.

Integration with AI and practical management protocols: Integrating the male effect into AI programs offers a practical, hormone-free framework for accelerating genetic progress and enhancing reproductive performance in caprine herds. By inducing and synchronizing estrus in anovulatory does, male introduction facilitates predictable AI scheduling and supports fixed-time AI protocols (Pellicer-Rubio *et al.*, 2016).

As discussed in the subsection on prior male separation, strict prior isolation is less critical when intensely active males are deployed: seasonally anovulatory goats previously kept in sensory contact with sexually inactive bucks showed estrous responses comparable to those of isolated females after the introduction of a photostimulated buck (Zarazaga *et al.*, 2017). This finding carries substantial practical value for tropical production systems, where achieving total spatial and sensory isolation between sexes is often challenging due to housing constraints.

Despite these management simplifications, operational challenges persist regarding the precise timing of insemination due to natural variations in estrus onset and the characteristic occurrence of short luteal cycles following initial male contact. Because the first induced ovulation is frequently followed by premature luteal regression and reduced fertility, insemination should preferably be targeted toward the second induced estrus, during which luteal function and fertility are fully established (Pellicer-Rubio *et al.*, 2016). Maximizing conception rates under these protocols requires rigorous estrus detection, typically accomplished through the strategic deployment of vasectomized or apron-fitted teaser bucks equipped with marking harnesses to identify receptive females accurately.

The buck-to-buck effect (social facilitation among males): A novel extension of male biostimulation is the "buck-to-buck effect", a socio-sexual phenomenon wherein sexually active males stimulate endocrine activity and courtship behavior in sexually inactive males during seasonal sexual rest (Delgadillo *et al.*, 2022). Social interaction with sexually active bucks triggers heightened secretion of LH and testosterone in sexually inactive recipient males, subsequently elevating their courtship behaviors. Remarkably, these socially activated males acquire sufficient biostimulatory capacity to induce a classical male effect in seasonally anestrous does, achieving reproductive performances comparable to those stimulated by directly photostimulated males (Delgadillo *et al.*, 2022).

Prolonged cohabitation with sexually active males maintains sustained endocrine and behavioral activation in recipient bucks. Interestingly, enhanced courtship behavior persists even after plasma testosterone concentrations decline, suggesting that social facilitation may involve central neuroendocrine mechanisms that operate independently of circulating androgen levels (Delgadillo *et al.*, 2026).

At the flock level, this socio-sexual hierarchy offers a highly practical and sustainable management strategy. A previous study reported that photostimulating only a small subset of bucks is sufficient to socially activate the remaining males, which can then collectively induce estrus and ovulation in anestrous does (Delgadillo *et al.*, 2022). Incorporating apron-fitted or fully intact sexually active males alongside untreated herdmates provides effective biostimulation across commercial flocks without compromising overall kidding rates (López-Magana *et al.*, 2025). This social facilitation framework substantially reduces the infrastructure, energy, and labor required for light-control facilities, offering a scalable, hormone-free approach to year-round reproductive management in small ruminant production systems.

Synthetic buck odor and pheromone applications: The identification of 4-ethyloctanal as the key primer pheromone activating the caprine GnRH pulse generator has expanded the framework for developing synthetic, pheromone-based reproductive management tools (Murata *et al.*, 2014). Synthetic 4-ethyloctanal activated the GnRH pulse generator in female goats, as assessed by MUA recordings, although with lower potency than the complete mixture of male volatiles (Murata *et al.*, 2014); its ability to induce ovulation has not yet been demonstrated. This response highlights the potential of synthetic pheromone formulations as non-living alternatives to bucks for inducing and synchronizing estrus. In contrast, synthetic 4-ethyloctanoic acid showed releaser but not primer pheromone activity (Iwata *et al.*, 2003; see the subsection on VOCs), confirming that odor-associated compounds should be distinguished from compounds with proven primer activity.

Crude pheromone extracts derived from male hair and wool also demonstrate considerable efficacy. Pheromones extracted from Awassi ram wool and Shami buck hair significantly elevated circulating LH and progesterone concentrations in Awassi ewes during the breeding season, suggesting that non-contact pheromonal stimulation can effectively drive neuroendocrine responses (Harba *et al.*, 2024); their efficacy during anestrus remains to be tested. These findings suggest that crude extracts provide a practical middle ground between live males and fully synthetic formulations.

Nevertheless, synthetic buck odor and pheromone-based protocols are not yet fully field-ready for

commercial deployment (Anakkul *et al.*, 2025). Critical challenges include establishing optimal dosages, effective delivery vectors, ambient stability under humid tropical conditions, and consistent fertility outcomes. Current evidence remains predominantly experimental; thus, implementing practical protocols in tropical herds will require comprehensive validation regarding breed-specific sensitivity, nutritional interactions, and cost-effectiveness. The expansion of these technologies provides key strategic benefits by minimizing reliance on live bucks while improving herd logistics and biosecurity, representing a crucial direction for future research.

Economic and sustainability benefits: The male effect provides a highly cost-effective, low-input, and non-invasive strategy for managing caprine reproduction (Lopez-Sebastián *et al.*, 2014; Viana Neto *et al.*, 2016). Traditional exogenous hormonal protocols incur recurring pharmaceutical costs (Khunmanee *et al.*, 2019), require direct veterinary intervention, and increasingly trigger animal welfare concerns. Conversely, male biostimulation relies entirely on natural neuroendocrine responses and can be executed with minimal farm infrastructure. Integrating artificial photoperiod treatments with the buck-to-buck effect further maximizes economic feasibility by reducing energy and facility demands, as a single photostimulated buck can socially activate multiple males across the herd (Delgadillo *et al.*, 2022; López-Magana *et al.*, 2025). For smallholder farmers in tropical and subtropical regions, this framework offers an exceptionally accessible and sustainable management tool requiring only simple facilities, particularly because strict prior isolation is not essential when sexually active bucks are used (Zarazaga *et al.*, 2017).

Key points: (i) The male effect can be integrated with buck photostimulation, nutritional management, the buck-to-buck effect, and AI as a sustainable, hormone-free reproductive strategy. (ii) Because the first induced ovulation is frequently followed by a short luteal phase, AI should preferably target the second induced estrus unless females are pretreated with progestagens. (iii) Synthetic pheromones remain experimental and require field validation prior to commercial adoption.

Opportunities and Future Perspectives

The integration of biostimulatory protocols, specifically the classical male effect, photoperiodic manipulation of bucks, and the newly described buck-to-buck effect, presents a valuable opportunity for small ruminant production systems worldwide. As global consumer demand shifts toward sustainable agriculture and stricter welfare regulations limit the routine use of exogenous hormones such as fluorogestone acetate sponges or equine chorionic gonadotropin, biostimulation offers a green, hormone-free, and ethically sound alternative for off-season estrus induction and synchronization. However, transitioning these socio-sexual phenomena from controlled experimental settings to widespread, commercial-scale adoption requires addressing several technical opportunities, mechanistic knowledge gaps, and field-level implementation challenges.

Refinement and optimization of social facilitation: The discovery of the buck-to-buck effect opens substantial avenues for simplifying flock management and lowering infrastructure investment. Because photoperiodic treatment of bucks requires light-proof facilities and automated lighting systems, the need to treat an entire male herd presents a significant financial barrier for smallholders. The buck-to-buck effect demonstrates that treating only a fraction of the male population is sufficient to socially activate untreated co-housed males, who then successfully stimulate anestrous females. Future research must prioritize establishing precise management thresholds for this social facilitation model. Specifically, studies are needed to determine the minimum ratio of photostimulated to non-photostimulated males required across varying herd densities, the exposure duration and social dominance dynamics necessary for recipient males to acquire biostimulatory capacity, and the spatial or acoustic parameters needed during male-male priming to prevent habituation while maximizing courtship behavior upon female exposure.

Unraveling neuroendocrine and physiological mechanisms: Although pathways involving both the main olfactory and vomeronasal systems, the medial amygdala, and ARC KNDy neurons have been partly characterized, mainly in rodents, sheep, and ovariectomized goats, key physiological mechanisms underpinning male biostimulation remain unresolved. Further investigation should focus on elucidating the relative contributions of the vomeronasal and main olfactory systems to the male effect in goats, particularly through selective sensory ablation studies.

A particularly intriguing observation in recipient males is that socially activated bucks maintain elevated courtship behavior and biostimulatory efficacy even after systemic testosterone concentrations decline. Decoupling socio-sexual behavior from circulating androgen status highlights a critical opportunity for neurobiological research. Priority should be given to mapping central c-Fos activation and the expression of kisspeptin, neurokinin B, and opioid peptides in recipient males during intra-male biostimulation. Furthermore, characterizing chemical changes in buck odor induced purely through socio-sexual facilitation will support the development of standardized, pheromone-based protocols for estrus induction and synchronization using synthetic compounds such as 4-ethyloctanal. Emerging evidence also points toward exploring the role of the gut microbiome and metabolome in mediating female biostimulatory responsiveness and pheromonal output (Liu *et al.*, 2026).

Development and application of synthetic buck odor: Building on identification of 4-ethyloctanal as a primer pheromone component (Murata *et al.*, 2014; see Synthetic buck odor and pheromone applications), the next challenge is to translate this signal into practical reproductive tools.

Translating this chemical signal into practical farming tools offers clear logistical advantages, including reduced buck housing costs, simplified herd biosafety, and broader application in AI programs. To maximize field efficacy, advanced delivery platforms such as microencapsulated formulations, controlled-release collars, or ambient diffuser systems are currently being conceptualized. Although such release technologies are well established in insect and mammalian pest management, their specific application to caprine reproductive management remains in its infancy and warrants rigorous field validation (Anakkul *et al.*, 2025).

Future research should therefore optimize dosage and delivery, confirm stability under humid tropical conditions, evaluate safety, and demonstrate consistent ovulation and pregnancy rates, breed-specific sensitivity, and cost-effectiveness under production conditions.

Breed sensitivity, genetic selection, and climatic resilience: Extending biostimulatory strategies across diverse climatic zones requires a deeper understanding of breed-specific sensitivity. Breeds exhibiting deep, rigid seasonal anestrus, such as the Blanca Andaluza or high-latitude temperate breeds, generally require photostimulated males or socially activated males to overcome the photoperiodic inhibition of females. Conversely, breeds with shallow seasonality, such as Murciano-Granadina or tropical Creoles, respond readily to less intense biostimulation. Optimizing photoperiodic and nutritional strategies tailored to specific breeds and production systems remains essential, particularly in tropical environments.

In tropical and subtropical regions, environmental heat stress acts as a primary stressor that compromises male libido, semen quality, and pheromonal output during dry seasons. Future perspectives should focus on incorporating male biostimulatory traits, including high sexual vigor, robust libido under thermal stress, and strong pheromone production, into genetic selection indices for breeding programs. Concurrently, developing cost-effective microclimate management strategies such as shade geometry, evaporative cooling, and strategic diurnal exposure timing will help preserve male stimulus strength. Integrating these strategies with Precision Livestock Farming technologies, including accelerometers, bio-logging collars, and thermal imaging, will allow real-time monitoring of male physical activity, mounting behavior, and scrotal temperature, enabling producers to objectively evaluate male readiness before initiating biostimulation.

Integration with assisted reproduction and socio-economic viability: The ultimate success of biostimulatory protocols relies on their seamless integration with overall farm management, particularly nutrition and modern reproductive technologies. In tropical systems where feed scarcity fluctuates with seasonal rainfall, body condition score and metabolic status dictate female responsiveness to male introduction. Biostimulation cannot overcome severe energy deficits; thus, combining photoperiodically or socially activated males with strategic, short-term nutritional flushing offers a holistic, low-input management package.

Furthermore, integrating the male effect with advanced reproductive technologies, including fixed-time AI and embryo transfer, provides a practical framework for accelerating genetic progress without relying on exogenous hormones. To ensure widespread adoption, future research must evaluate the economic cost-effectiveness, logistical feasibility, and socio-economic adoption barriers of these integrated biostimulatory protocols within smallholder goat farming systems in tropical regions. Communicating these evidence-based, low-cost strategies through practical field guidelines will be crucial to achieving sustainable, year-round reproductive management and enhancing global small ruminant productivity.

Key points: (i) Research priorities include defining the relative roles of the MOS and VNS in goats and the central mechanisms of the buck-to-buck effect. (ii) Synthetic pheromone tools require optimized dosage, delivery, and stability, and must demonstrate ovulation and pregnancy outcomes under field conditions. (iii) Breed-specific, climate-resilient protocols and their cost-effectiveness in smallholder systems should be evaluated.

Conclusion

The male effect represents a promising hormone-free strategy in small ruminant reproductive management, supported by substantial experimental and field evidence for sustainable, year-round caprine production. Harnessing the neuroendocrine cascades triggered by male socio-sexual biostimulation enables livestock production systems to effectively overcome seasonal anestrus while minimizing reliance on exogenous hormonal therapies. Integrating classical biostimulatory frameworks with strategic photoperiodic manipulation, optimal male-to-female ratios, and tactical nutritional flushing optimizes reproductive efficiency, and synthetic buck odorants may further contribute once validated under field conditions. Furthermore, this integrated approach aligns livestock operations with stringent standards of animal welfare and environmental sustainability.

Translating these biostimulatory concepts into widespread, successful field applications necessitates addressing environmental constraints. Heat stress and seasonal nutritional deficits in tropical regions directly dictate male libido and female hypothalamic responsiveness; therefore, bridging remaining knowledge gaps across neuroendocrinology, sensory biology, and farm-level feasibility through interdisciplinary research remains essential to establish climate-resilient, breed-specific management protocols. Ultimately, integrating male biostimulation into modern reproductive technologies and precision farming systems harmonizes fundamental neurobiology with practical husbandry, driving long-term productivity, genetic progress, and sustainability in global livestock production.

Acknowledgments

This review was financially supported by the Faculty of Veterinary Science Research Fund, Chulalongkorn University (Grant No. RI 7/2568, 2025). The authors would like to thank Professor Emeritus Dr. Mongkol Techakumphu and Professor Dr. Tirayut Vilaivan for conceptualizing and initiating the project on synthetic odor in small ruminants, which served as the primary catalyst for this review and our broader research program.

Conflict of interest: The authors declare no conflict of interest.

Statement of author contributions: **Nitira Anakkul:** Conceptualization, Methodology, Visualization, Writing – original draft, Funding Acquisition. **Sopita Suttikrai:** Writing – original draft. **Ratree Jintana:** Writing – original draft. **Theerawat Swangchan-Uthai:** Conceptualization, Supervision, Writing – review & editing. All authors have read and approved the final version of the manuscript.

Declaration of artificial intelligence use: Perplexity AI was employed to conduct literature verification and cross-check the accuracy of reference citations. Additionally, Google Gemini (version 2.0 Flash) was used for English language proofreading, and enhancing the academic tone of the text. After this process, the authors thoroughly reviewed and edited the content as needed and took full responsibility for the accuracy, originality, and integrity of the publication.

References

Abecia JA, Forcada F and González-Bulnes A 2012. Hormonal control of reproduction in small ruminants. Anim Reprod Sci. 130(3-4): 173–179.

Anakkul N, Suwimonteerabutr J, Tharasanit T, Panyaboriban S, Khunmanee S, Thanomsuksinchai N and Techakumphu M 2013. Production of black goat using laparoscopic artificial insemination and embryo transfer. Thai J Vet Med. 43(2): 259–263.

Anakkul N, Vilaivan T, Yukhet P, Nakkhao W, Suttikrai S, Jintana R and Techakumphu M 2025. Preliminary study on estrus detection using synthetic buck scent. Thai J Vet Med. 55(Suppl. 1): 167.

Baum MJ and Kelliher KR 2009. Complementary roles of the main and accessory olfactory systems in mammalian mate recognition. Annu Rev Physiol. 71: 141–160.

Bedos M, Flores JA, Fitz-Rodríguez G, Keller M, Malpaux B, Poindron P and Delgadillo JA 2010. Four hours of daily contact with sexually active males is sufficient to induce fertile ovulation in anestrous goats. Horm Behav. 58: 473–477.

Bedos M, Portillo W, Dubois J, Duarte G, Flores JA, Chemineau P, Keller M, Paredes R and Delgadillo JA 2016. A high level of male sexual activity is necessary for the activation of the medial preoptic area and the arcuate nucleus during the 'male effect' in anestrous goats. Physiol Behav. 165: 173–178.

Caraty A, Delaleu B, Chesneau D and Fabre-Nys C 2002. Sequential role of E2 and GnRH for the expression of estrous behavior in ewes. Endocrinology 143(1): 139–145.

Caraty A, Fabre-Nys C, Delaleu B, Locatelli A, Bruneau G, Karsch FJ and Herbison A 1998. Evidence that the mediobasal hypothalamus is the primary site of action of estradiol in inducing the preovulatory gonadotropin releasing hormone surge in the ewe. Endocrinology 139(4): 1752–1760.

Caraty A and Skinner DC 1999. Progesterone priming is essential for the full expression of the positive feedback effect of estradiol in inducing the preovulatory gonadotropin-releasing hormone surge in the ewe. Endocrinology 140(1): 165–170.

Chasles M, Chesneau D, Moussu C, Delgadillo JA, Chemineau P and Keller M 2016. Sexually active bucks are efficient to stimulate female ovulatory activity during the anestrous season also under temperate latitudes. Anim Reprod Sci. 168: 86–91.

Chasles M, Chesneau D, Moussu C, Poissenot K, Beltramo M, Delgadillo JA, Chemineau P and Keller M 2018. Sexually active bucks are a critical social cue that activates the gonadotrope axis and early puberty onset in does. Horm Behav. 106: 81–92.

Chemineau P 1983. Effect on oestrus and ovulation of exposing Creole goats to the male at three times of the year. J Reprod Fertil. 67: 65–72.

Chemineau P 1987. Possibilities for using bucks to stimulate ovarian and oestrous cycles in anovulatory goats: A review. Livest Prod Sci. 17: 135–147.

Chemineau P, Daveau A, Cognié Y, Aumont G and Chesneau D 2004. Seasonal ovulatory activity exists in tropical Creole female goats and Black Belly ewes subjected to a temperate photoperiod. BMC Physiol. 4: 12.

Chemineau P, Pellicer-Rubio MT, Lassoued N, Khaldi G and Monniaux D 2006. Male-induced short oestrous and ovarian cycles in sheep and goats: A working hypothesis. Reprod Nutr Dev. 46(4): 417–429.

Claus R, Over R and Dehnhard M 1990. Effect of male odour on LH secretion and the induction of ovulation in seasonally anoestrous goats. Anim Reprod Sci. 22: 27–38.

Danso F, Iddrisu L, Lungu SE, Zhou G and Ju X 2024. Effects of heat stress on goat production and mitigating strategies: A review. Animals 14: 1793.

Delgadillo JA, Carrillo E, Moran J, Duarte G, Chemineau P and Malpaux B 2001. Induction of sexual activity of male creole goats in subtropical northern Mexico using long days and melatonin. J Anim Sci. 79: 2245–2252.

Delgadillo JA, Duarte G, Flores JA, Vielma J, Hernández H, Fitz-Rodríguez G, Bedos M, Fernández I, Munoz-Gutierrez M, Retana-Marquez S and Keller M 2012a. Control of the sexual activity of goats without exogenous hormones: Use of photoperiod, male effect and nutrition. Trop Subtrop Agroecosyst. 15(S1): S15–S27.

Delgadillo JA, Espinoza-Flores LA, Abecia JA, Hernández H, Keller M and Chemineau P 2022. Sexually active male goats stimulate the endocrine and sexual activities of other males in seasonal sexual rest through the "buck-to-buck effect". Domest Anim Endocrinol. 78: 106746.

Delgadillo JA, Fitz-Rodríguez G, Duarte G, Véliz FG, Carrillo E, Flores JA, Vielma J, Hernández H and Malpaux B 2004. Management of photoperiod to control caprine reproduction in the subtropics. Reprod Fertil Dev. 16: 471–478.

Delgadillo JA, Flores JA, Hernández H, Poindron P, Keller M, Fitz-Rodríguez G, Duarte G, Vielma J, Fernández IG and Chemineau P 2015. Sexually active males prevent the display of seasonal anestrus in female goats. Horm Behav. 69: 8–15.

Delgadillo JA, Flores JA, Véliz FG, Duarte G, Vielma J, Hernández H and Fernández IG 2006. Importance of the signals provided by the buck for the success of the male effect in goats. Reprod Nutr Dev. 46: 391–400.

Delgadillo JA, Flores JA, Véliz FG, Hernández H, Duarte G, Vielma J, Poindron P, Chemineau P and Malpaux B 2002. Induction of sexual activity in lactating anovulatory female goats using male goats treated only with artificially long days. J Anim Sci. 80: 2780–2786.

Delgadillo JA, Gelez H, Ungerfeld R, Hawken PAR and Martin GB 2009. The 'male effect' in sheep and goats—revisiting the dogmas. Behav Brain Res. 200: 304–314.

Delgadillo JA, López-Magana N, Tejada LM, López-Magana D, Hernández H, Abecia J, Keller M and Chemineau P 2026. Long-term male-to-male effect progressively activates testosterone and socio-sexual behavior in seasonally resting male goats. Domest Anim Endocrinol. 97: 107025.

Delgadillo JA and Vélez LI 2010. Stimulation of reproductive activity in anovulatory Alpine goats exposed to bucks treated only with artificially long days. Animal 4(12): 2012–2016.

Delgadillo JA, Vielma J, Hernández H, Flores JA, Duarte G, Fernández IG, Keller M and Gelez H 2012b. Male goat vocalizations stimulate the estrous behavior and LH secretion in anestrous goats that have been previously exposed to bucks. Horm Behav. 62: 525–530.

Endo N and Tanaka T 2014. Effects of senktide, a neurokinin 3 receptor agonist, on luteinizing hormone secretion and follicular development in anestrous Shiba goats: A pilot study. BMC Res Notes. 7: 773.

Espinoza-Flores LA, Andrade-Esparza JD, Vielma J, López Magaña D, Zarazaga LA, Hernández H, Keller M, Chemineau P and Delgadillo JA 2024. Two sexually active bucks housed with four successive groups of anovulatory does induced high pregnancy rates during seven-day mating period. Trop Subtrop Agroecosyst. 27: 028.

Flores JA, Véliz FG, Perez-Villanueva J, Martinez de la Escalera G, Chemineau P, Poindron P, Malpaux B and Delgadillo JA 2000. Male reproductive condition is the limiting factor of efficiency in the male effect during seasonal anestrus in female goats. Biol Reprod. 62: 1409–1414.

Freitas VJF, Rondina D, Lopes ES Jr, Teixeira DIA and Paula NRO 2004. Hormonal treatments for the synchronisation of oestrus in dairy goats raised in the tropics. Reprod Fertil Dev. 16: 415–420.

Gallego-Calvo L, Gatica MC, Celi I, Guzmán JL, Delgadillo JA and Zarazaga LA 2014. No previous isolation of female goats is required for novel males to induce a male effect, especially if direct physical contact is established. Theriogenology 82(9): 1310–1315.

Gallego-Calvo L, Gatica MC, Guzmán JL and Zarazaga LA 2015. Reproductive performance response to the male effect in goats is improved when doe live weight/body condition score is increasing. Anim Reprod Sci. 156: 51–57.

Gelez H and Fabre-Nys C 2004. The "male effect" in sheep and goats: A review of the respective roles of the two olfactory systems. Horm Behav. 46: 257–271.

Gelez H and Fabre-Nys C 2006. Neural pathways involved in the endocrine response of anestrous ewes to the male or its odor. Neuroscience 140(3): 791–800.

Gómez-Brunet A, Santiago-Moreno J, Toledano-Diaz A and Lopez-Sebastián A 2012. Reproductive seasonality and its control in Spanish sheep and goats. Trop Subtrop Agroecosyst. 15: S47–S70.

González-Bulnes A, Carrizosa JA, Urrutia B and Lopez-Sebastián A 2006. Oestrous behaviour and development of preovulatory follicles in goats induced to ovulate using the male effect with and without progesterone priming. Reprod Fertil Dev. 18(7): 745–750.

Harba H, Moussa MA, Al Yasin AO, Zarkawi M and Amirat L 2024. The application of pheromones extracted from Shami goats' male hair and Awassi sheep male wool during the breeding season on LH and progesterone concentrations in Awassi ewes in Syria. Open Vet J. 14: 2564–2571.

Hebets EA and Papaj DR 2005. Complex signal function: Developing a framework of testable hypotheses. Behav Ecol Sociobiol. 57(3): 197–214.

Ichimaru T, Takeuchi Y and Mori Y 1999. Stimulation of the GnRH pulse generator activity by continuous exposure to the male pheromones in the female goat. J Reprod Dev. 45: 243–248.

Iwata E, Kikusui T, Takeuchi Y and Mori Y 2003. Substances derived from 4-ethyl octanoic acid account for primer pheromone activity for the "male effect" in goats. J Vet Med Sci. 65: 1019–1021.

Iwata E, Wakabayashi Y, Kakuma Y, Kikusui T, Takeuchi Y and Mori Y 2000. Testosterone-dependent primer pheromone production in the sebaceous gland of male goat. Biol Reprod. 62: 806–810.

Kang N, Baum MJ and Cherry JA 2009. A direct main olfactory bulb projection to the 'vomeronasal' amygdala in female mice selectively responds to volatile pheromones from males. Eur J Neurosci. 29(3): 624–634.

Karsch FJ, Bittman EL, Foster DL, Goodman RL, Legan SJ and Robinson JE 1984. Neuroendocrine basis of seasonal reproduction. Recent Prog Horm Res. 40: 185–232.

Kendrick KM, Fabre-Nys C, Blache D, Goode JA and Broad KD 1993. The role of oxytocin release in the mediobasal hypothalamus of the sheep in relation to female sexual receptivity. J Neuroendocrinol. 5: 13–21.

Khunmanee S, Swangchan-Uthai T, Suwimonteerabutr J, Thiangthientham P, Supappornchai S and Techakumphu M 2019. Development of business models for indigenous genetic improvement in small ruminant farms through reproductive biotechnology. Thai J Vet Med. 49(3): 217–225.

Lehman MN, Merkley CM, Coolen LM and Goodman RL 2010. Anatomy of the kisspeptin neural network in mammals. Brain Res. 1364: 90–102.

Liu QQ, Wang YL, Shi CB, Yu K, Liu LH, Wang W, He QY and Luo J 2026. Associations of short photoperiod and the male effect with fecal microbiota, metabolomic profiles, serum metabolites, and reproductive performance in dairy goats during the nonbreeding season. J Dairy Sci. In press.

López-Magana N, Tejada LM, López-Magana D, Millan-Orozco J, Hernández H, Millan-Orozco J, Bedos M, Abecia J, Keller M, Chemineau P and Delgadillo JA 2025. Male goats exposed to the "male-to-male effect" stimulate the reproductive activity and ensure high fertility of both does and male goats during the non-breeding season. Theriogenology 243: 117476.

Lopez-Sebastián A, Coloma MA, Toledano A and Santiago-Moreno J 2014. Hormone-free protocols for the control of reproduction and artificial insemination in goats. Reprod Domest Anim. 49(Suppl 4): 22–29.

Martínez-Alfaro JC, Hernández H, Flores JA, Duarte G, Fitz-Rodríguez G, Fernández IG, Bedos M, Chemineau P, Keller M, Delgadillo JA and Vielma J 2014. Importance of intense male sexual behavior for inducing the preovulatory LH surge and ovulation in seasonally anovulatory female goats. Theriogenology 82(7): 1028–1035.

Matsuda F, Nakatsukasa K, Suetomi Y, Naniwa Y, Ito D, Inoue N, Wakabayashi Y, Okamura H, Maeda KI, Uenoyama Y, Tsukamura H and Ohkura S 2015. The luteinising hormone surge-generating system is functional in male goats as in females: Involvement of kisspeptin neurones in the medial preoptic area. J Neuroendocrinol. 27(1): 57–65.

Merkley CM, Porter KL, Coolen LM, Hileman SM, Billings HJ, Drews S, Goodman RL and Lehman MN 2012. KNDy (kisspeptin/neurokinin B/dynorphin) neurons are activated during both pulsatile and surge secretion of LH in the ewe. Endocrinology. 153(11): 5406–5414.

Mori Y, Nishihara M, Tanaka T, Shimizu T, Yamaguchi M, Takeuchi Y and Hoshino K 1991. Chronic recording of electrophysiological manifestation of the hypothalamic gonadotropin-releasing hormone pulse generator activity in the goat. Neuroendocrinology 53(4): 392–395.

Murata K, Tamogami S, Itou M, Ohkubo Y, Wakabayashi Y, Watanabe H, Okamura H, Takeuchi Y and Mori Y 2014. Identification of an olfactory signal molecule that activates the central regulator of reproduction in goats. Curr Biol. 24: 681–686.

Murata K, Wakabayashi Y, Sakamoto K, Tanaka T, Takeuchi Y, Mori Y and Okamura H 2011. Effects of brief exposure of male pheromone on multiple-unit activity at close proximity to kisspeptin neurons in the goat arcuate nucleus. J Reprod Dev. 57: 197–202.

Nestor CC, Merkley CM, Lehman MN, Hileman SM and Goodman RL 2023. KNDy neurons as the GnRH pulse generator: Recent studies in ruminants. Peptides 164: 171005.

Ohara H, Okamura H, Mogi K, Ohkura S, Ichimaru T, Mori Y and Takeuchi Y 2014. Effects of exposure to male goat hair extracts on luteinizing hormone secretion and neuronal activation in seasonally anestrous ewes. J Vet Med Sci. 76: 1329–1337.

Ohkura S and Nakamura S 2026. Neuroendocrine mechanisms leading to novel control techniques of reproduction in livestock: Regulation of the GnRH pulse generator activity. J Reprod Dev. 72: 398–402.

Okamura H, Murata K, Sakamoto K, Wakabayashi Y, Ohkura S, Takeuchi Y and Mori Y 2010. Male effect pheromone tickles the gonadotrophin-releasing hormone pulse generator. J Neuroendocrinol. 22: 825–832.

Partan S and Marler P 1999. Communication goes multimodal. Science 283(5406): 1272–1273.

Pellicer-Rubio MT, Boissard K, Forgerit Y, Pougnard JL, Bonne JL and Leboeuf B 2016. Evaluation of hormone-free protocols based on the "male effect" for artificial insemination in lactating goats during seasonal anestrus. Theriogenology 85: 960–969.

Pellicer-Rubio MT, Leboeuf B, Bernelas D, Forgerit Y, Pougnard JL, Bonne JL, Senty E, Breton S, Brun F and Chemineau P 2008. High fertility using artificial insemination during deep anoestrus after induction and synchronisation of ovulatory activity by the "male effect" in lactating goats subjected to treatment with artificial long days and progestagens. Anim Reprod Sci. 109: 172–188.

Ponce-Covarrubias JL, García y González EC, Pineda-Burgos BC, Guevara-Arroyo AM, Hernández-Ruiz PE, Torres-Agatón F, Ruiz-Ortega M, Paredes-Alvarado M, Robles-Robles JM, Rodríguez-Castillo JC, Ángel-García O and Valencia-Franco E 2023. Annual sexual behavior in Boer bucks located in the Guerrero tropics in Mexico. Ruminants 3(2): 149–157.

Rekwot PI, Ogwu D, Oyedipe EO and Sekoni VO 2001. The role of pheromones and biostimulation in animal reproduction. Anim Reprod Sci. 65: 157–170.

Rivera Lozano MT, Díaz Gómez MO, Urrutia Morales J, Vera Ávila H, Gamez Vázquez H, Villagomez-Amezcua Manjarrez E, Aréchiga Flores CF and Escobar Medina FJ 2011. Seasonal variation in ovulatory activity of Nubian, Alpine and Criollo × Nubian goats under tropical photoperiod. Trop Subtrop Agroecosyst. 14(3): 973–980.

Rosa HJD and Bryant MJ 2002. The 'ram effect' as a way of modifying reproductive activity in the ewe. Small Rumin Res. 45: 1–16.

Rosa HJD and Bryant MJ 2003. Seasonality of reproduction in sheep. Small Rumin Res. 48: 155–171.

Sakamoto K, Wakabayashi Y, Yamamura T, Tanaka T, Takeuchi Y, Mori Y and Okamura H 2013. A population of kisspeptin/neurokinin B neurons in the arcuate nucleus may be the central target of the male effect phenomenon in goats. PLoS One 8: e81017.

Salles MGF, Viana Neto AM, Vieira Neto MF, Rodrigues ICS, Rocha DR, Carneiro PTS and Araújo AA 2020. Tropical climate induces seasonal changes in the reproductive parameters and hormonal profile of Saanen bucks. Vet Arh. 90(3): 235–242.

Sankarganesh D, Annis Inncia GT and Shibu A 2025. Buck effect in goat reproduction: A review. J Endocrinol Reprod. 29: 1–12.

Scalia F and Winans SS 1975. The differential projections of the olfactory bulb and accessory olfactory bulb in mammals. J Comp Neurol. 161: 31–55.

Schumacher M, Coirini H, Pfaff DW and McEwen BS 1990. Behavioral effects of progesterone associated with rapid modulation of oxytocin receptors. Science 250: 691–694.

Skinner DC, Caraty A, Malpaux B and Evans NP 1997. Simultaneous measurement of gonadotropin-releasing hormone in the third ventricular cerebrospinal fluid and hypophyseal portal blood of the ewe. Endocrinology 138(11): 4699–4704.

Smith JT, Li Q, Pereira A and Clarke IJ 2009. Kisspeptin neurons in the ovine arcuate nucleus and preoptic area are involved in the preovulatory luteinizing hormone surge. Endocrinology 150(12): 5530–5538.

Smith PW, Parks OW and Schwartz DP 1984. Characterization of male goat odors: 6-trans nonenal. J Dairy Sci. 67: 794–801.

Tanaka T, Ohgata N, Kamomae H, Takeuchi Y, Mori Y and Karsch FJ 1997. Hypophyseal portal blood collection for analysis of GnRH neurosecretion in Shiba goats. J Reprod Dev. 43(1): 101–106.

Thiangthientham P, Anakkul N, Suwimonteerabutr J, Kallayanathum W, Santiviparat S, Techakumphu M and Tharasanit T 2022. Ovarian stimulation with a low dose of follicle stimulating hormone improved recovery rates and developmental competence of goat oocytes. Thai J Vet Med. 52(3): 507–513.

Ungerfeld R, Forsberg M and Rubianes E 2004. Overview of the response of anoestrous ewes to the ram effect. Reprod Fertil Dev. 16: 479–490.

Véliz FG, Moreno S, Duarte G, Vielma J, Chemineau P, Poindron P, Malpaux B and Delgadillo JA 2002. Male effect in seasonally anovulatory lactating goats depends on the presence of sexually active bucks, but not estrous females. Anim Reprod Sci. 72: 197–207.

Vera-Avila H, Urrutia-Morales J, Espinosa-Martinez MA, Gamez-Vazquez HG, Jimenez-Severiano H and Villagomez-Amezcua E 2017. Body condition and stage of seasonal anestrus interact to determine the ovulatory response after male biostimulation in anovulatory Criollo × Nubian goats. Anim Sci J. 88: 841–846.

Viana Neto AM, Salles MG, Araújo ÉP, Rodrigues IC, Rocha DR and Araújo AD 2016. Male effect: Sustainability and effectiveness in inducing estrus in goats/efecto macho: Sostenibilidad y eficiencia en la inducción del celo en cabras. J Vet Androl. 1(1): 13–23.

Wakabayashi Y, Iwata E, Kikusui T, Takeuchi Y and Mori Y 2000. Regional differences of pheromone production in the sebaceous glands of castrated goats treated with testosterone. J Vet Med Sci. 62: 1067–1072.

Wakabayashi Y, Mori Y, Ichikawa M, Yazaki K and Hagino-Yamagishi K 2002. A putative pheromone receptor gene is expressed in two distinct olfactory organs in goats. Chem Senses. 27(3): 207–213.

Wakabayashi Y, Nakada T, Murata K, Ohkura S, Mogi K, Navarro VM, Clifton DK, Mori Y, Tsukamura H, Maeda K, Steiner RA and Okamura H 2010. Neurokinin B and dynorphin A in kisspeptin neurons of the arcuate nucleus participate in generation of periodic oscillation of neural activity driving pulsatile gonadotropin-releasing hormone secretion in the goat. J Neurosci. 30(8): 3124–3132.

Wakabayashi Y, Ohkura S, Okamura H, Mori Y and Ichikawa M 2007. Expression of a vomeronasal receptor gene (V1r) and G protein alpha subunits in goat, *Capra hircus*, olfactory receptor neurons. J Comp Neurol. 503(2): 371–380.

Wakabayashi Y, Yamamura T, Sakamoto K, Mori Y and Okamura H 2013. Electrophysiological and morphological evidence for synchronized GnRH pulse generator activity among kisspeptin/neurokinin B/dynorphin A (KNDy) neurons in goats. J Reprod Dev. 59: 40–48.

Walkden-Brown SW, Martin GB and Restall BJ 1999. Role of male-female interaction in regulating reproduction in sheep and goats. J Reprod Fertil Suppl. 54: 243–257.

Walkden-Brown SW, Restall BJ and Henniawati 1993. The male effect in the Australian cashmere goat. 2. Role of olfactory cues from the male. Anim Reprod Sci. 32: 55–67.

Zarazaga LA, Gatica MC, Delgado-Pertínez M, Hernández H, Guzmán JL and Delgadillo JA 2021. Photoperiod-treatment in Mediterranean bucks can improve the reproductive performance of the male effect depending on the extent of their seasonality. Animals 11: 400.

Zarazaga LA, Gatica MC, de la Rosa I, Delgado-Pertínez M and Guzmán JL 2022. The high testosterone concentrations of the bucks used in the "male effect" is not a prerequisite for obtaining high ovarian activity in goats from Mediterranean latitudes. Animals 12: 954.

Zarazaga LA, Gatica MC, Gallego-Calvo ML and Guzmán JL 2018. When using photostimulated bucks to induce the male effect in female goats living at Mediterranean latitudes, a male:female ratio of 1:20 is optimum. J Appl Anim Res. 46: 883–887.

Zarazaga LA, Gatica MC, Hernández H, Gallego-Calvo L, Delgadillo JA and Guzmán JL 2017. The isolation of females from males to promote a later male effect is unnecessary if the bucks used are sexually active. Theriogenology 95: 42–47.

Zarazaga LA, Gatica MC, Hernández H, Keller M, Chemineau P, Delgadillo JA and Guzmán JL 2019. The reproductive response to the male effect of 7-

or 10-month-old female goats is improved when photostimulated males are used. Animal 13: 1658–1665.