Uttar Pradesh Journal of Zoology

Volume 45, Issue 20, Page 210-219, 2024; Article no.UPJOZ.4252
ISSN: 0256-971X (P)

Unlocking the Secrets of Pheromones: Reproductive and Social Communication in Domestic Mammals

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Authors' contributions

This work was carried out in collaboration among all authors. Authors KD, PA and TAK conceptualized the title and wrote the first draft of the manuscript. Authors VBJ, PS and RG corrected the manuscript and arranged the manuscript as per the format. All authors read and approved the final manuscript.

Article Information

DOI: https://doi.org/10.56557/upjoz/2024/v45i204578

Open Peer Review History:
This journal follows the Advanced Open Peer Review policy. Identity of the Reviewers, Editor(s) and additional Reviewers, peer review comments, different versions of the manuscript, comments of the editors, etc are available here: https://prh.mbimph.com/review-history/4252

Review Article

Received: 22/08/2024
Accepted: 24/10/2024
Published: 28/10/2024

ABSTRACT

Pheromones play a pivotal role in the reproductive and behavioural management of livestock, influencing various physiological and behavioural responses within and across species. This review explores the application of pheromones in cattle, buffalo, sheep, goats, pigs, and equines,

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Cite as: *Dharani, K., P. Abinaya, Violet Beaulah J, P. Sridevi, R. Gnanadevi, and T. A. Kannan. 2024. "Unlocking the Secrets of Pheromones: Reproductive and Social Communication in Domestic Mammals". UTTAR PRADESH JOURNAL OF ZOOLOGY 45 (20):210-19. https://doi.org/10.56557/upjoz/2024/v45i204578.*

highlighting their significant impact on reproductive efficiency, stress reduction, and animal welfare. In cattle, pheromones are essential for estrus detection and the enhancement of maternal bonding. Similarly, in buffaloes, urinary pheromones have been identified as markers for estrus detection, aiding in overcoming the challenge of silent ovulation, while also contributing to penis erection and sperm quantity enhancement. In small ruminants such as sheep and goats, the "male effect" accelerates puberty and synchronizes estrus, which is crucial for optimizing breeding cycles. In pigs, the presence of boars accelerates puberty in gilts and reduces postpartum anestrus in sows, enhancing reproductive outcomes. Equines benefit from appeasing pheromones, which alleviate stress in foals and adult horses, particularly during transportation and other stressful events. The synthesis and application of synthetic analogs of these pheromones have demonstrated practical benefits in animal husbandry, offering promising avenues for improving reproductive performance and animal welfare. However, despite these advancements, the identification and characterization of specific pheromones across different species remain incomplete. Future research should focus on the molecular identification of these pheromones, their mechanisms of action, and the development of innovative applications to further enhance their utility in animal management.

Keywords: Pheromones; mammals; communication; animal behaviour.

ABBREVIATIONS

CNS : Central Nervous System
MOE : Main Olfactory Epithelium
VNO : Vomeronasal Organ
OBP : Odorant-Binding Proteins
LH-RH : Luteinizing Hormone-Releasing Hormone
LH : Luteinizing Hormone
FSH : Follicle Stimulating Hormone
EAP : Equine Appeasing Pheromone
NA : Norepinephrine
Ach : Acetylcholine
GABA : γ-aminobutyric acid

1. INTRODUCTION

Communication is vital for the well-being of animals, with many species relying on chemical signals produced by internal glands. A pheromone is a chemical substance produced and released into the environment by one animal, influencing the behaviour of another animal, either within the same species or across different species. The term "pheromone" was introduced by Karlson and Luscher in 1959, derived from the Greek words *pherein* (to carry) and *hormōn* (to excite). The first identified pheromone, named Bombykal, was extracted from honey bees. Originally, pheromones were defined as substances secreted by one individual and detected by another of the same species, triggering specific behavioural or developmental responses. Although the concept initially applied to insect sex attractants, it has since expanded to encompass a wide range of chemicals released by animals, serving various functions.

Pheromones are typically species-specific and are often hormones secreted by modified ectodermal glands. These ectohormones, even when released in minute quantities, can have significant effects by acting as chemical messengers, playing a crucial role in intraspecific communication (Meghna 2024).

Animals of the same species communicate with one another to coordinate reproductive activities. These communications involve biologically active substances similar to hormones, such as airborne chemical compounds that are secreted externally through urine, feces, or modified subcutaneous glands. These substances trigger specific responses in receiving animals, leading to changes in behaviour or physiological alterations in the recipient's endocrine or reproductive system (Rekwot et al. 2000a, Rekwot et al. 2000b).

Exteroceptive cues, which are crucial in male and female interactions, include olfactory, visual, auditory, and tactile stimuli (Zalesky et al. 1984). These chemical molecules are released not only in animals but also in humans and insects, and they serve to elicit specific behavioural responses or hormonal changes in the opposite sex, the same sex, or both sexes of the same species (Mostafa et al. 2012).

Bio-stimulation refers to the stimuli induced by the presence of males, which can provoke estrus and ovulation through genital stimulation, pheromones, or other external cues (Chenoweth 1983).

2. DIFFERENCES BETWEEN HORMONES AND PHEROMONES

To start, hormones function within the same body, facilitating intracellular communication, whereas pheromones operate between individuals of the same species or between the species. Additionally, the molecular structures of hormones and pheromones are distinct. Hormones are subject to natural selection based on individual fitness, while pheromones must consider inclusive fitness and the honesty of signalling.

Pheromones are detected according to the labelled line principle, meaning their receptors are highly specific and less sensitive, so even a minor alteration in pheromone composition could disrupt or lose the signal. In contrast, general odours are processed through the fiber pattern principle, which allows for the detection of a wide range of smells.

In essence, pheromones are inherently social, evolving under selective pressures to become species-specific, thereby preventing cross-species communication, known as crosstalk. Hormones, however, do not undergo such changes due to evolutionary pressures. The interaction between the hormone transmitter and receiver is typically reliable, whereas pheromones may not always convey honest signals. For instance, a predator might mimic a pheromone signal to deceive prey (Anne van der Geest 2015).

3. CLASSIFICATION OF PHEROMONES

Pheromones can be categorized into various types, including aggregation, alarm, signal, epideictic, information, territorial, trail, and sex pheromones (Sobel and Brown 2001, Wyatt 2010).Despite their diversity, all pheromones share a common function: facilitating communication between animals of the same species, thereby triggering changes in behaviour and/or physiology. However, the secretion and detection of pheromones vary across species, life cycles, and environmental conditions, meaning that pheromones do not function uniformly across different animal species (Anne van der Geest 2015).

3.1 Releaser Pheromones

Releaser pheromones trigger immediate and reversible behavioural responses, directly mediated by the central nervous system (CNS). These pheromones are primarily involved in species recognition, sexual attraction, determining sexual status, inducing or inhibiting aggression, facilitating milk ejection, and serving as trail or alarm signals. These substances referred as signalling pheromones due to their role in eliciting immediate motor responses (Meghna 2024).

For instance, certain organisms release powerful attractant molecules that can draw mates from distances of two miles or more. Generally, releaser pheromones elicit rapid responses but are quickly degraded (Patel and Gohil 2014). In mammals, releaser pheromones are found in urine and footpads. The pheromones in footpads can provoke aggressive behaviour when they encounter unfamiliar males. In stallion, urine contains releaser pheromones that attract females or stimulate aggressive behaviour. Vaginal secretions in sheep also act as releaser pheromones (Meghna 2024).

3.2 Priming Pheromones

Priming pheromones induce prolonged or long-term endocrine or physiological responses in the receiver, mediated by neuroendocrine pathways or through direct effects on target organs. These pheromones can stimulate the production of oestrogen and progesterone, leading to estrus (either inducing or inhibiting), pregnancy termination, and the regulation of sexual maturation cycles (Meghna 2024). Unlike releaser pheromones, the priming pheromones have a slower onset but a longer duration of effect (Wani et al. 2013). They modulate physiological processes by either inhibiting or stimulating various endocrine, reproductive, and other bodily systems (Kekan et al. 2017). Bruce effect and Whitten effect are the results of priming pheromone (Meghna 2024).

In domestic animals, priming pheromones released by males act as bio stimulants to induce early puberty, terminate seasonal anestrus, and shorten postpartum anestrus. This can serve as an effective management tool in tropical regions, offering economic benefits (Kekan et al. 2017, Patra et al. 2012).

3.3 Imprinting Pheromones

Imprinting pheromones exert their influence during critical developmental periods, resulting in permanent changes in adult behaviour .Though, this pheromone is not released in domestic animals, secreted by rodents (Meghna).

3.4 Alarm Pheromones

Alarm pheromones are secreted to alert nest mates of potential threats. Upon detecting these pheromones, animals may respond by fleeing from the source of the scent, freezing and playing dead, or rushing toward the scent's origin to attack any nearby enemies. Most commonly observed in ants (Meghna 2024).

3.5 Recruit Pheromones

Recruit pheromones are used not only to gather food but also to recruit others for territorial defence and disputes. It is also most commonly noticed in ants (Meghna 2024).

3.6 Signal Pheromones

Signal pheromones trigger short-term changes, such as the release of neurotransmitters that activate a specific response. These pheromones prompt immediate behavioural reactions and follow a classical stimulus-response paradigm mediated by the CNS. For example, during parading, a teaser bull receives estrus-specific chemical signals from females, prompting the bull to exhibit flehmen behaviour. Observations of bulls interacting with cows provide reliable biological indicators of pheromone presence and forms the basis for laboratory analysis of the compounds involved in chemical communication (Patra et al. 2012). Signal pheromones also convey information about the sender, such as individual or group identity, which is crucial for parent-offspring recognition and mate selection (Kekan et al. 2017, Pageat and Gauliter 2003).

3.7 Aggregation Pheromones

Aggregation pheromones play a role in defence against predators, mate selection, and overcoming host resistance through mass attacks. An aggregation refers to a group of individuals gathered at one location, which can include either one sex or both sexes. Male-produced sex attractants are often called aggregation pheromones because they typically result in the convergence of both sexes at a calling site, thereby increasing the density of conspecifics around the pheromone source. Aggregation pheromones are among the most ecologically selective methods for pest suppression, as they are non-toxic and effective at very low concentrations (Landolt 1997).

3.8 Sex Pheromones

In animals, sex pheromones signal a female's availability for breeding. Males may also emit pheromones that convey information about their species and genotype. While most sex pheromones are produced by females, a small percentage are produced by males (Kekan et al. 2017).

4. REGULATION AND MECHANISM OF ACTION

In mammals, the nasal cavity is composed of two distinct regions: the main olfactory epithelium (MOE) and the vomeronasal organ (VNO). The MOE serves a general function, acting as a molecular analyzer for a wide range of odours and environmental chemicals without any specific predetermined meaning. In contrast, the VNO is specialized for detecting species-specific chemical signals, or pheromones, that convey critical information about gender, reproductive status, or dominance. The VNO contains neuron receptors that are activated by specific ligands or pheromones, which likely trigger a cascade of neuroendocrine responses independent of cognitive recognition (Patra et al. 2012).

Pheromones are released into the environment as small, hydrophobic airborne chemicals. Upon entering the VNO, these pheromones bind to odorant-binding proteins (OBP). Once bound, OBP delivers the pheromones to the dendritic microvilli of bipolar chemosensory neuron receptors within the VNO. These neurons possess the ability to encode the strength of the stimulus. When the stimulus reaches a certain threshold, it activates a subpopulation of neurons, leading to the generation of an action potential and the transmission of a strong electrochemical signal to the brain. This signal can directly stimulate the hypothalamus, eliciting a neuroendocrine response specific to the particular subpopulation of neurons activated in the VNO. The reproductive effects are primarily mediated by the release of luteinizing hormone-releasing hormone (LH-RH) in the hypothalamus (Kekan et al. 2017).

5. ROLE OF PHEROMONES IN SOCIAL COMMUNICATION

Pheromones are volatile chemical signals that plays a crucial role in social communication among animals. They are often used for marking trails or territories. Many mammals rely on pheromones present in the urine and feces to delineate their core area, home range, or territory. In addition to marking territory, animals use urine and feces to mark pathways, resting grounds, feeding areas, and sleeping sites. Pheromones are also employed to mark rivals, opponents, or defeated animals (Meghna 2024).

Certain pheromones are species-specific and perform unique functions depending on the species. For example, in buffalo and mares, pheromones are found in feces (Karthikeyan and Archunan 2013). In pigs and cows, pheromones are secreted by the submaxillary salivary glands (Sankar and Archunan 2004). In rams, pheromones are present in wool wax (Patra et al. 2012), while in cows, they are found in the perineal skin glands (sweat and sebaceous glands) and milk secretions (Bendall 2001). Cow's milk even contains volatile compounds that may function as pheromones, facilitating olfactory communication (Patra et al. 2012).

6. ROLE OF PHEROMONES IN SEXUAL COMMUNICATION

Pheromones play a significant role in sexual communication among mammals, including farm animals. Urine, in particular, serves as a fundamental source for chemical communication, containing sexually stimulating odours that are crucial in signalling reproductive status across various species (Karthikeyan and Archunan 2013, Patra et al. 2012). It is also a key source of estrus signals in domestic animals (Crowell-Davis and Houpt 1985).

6.1 Bovine

The role of priming pheromones in bovine reproduction is less clearly defined compared to other species. However, research supports the hypothesis that social interactions between bulls and prepubertal heifers can reduce the age of puberty onset. Heifers exposed to bull urine or vasectomized bulls attain puberty earlier than those not exposed (Izard and Vandenbergh 1982, Rekwot et al. 2000a).

6.1.1 Bull effect

The "bull effect" is hypothesized to increase the sensitivity of the hypothalamus to oestrogen, potentially overriding the inhibitory effects of low oestrogen concentrations. This effect may also involve an increase in the number of LH receptors in the ovary, promoting quicker resumption of estrous cycles post-partum (Custer et al. 1990, Patra et al. 2012).

6.1.2 Estrous pheromones and reproductive timing

Estrus pheromones in cows are influenced by hormonal changes. High progesterone levels inhibit the synthesis of these pheromones, while luteolysis increases their production. These pheromones, such as (Z)-7-dodecen-1-yl-acetate, are present in high concentrations in pre-ovulatory urine and elicit strong behavioural responses in males (Rasmussen et al. 1982, Rasmussen et al. 1996, Rasmussen et al. 1997). Continuous exposure to bull urine has been shown to reduce postpartum anestrus intervals, leading to a higher proportion of cows exhibiting estrus within 60-90 days post-calving (Custer et al 1990, Fernandez et al. 1996). The specific pheromone signals in bull urine remain unidentified (Kekan et al. 2017).

6.2 Buffalo

6.2.1 Estrus detection by female pheromones

Buffaloes often experience silent ovulation, where there are no visible signs of estrus, which complicates reproductive management (Dobson and Kamonpatana 1986). The identification of urinary sex pheromones in buffalo provides a promising solution to this issue (Rajanarayanan and Archunan 2011). Research on urinary volatiles in cows (Archunan and Rameshkumar 2012, Rameshkumar 2000) and horses (Buda et al. 2012) has demonstrated the potential of using these pheromones as markers for estrus detection. In buffaloes, estrus can be identified by evaluating the concentration of specific volatile compounds, such as those found in urine, feces, saliva, and vaginal mucus, with a minimum detectable concentration of 0.1 µg/g from vaginal secretions (Preti 1984). Unlike in cows and other ungulates, visual signs of estrus are not prominent in buffaloes, making it difficult to detect heat. However, buffaloes do exhibit reproductive behaviours and release chemo signals that can be utilized for estrus detection (Archunan 2009).

6.2.2 Enhancement of penis erection and sperm quantity

Research has shown that female urinary sex pheromones in buffaloes significantly enhance penis erection and increase sperm quantity. This discovery was notable enough to secure an Indian National Patent (Archunan and Rajanarayanan 2010).

6.2.3 Reduction in *Postpartum anestrus*

Prolonged postpartum an estrus in buffaloes can lead to significant economic losses for farmers. Studies have shown that continuous exposure of postpartum buffaloes to vasectomized bulls from 40 days onwards can reduce the interval to the resumption of ovarian cyclicity, with exposed buffaloes resuming cycles at 47.4 days compared to 56.0 days in non-exposed buffaloes (Gokuldas et al. 2010).

6.3 Sheep and Goat

6.3.1 Puberty acceleration

Priming pheromones from rams and bucks have been shown to accelerate the onset of puberty and estrus in sheep and goats, a phenomenon known as the "ram effect" or "male effect." Introducing sexually active males before the normal breeding season can induce estrus in seasonally anestrus ewes (Knight et al. 1978). In these species, the exposure of anestrus females to sexually active males stimulates luteinizing hormone (LH) secretion and synchronized ovulation. This effect is mediated by olfactory cues, likely involving the vomeronasal organ (VNO), which is connected to the hypothalamus and plays a crucial role in reproductive regulation (Wani et al. 2013).

Research indicates that urine, wool, and wax from rams are as effective as direct contact in inducing ovulation in ewes (Knight et al. 1980). Similarly, introducing a buck to does can synchronize estrus within 5-10 days (Shelton 1960). Pheromones secreted through the ewe’s wool, wax, and vaginal secretions attract rams, although the specific pheromonal compounds involved are yet to be fully identified (Kekan et al. 2017).

6.3.2 Effect in anestrus ewes

In domestic sheep, priming pheromones play a vital role in sociosexual stimulation, influencing reproductive processes and male-female interactions. The presentation of an anestrus female to a male can trigger a pulse of LH within minutes, leading to a sustained high rhythm of LH secretion and a preovulatory surge within 36 hours. This LH pulse likely stimulates ovarian estradiol secretion via positive feedback at the hypothalamic level, inducing the preovulatory surge (Signoret 1991).

6.3.3 Estrus induction and synchronization

Introducing a male to a group of anestrus females during the non-breeding season can activate LH secretion and synchronize ovulation. This is a widely used practice in the husbandry of sheep and goats, and the male pheromones responsible are reported to be produced in the fleece (Van den Hurk 2007).

6.3.4 Maternal responsiveness by neonatal pheromones

In sheep, maternal recognition of offspring is established within the first hour after birth, with olfactory cues playing a crucial role. The mother learns the olfactory signature of her lamb, facilitating acceptance and bonding (Nowak et al. 2011). The cortical and medial amygdala regions of the brain are involved in forming olfactory memory for the lamb (Keller et al. 2004, Meurisse et al. 2009). Oxytocin and vasopressin are released in the olfactory bulb, modulating neurotransmitters such as norepinephrine (NA), acetylcholine (ACh), and γ-aminobutyric acid (GABA), which are essential for olfactory memory (Lévy et al. 2004). However, the specific odours produced by lambs that facilitate maternal recognition are still under investigation (Kekan et al. 2017).

6.4 Pig

6.4.1 Puberty acceleration

In domestic pigs, the presence of a male has been shown to accelerate puberty in gilts. Gilts exposed to a boar in confinement reach puberty about 30 days earlier than unexposed gilts (Dyck 1988). The boar's scent is believed to be the primary olfactory cue that induces early puberty in gilts. Even exposure to a pen previously occupied by a boar can stimulate early puberty, demonstrating the potency of the pheromones left behind. This effect is attributed to olfactory cues, with exposure to a pen where boar pheromones remain after the boar’s removal being sufficient to induce early puberty (Signoret and Lindsay 1982). The presence of the boar helps overcome some adverse effects of confinement on puberty, resulting in earlier farrowing and increased lifetime productivity (Thomson and Savage 1978). Gilts that experience early puberty through boar contact tend to have higher ovulation rates and more estrous cycles, thus higher reproductive potential (Izard 1983). The presence of a boar during the insemination of a sow enhances sperm transport and ovulation (Wani et al. 2013).

The age of the boar also influences the effectiveness of puberty induction. Boars that are older and more mature tend to have a greater effect on inducing puberty due to their increased ability to produce pheromones. Gilts exposed to 2-year-old or 11-month-old boars attain puberty about 24 days earlier than those exposed to younger boars (Kirkwood et al. 1981). This difference is likely due to the younger boar’s lower production of priming pheromones or less effective pheromone production compared to older boars. The puberty-accelerating pheromone is secreted in saliva from the sub-mandibular salivary gland (Kirkwood et al. 1981) which is crucial for inducing early puberty in gilts (Pageat and Teyssier 1998).

6.4.2 Postpartum anestrus

Sows experience postpartum anestrus, which is thought to result from inhibited LH synthesis and reduced FSH release due to suckling stimuli. Successful induction of estrus in lactating sows has been achieved by grouping sows with their litters in the presence of a boar (Izard 1983). Boar stimuli are critical for the onset of estrus in sows post-weaning (Soede 1993). This practice is essential for efficient rebreeding and productivity in pig farming systems (Izard 1983).

6.4.3 Influence on standing posture

Boar pheromones, such as 5α-androstenone and 3α-androstenol, released in saliva, play a role in stimulating the immobilization reflex in sows (Wani et al. 2013).These pheromones are involved in attracting estrus females and facilitating receptive postures for mating (Signoret 1970). The presence of these odors is crucial for prolonged coitus. A synthetic aerosol boar mate pheromone is now used in artificial insemination practices to induce the immobilization reflex in estrus females (Booth 1984).

6.4.4 Appeasing pheromone

The pig appeasing pheromone (PAP) is important in mother-young interactions, reducing aggression and stress responses in young and adult pigs (Temple et al. 2016). It also stimulates feeding behaviour, resulting in significant weight gain. A synthetic analog of the porcine appeasing pheromone is available commercially and widely used in the pig industry (Pageat 2001).

6.5 Equine

6.5.1 Appeasing pheromone

Nursing mares produce an appeasing pheromone that helps their new foals feel safe and secure, especially in new or stressful environments. This pheromone plays a crucial role in reducing stress and promoting confidence in foals (Falewee 2006). Studies have confirmed the effectiveness of this pheromone in controlling stress, including during transportation (Cozzi et al. 2012).

Commercial products based on this natural pheromone are available for horses, such as Equine Appeasing Pheromone (EAP) marketed as Pherocalm® in Europe and Modipher EQR in the United States (Riley et al. 2002). These products are used to manage stress and anxiety in horses of all ages.

6.5.2 Estrus pheromone and reproductive behaviour

The urinary pheromone of mares during estrus has been reported to influence penile erection in stallions (Wierzbowski and Hafez 1961). This indicates the role of mare estrus pheromones in stimulating reproductive behaviour in stallions, highlighting the importance of chemical communication in equine reproduction.

7. PHEROMONE THERAPY

Pheromone therapy, the therapeutic use of pheromones, has been applied in dogs and cats (Levine and Mills 2008) and has the potential to be extended to other mammalian species, including cattle. This therapy is valuable for calming animals, reducing anxiety and phobias, and enhancing grooming behaviours in various clinical situations. Neonatal pheromones, in particular, have been shown to play a critical role in establishing the mother-young bond in sheep (Kekan et al. 2017).

8. CONCLUSION

In conclusion, pheromones play a pivotal role in the reproductive and social behaviours of various mammalian species. From enhancing reproductive efficiency and synchronizing estrus to easing stress and facilitating maternal bonding, these chemical signals are crucial for both individual well-being and broader management practices. In species ranging from cattle and buffalo to sheep, goats, pigs, and equines, pheromones such as those involved in puberty acceleration, estrus detection, and stress reduction highlight their diverse and significant impacts. The application of these findings, whether through natural pheromone sources or synthetic analogs, offers valuable tools for improving animal management, welfare, and productivity. Ultimately, understanding and harnessing the power of pheromones can lead to significant advancements in animal welfare and agricultural practices.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc) and text-to-image generators have been used during writing or editing of this manuscript.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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