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Dishin S Goyani

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Dhiren B Bhoi

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Alvin V Thoriya

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Anju D Bhagariya

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Sneh A Patel

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Ishwar B Chavan

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Corresponding Author:

Dishin S Goyani

Department of Veterinary
Gynaecology and Obstetrics,
College of Veterinary Science and
Animal Husbandry, Kamdhenu
University, Navsari, Gujarat, India

Insights of pheromones in domestic animal reproduction

**Dishin S Goyani, Dhiren B Bhoi, Alvin V Thoriya, Anju D Bhagariya,
Sneh A Patel and Ishwar B Chavan**

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Abstract

Pheromones are species-specific chemical-based messengers that play an important role in regulating behavioural, reproductive and social interactions among domestic animals. It provides advances in understanding applications and functions of pheromones in animal reproduction and management. This deliberate review paper summarizes the sources, classification, mechanism of perception, functions and also emerging applications of pheromones in domestic animal reproduction and reproductive biotechnologies. Pheromones are secreted through faeces, urine, vaginal secretions, saliva, milk in animals etc but varies in different species. They are primarily detected by the vomeronasal organ. Based on their biological activities, pheromones are classified as territorial, alarm, aggregation, calming and sex pheromones. Pheromones helps in estrus detection, male attraction, reproductive behaviour, maternal bonding, territorial marking and stress responses. Experimental studies showed that pheromones can trigger puberty, overcome postpartum anoestrus, improves estrus exhibition, enhance libido and semen quality also. It stimulates proper penile erection and improve reproductive efficiency. Maternal appeasing pheromones also showed stress reduction, reduced aggressive behaviour, improved feed intake, growth and welfare in animals. Recent technological advancements have showed use of pheromones in animal reproduction. Rapid and non-invasive methods for estrus detection using portable electronic nose systems and urine-based pheromone detection kits are now a days available particularly for cattle and buffaloes. In addition, several synthetic pheromones have also been commercialized to improve reproductive efficiency, reduce stress associated with transport, weaning, and handling and to facilitate artificial insemination.

Keywords: Domestic animals, pheromones, reproduction, vomeronasal organ

Introduction

Communication can be understood as the process of transmitting information from a sender to a receiver. Many species rely on chemical signals produced by bodily glands for such communication (Dharani *et al.*, 2024; Górski *et al.*, 2026) ^[13]. Communication in animal is the process by which one animal transmits information that influences the behaviour of another. (Bradbury and Vehrencamp, 1998) ^[7]. Mammals communicate with one another using many different signals such as facial expressions, body posture, sounds, touch, smells etc. (Górski *et al.*, 2026). Chemical communication is the most ancient way for exchange of information between organisms. These chemicals for animal communication are known as semiochemicals or infochemicals.

Pheromones are volatile chemical signals that are crucial in social communication among animals (Dharani *et al.*, 2024) ^[13]. The term 'Pheromone' was introduced by Karlson and Luscher in 1959. It derives from the Greek words 'pherein' (to carry) and 'hormon' (to excite). Pheromones are also referred as 'ecto-hormones' as they are chemical messengers emitted from the body of a sender and received by a receiver of the same species to which they release a specific reaction (Grammer *et al.*, 2005; Brennan and Zufall, 2006) ^[9, 20].

History

The study of pheromones and chemosensory communication has evolved through several important historical milestones. Some of them are listed here. The vomeronasal organ (VNO) was first described by Ludvig Jacobson in 1813, and is therefore commonly referred to as the Organ of Jacobson (Brennan, 2001) ^[8]. Meredith Halpern (1976) clarified function of VNO as it processes pheromonal signals. The term Flehmen was introduced by Karl Max Schneider in 1934. It originates from a German word meaning 'to show the upper teeth', describing a characteristic behaviour seen in many mammals during pheromone detection. In 1954, Peter G. Schinckel described the 'Ram effect'. Hilda Bruce (1959) discovered the Bruce effect in female mice. J. G. Vandenbergh (1975) described the Vandenbergh effect in prepubertal female mice. Wesley K. Whitten (1962) reported the Whitten effect in female mice. D. W. Patterson (1968) isolated the first mammalian sex pheromones in pigs. In 1979, M. Goodwin isolated hydroxybenzoate from vaginal secretions of estrus bitches and showed its role in stimulating mounting behaviour in male dogs. David Izard (1982) ^[24] identified acetic acid and propionic acid in feces and urine of estrus cattle, which trigger sexual excitations in bulls. In

2003, Pageat and Gaultier identified Bovine Appeasing Pheromone (BAP) and Dog Appeasing Pheromone (DAP) from mammary gland and sebaceous gland secretions, which are known to have calming effects and reduce anxiety in young animals. Rajnarayan and Archunan in 2011 ^[2] identified 4-methylphenol (strong male attractant) and 9-octadecenoic acid (induces mounting behaviour) as pheromonal compound in buffalo. Būda *et al.* (2012) identified *p*-cresol in the urine of estrus mares as a sex pheromone responsible for triggering the Flehmen response in stallions.

Source of pheromones

Pheromones are secreted in animals by various bodily fluids and excreta (urine, faeces, cervical and vaginal secretions) as well as exocrine gland secretions. Urine is a prime medium that is useful in mammalian chemical communication (Rivard and Klemm, 1989) ^[44]. Some pheromones are secreted by specialized glands or through particular body regions viz, flank, special scent glands, peri ocular region, perineal region, areas around the external genitalia, anal glands (Sankar and Archunan, 2004) ^[46].

Table 1: Sources of pheromone secretion in various animals

Species	Source	Reference
Cattle	Urine, milk, saliva, cervico-vaginal mucus, perineal skin glands (sweat and sebaceous)	Blazquez <i>et al.</i> (1988) ^[5]
Buffalo	Urine, feces	Karthikeyan and Archunan (2013) ^[26]
Sheep	Urine, sebaceous gland	Ichimaru <i>et al.</i> (2008) ^[22]
Goat	Urine, hair	Iwata <i>et al.</i> (2003) ^[23]
Pig	Submaxillary salivary gland, mammary skin secretion	Signoret <i>et al.</i> (1962) ^[49]
Horse	Urine	Būda <i>et al.</i> (2012)
Dog	Urine, mammary gland, anal gland	Goodwin <i>et al.</i> (1979) ^[18]
Cat	Sebaceous gland of cheek and perioral region	Pageat and Gaultier (2003) ^[15, 36]

Vomeronasal organ

The vomeronasal organ (VNO) is an important part of the accessory olfactory system which helps to detect pheromones and chemical signals involved in social and reproductive communications. Anatomically, it is located between the vomer bone and hard palate. It is a blind-ended tubular structure located bilaterally at the base of nasal septum which connects nasal cavity via narrow vomeronasal duct. In cross-section the VNO has a typical crescent shape with a thick pseudostratified sensory epithelium medially and a thinner and ciliated non-sensory epithelium laterally. Vomero nasal receptors are continually being replaced from basal stem cells because of its limited life span (Brennan, 2001) ^[8].

Production, transport, excretion and perception of pheromones

Pheromones are synthesized from various body tissues and secreted into bloodstream. In circulation, they bind with specific carrier proteins known as lipocalins. Function of lipocalins is to bind and transport small hydrophobic molecules such as pheromones, odorants and steroids. The binding of pheromones with lipocalins protects it from degradation in the bloodstream and facilitates their transport to different body fluids.

The perception of pheromones in animals begins at the mucosal epithelium of the VNO, where the odorant binding proteins (OBPs) are present. OBPs are a carrier protein which are present in both the main olfactory system and the vomeronasal organ. This dual presence enables the animals to detect a wide range of pheromonal signals that influence social and reproductive behaviours. OBPs possess multiple

binding sites where pheromones are bind. These OBPs delivers the pheromone molecules to the chemosensory neuron receptors. These neurons encode the type and strength of pheromone signal. The signal is transmitted as a strong electrochemical impulse to brain and stimulates hypothalamus and ultimately results in a neuroendocrine response (Pevsner *et al.*, 1985) ^[37].

Active pump mechanism is an alternative method used by domestic animals to detect pheromones. This mechanism is mainly associated with a behavioural response called Flehmen reaction. During this reaction, animal stands rigidly with extended neck and curling of upper lip to expose teeth. This specific movement alters the pressure in the nasal cavity, and helps vomeronasal organ to detect pheromones.

Classification of pheromones

1) Territorial Pheromones:

Mammals rely on pheromones to define their home range or territory. In addition to marking territory, animals use urine and faeces to mark pathways, resting grounds, feeding areas and sleeping sites. Dogs clearly scent mark and overmark urinary signals, which may relay information like age, sex, general health and when the animal was present at that place (McGlone and Hendersen, 2022; Dharani *et al.*, 2024) ^[13, 29].

2) Alarm Pheromones

In response to attack by natural enemies, aphids secrete droplets of fluid from cornicles, (located on the upper, posterior surface of the abdomen). These secretions contain an alarm pheromone that induces behavioural responses in other receiving insects. β -farnesene and germacrene A are

primary component of this pheromone in aphids (Vandermoten *et al.*, 2012) ^[51].

3) Aggregation Pheromones

Aggregation pheromone is defined as a pheromone which helps to form an aggregation that serves for protection, reproduction or feeding. Through attraction; aggregation pheromones help to form a group of individuals in a particular location. Aggregation pheromones are beneficial because they help to find a food source, protection or reproduction (Wertheim *et al.*, 2005; Dharani *et al.*, 2024) ^[13, 53].

4) Calming Pheromones

Calming pheromones play a significant role in reducing stress and promoting comfort among animals. Pig Appeasing Pheromone (PAP) is secreted by sow and it helps in calming and comforting the young piglets by reducing anxiety and distress during weaning or transport. Fecal semiochemical also contain Myristic acid as calming compound. When weaned piglets are exposed to sow feces containing myristic acid, they display a noticeable calming effect and reduced aggressive behaviour. Additionally, this compound has been associated with an increased feed intake, which ultimately contributes to improved growth rates among piglets. Thus, both Pig Appeasing Pheromone and Myristic acid play a crucial role in maintaining the well-being of piglets by promoting calmness (Borpujari *et al.*, 2020) ^[6]. Likewise, Bovine Appeasing Pheromone (BAP) (Pageat, 2001) ^[35] and Equine Appeasing Pheromone (EAP) (Riley *et al.*, 2002) ^[43] also act as calming agent and growth promoter to young one.

5) Sex Pheromones

Sex pheromones are volatile chemical compound which signal that a female animal is physically ready to mate. These signals are usually produced by females; however, males can also release some pheromones that give information about their species and genetic makeup. When a female is in estrus, she releases pheromones into the environment that act on male animals, causing an immediate change in the behaviour of than male animal (Dzięcioł *et al.*, 2012; Kekan *et al.*, 2017) ^[27].

5.1) Releaser Pheromones

Releaser pheromones are those chemical signals that cause a short-term alteration in the behaviour of the recipient (within seconds or minutes) and act as attractants (Gokuldas *et al.*, 2023) ^[16]. Ex. Boar sex pheromone. This Boar sex pheromones contain androstenone & androstanol which are secreted through saliva. Which induces immobilization reflex in estrus sow (Sankarganesh *et al.*, 2022) ^[48].

5.2) Priming Pheromones

Priming pheromones are substances that cause physiological events and comparatively long-term effects either through inhibition or stimulation of hormone. In domestic mammals, priming pheromones from the male have potential influence on induction of puberty, shortening of seasonal anoestrus and resumption of ovarian activity and estrus (Gokuldas *et al.*, 2023) ^[16].

Roles of pheromones in different domestic animals

Chemical communication is very important in mammalian reproduction. The sense of smell plays a major role in sexual and mating behaviours in mammals. It helps animals to find

animal of the opposite sex. In addition, scents help animals choose the most suitable partner (Coombes *et al.*, 2018) ^[12].

Cattle

Acetic acid, propionic acid and 1-iodo-undecane are chemical compounds found in milk, urine and feces. These substances act as indicators of estrus and also help in attracting males during the reproductive period. Similarly, trimethylamine, 4-propyl phenol and pentanoic acid are present in saliva. These compounds mainly play a role in attracting males and influencing mating behaviour (Sankar *et al.*, 2007; Archunan and Rameshkumar, 2012) ^[39, 47].

Buffalo

4-methylphenol, 9-octadecenoic acid, 1-chlorooctane and *p*-cresol are chemical compounds present in urine of estrus buffalo. 9-octadecenoic acid is also found in vaginal secretions. These compounds play an important role in attracting males and stimulating mounting behaviour in buffalo bull (Rajanarayanan and Archunan, 2011; Karthikeyan and Archunan, 2013) ^[2, 26, 38].

Goat

The pheromonal compounds of bucks are octanoic acid and 2,6-di-tert-butyl-4-methyl phenol. These compounds are mainly secreted from the fleece of the buck which influence the reproductive cycle of does by stimulating release of LH from anterior pituitary, which plays an important role in inducing ovulation (Iwata *et al.*, 2003) ^[23].

Sheep

In rams, certain compounds such as Fatty Acid I, Fatty Acid II and long-chain alcohols like hexadecane-1,2-diol and octadecane-1,2-diol have been identified as pheromonal substances. These compounds are secreted from the fleece of the ram. They play an important role in stimulating the release of LH in ewes, which is a key hormone requires for ovulation (Over *et al.*, 1990) ^[34].

Pig

In boars, the salivary glands produce saliva that contains steroid pheromones such as 5 α -androstenone, 3 α -androstanol and 3 β -androstanol. These compounds are mainly produced in the testes, transported through bloodstream and stored in adipose tissues. They are known for standing reflex in sow. In addition, non-steroid pheromones known as pig appeasing pheromones (PAP) have been identified in the mammary skin secretions of lactating sows, which modifies the behaviour of weaned piglets by promoting calmness and reducing stress or aggressive behaviours (Sankarganesh *et al.*, 2022) ^[48].

Horse

In horses, the main compounds identified are *p*-cresol and *m*-cresol, which are present in urine of estrus mare. These compounds act as indicators of ovulation in mare and helping stallion to detect right time for mating. This improves the timing and efficiency of reproduction in horse. In addition, *p*-cresol has been shown to enhance penile erection in stallion, indicating its role in stimulating sexual arousal and readiness for mating (Büda *et al.*, 2012; Mozūraitis *et al.*, 2012).

Dog

In female dogs, methyl-*p*-hydroxybenzoate has been identified as a sex pheromone that is released in urine during estrus. This compound helps to communicate and identity

reproductive status to male dogs (Goodwin *et al.*, 1997; McGlone and Hendersen, 2022) ^[18, 29]. Another important pheromone is the Dog Appeasing Pheromone (DAP), which is secreted from the mammary glands of lactating females. DAP plays a key role in promoting calmness, strengthening social bonding and reducing anxiety in puppies as well as adult dogs (Şafak and Sulu, 2026).

Cat

Pheromones in cats are very important for communication and marking their territory. Chemicals involved are oleic acid, pimelic acid and palmitic acid. These are produced by sebaceous glands located on the cat's cheeks. When cat rubs its face on objects, these chemicals are deposited and helping the cat to recognize familiar places and feel comfortable (Goodwin *et al.*, 1979) ^[18]. Another group of chemicals, such as 5 β -cholestan acid is also released from the cheek glands. These are mainly involved in marking territory and creating a sense of calmness for the cat (Pageat and Gaultier, 2003) ^[15, 36].

Effects of pheromones

1) Puberty acceleration: Puberty acceleration plays a crucial role in reproductive management of livestock. Early onset of puberty improves breeding efficiency and overall productivity. Research has shown that a male primer pheromone, 1-iodo-undecane can accelerate puberty in females of various species. This suggests that pheromones play a significant role in regulating reproductive maturity (Rekwot *et al.*, 2001) ^[41].

Species	Material Method	Onset of Puberty	Reference
Cattle	Heifers exposed to vasectomized bull	3 months earlier	Rekwot <i>et al.</i> , 2000 ^[42]
Goat	Pre-pubertal goat exposed to sexually mature buck	2 weeks earlier	Augusto <i>et al.</i> , 2020 ^[3]

2) Reduction in postpartum anoestrus: Reduction in postpartum anoestrus is an important factor for improving reproductive efficiency in livestock. In ewes, introducing rams during the postpartum period reduces the interval between parturition and conception, particularly during the autumn and spring seasons (Gokuldas *et al.*, 2010) ^[17].

Species	Exposure	First post-partum estrus	Reference
Cattle	Not exposed	62 days	Berardinelli <i>et al.</i> , 2005 ^[4]
	Teaser bull	43 days	
	Excretory product of bulls	45 days	
Buffalo	Not exposed	61 days	Gokuldas <i>et al.</i> , 2010 ^[17]
	Vasectomized bull	55 days	
Cattle	Normal saline	92 days	Kamal, 2023 ^[25]
	Bull urine	60 days	
	Synthetic pheromone compound	85 days	

3) Influencing the standing posture by male pheromones in sow: The steroid chemo signals identified in boar saliva have been demonstrated to evoke the immobilization reflex to sows in heat and characterize their readiness to mate (Brooks and Cole, 1970) ^[10].

4) Estrus detection by female pheromones: Effective estrus detection would greatly help cattle reproduction for artificial insemination. Silent heat is common issue in buffalo.

Successful recognition of estrus prior to the actual time of ovulation may improve conception rate in cattle and buffaloes (Rao *et al.*, 2013) ^[40]. Hence, successful identification of urinary sex pheromones in the farm animals provides a tool to overcome this problem (Rameshkumar *et al.*, 2002) ^[39].

Species	Sample	Measured chemical compound	Result	Reference
Cattle	Faeces	Acetic acid	Estrus - 36 $\pm$ 8 ng	Mozuraitis <i>et al.</i> , 2017 ^[32]
			Diestrus - 19 $\pm$ 5 ng	
		Propionic acid	Estrus - 10 $\pm$ 3 ng	
			Diestrus - 2.3 $\pm$ 1 ng	
Buffalo	Urine	<i>p</i> -cresol	Estrus - No colour	Muthukumar <i>et al.</i> , 2018 ^[33]
			Pro/Diestrus - Pink colour	

6) Penis erection and sperm motility: Female urinary sex pheromones have been shown to enhance penile erection and improve semen quality in buffalo. Similarly, urinary pheromones from estrus mare are reported to stimulate penile erection in stallion. These findings suggest that female sex pheromones can be utilized in assisted reproductive technologies under specific conditions in certain species (Kekan *et al.*, 2017) ^[17].

Rabbit exposed to female rabbit urine and vaginal swab			
Criteria	Control	Female Urine	Vaginal swab
Sperm conc. (Million/ml)	797.50 ^b $\pm$ 466.55	1173.47 ^a $\pm$ 400.32	1112.22 ^a $\pm$ 332.45
Motility (%)	22.65 ^b $\pm$ 23.69	70.15 ^a $\pm$ 23.50	51.80 ^a $\pm$ 32.14
(<i>p</i> < 0.05)	(Villamayor <i>et al.</i> , 2024) ^[52]		

Exposure to acetic acid and 1-iodoundecane in Zebu bull with reduced libido			
Criteria	Control	1-iodoundecane	Acetic acid
Semen volume (ml)	3.72 $\pm$ 0.19	4.03 $\pm$ 0.24	4.17 $\pm$ 0.24
Sperm conc. (Million/ml)	1027.00 $\pm$ 34.80	1080.00 $\pm$ 42.85	1106.00 $\pm$ 42.88
Reaction time (s)	59.40 ^a $\pm$ 9.09	42.57 ^a $\pm$ 4.31	33.27 ^b $\pm$ 2.96
(<i>p</i> < 0.05)	(Mondal <i>et al.</i> , 2019) ^[30]		

Exposure to cervical mucus of estrus female and normal saline spray in Sahiwal bull with reduced libido		
Criteria	Cervical Mucus Spray	Normal Saline Spray
Semen volume (ml)	3.78 $\pm$ 0.33	3.22 $\pm$ 0.33
Sperm conc. (Million/ml)	1149.67 $\pm$ 65.50	1125.79 $\pm$ 43.86
Initial motility (%)	72.33 $\pm$ 2.56	72.88 $\pm$ 3.29
Sperm abnormality (%)	5.27 $\pm$ 0.40	7.97 $\pm$ 0.38
	(Singh <i>et al.</i> , 2016) ^[50]	

6) Reducing fighting behaviour and growth promoting maternal pheromones: Maternal appeasing pheromones, which reduce aggressive behaviour in young ones and promotes growth. Their use as pheromone therapy is well documented and has been applied to simplify the management of anxiety and phobia related conditions in various animal species (Griffith *et al.*, 2000; McGlone and Anderson, 2002; Gaultier *et al.*, 2005) ^[15, 21, 28].

Advances in pheromone based estrus detection

Reproductive performance is one of the most important factors that determines the economic success of a farm. Reproduction related problems are a major reason to cull animals. To enhance fertility of farm, detecting estrus at the

right time and accurately is very important (Ali *et al.*, 2022) ^[1]. To overcome silent heat and for assisted reproductive techniques, a need for simple, non-invasive and reliable methods for heat detection.

Portable E-Nose device can detect estrus by sensing changes in volatile compound from perineal region of cattle and buffalo. It was developed by GmbH, Germany. A prototype called MENT-EGAS (Milking Machine and Electronic Nose Technology-Egypt, Asmaa Shaaban prototype) was used to detect odour changes from the perineal region of cows.



Fig 1: Portable Electronic Nose (PEN) device

It detects pheromones released by cows during estrus. This system includes three main parts: (1) a unit to collect samples, (2) a unit to detect, analyse and identify odour (3) a unit to interpret and display results. It contains 10 metal oxide chemical sensors that respond to different gases. These sensors create a pattern based on the smell of the sample. This device can give a general idea about the vapor composition based on its trained database. This technology helps to determine the best time for artificial insemination, which improves fertility and ultimately economy of farm. In contrary, feces also produce other volatile organic compounds that are not estrus-related, which may interfere with the response of PEN's during the measurements. However, MENT-EGAS was able to differentiate estrus from non-estrus phases, even with the presence of possible error sources such as fecal contamination. (Wiegerinck *et al.*, 2011; Ali *et al.*, 2022) ^[1, 54].

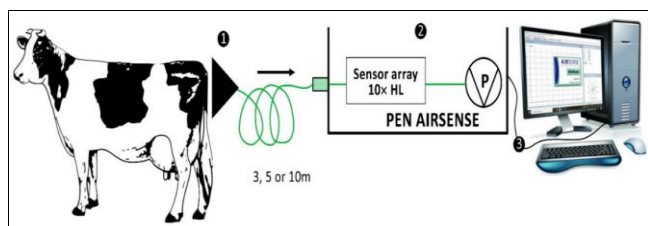


Fig 4: Schematic diagram of the Electronic Nose Technology-Egypt, Asmaa Shaaban prototype system

Muthukumar *et al.* (2018) ^[33] developed a simple urine-based kit to detect estrus in buffaloes. This kit works by identifying a specific chemical called *p*-cresol (estrus specific compound)

in urine. In this method, a drop of the reagent is added to a urine sample collected from the animal. If no colour develops, it indicates a positive result, meaning the animal is in estrus. In contrast, a pale pink colour shows the proestrus stage, while a dark pink colour indicates the diestrus. This method is simple, quick and useful for identifying the correct time for breeding.

Synthetic maternal pheromones:

A synthetic mixture of androstenone, androstanol and quinoline mimics function of boar saliva, which can stimulate estrus behaviour in sows ex. Boar Mate[®], Hog Mate[®] etc. This mixture also helps to reduce the time between weaning and the onset of estrus (Sankarganesh *et al.*, 2022) ^[48]. In addition, a synthetic product known as porcine appeasing pheromone (PAP) is commercially available and widely used in the pig industry, such as FerAppease[®] (Brooks and Cole, 1970; Pageat, 2001) ^[10, 35].

Reducing stress in foals is important for improving growth, welfare and training. To address this, researchers developed the Equine Appeasing Pheromone (EAP), with brand name ConfidenceEQ[®]. Synthetic pheromone products based on natural compounds are commercially available for horses, as ModipherEQ[®] in the United States and StressLess[®] in European country. EAP works by imitating the natural calming signals released by a mare. It helps to reduce fear and anxiety in horses, especially during stressful situations like transportation, veterinary procedures or training sessions (Riley *et al.*, 2002) ^[43].

Conclusions

Pheromones are powerful natural chemical signals that play a crucial role in regulating reproduction, behaviour and social bonding in domestic animals. They help in estrus detection and to optimize the best timing of artificial insemination to improve fertility. Pheromones can also help to accelerate puberty, early resumption of ovarian cyclicity, overcome postpartum anestrus and improve semen quality. In addition, maternal appeasing pheromones reduce stress and promote growth in young animals, which ultimately leads to improved reproductive efficiency and productivity. In nut shell, pheromone therapy is a safe, natural and effective approach to enhance production, reproduction and welfare in animals, making it an important tool in modern livestock management system.

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