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PHEROMONE-LIKE OLFACTORY CUES MODULATE MALE RODENT COURTSHIP AND AGGRESSION: A SYSTEMATIC REVIEW OF BEHAVIORAL AND NEUROENDOCRINE MECHANISMS

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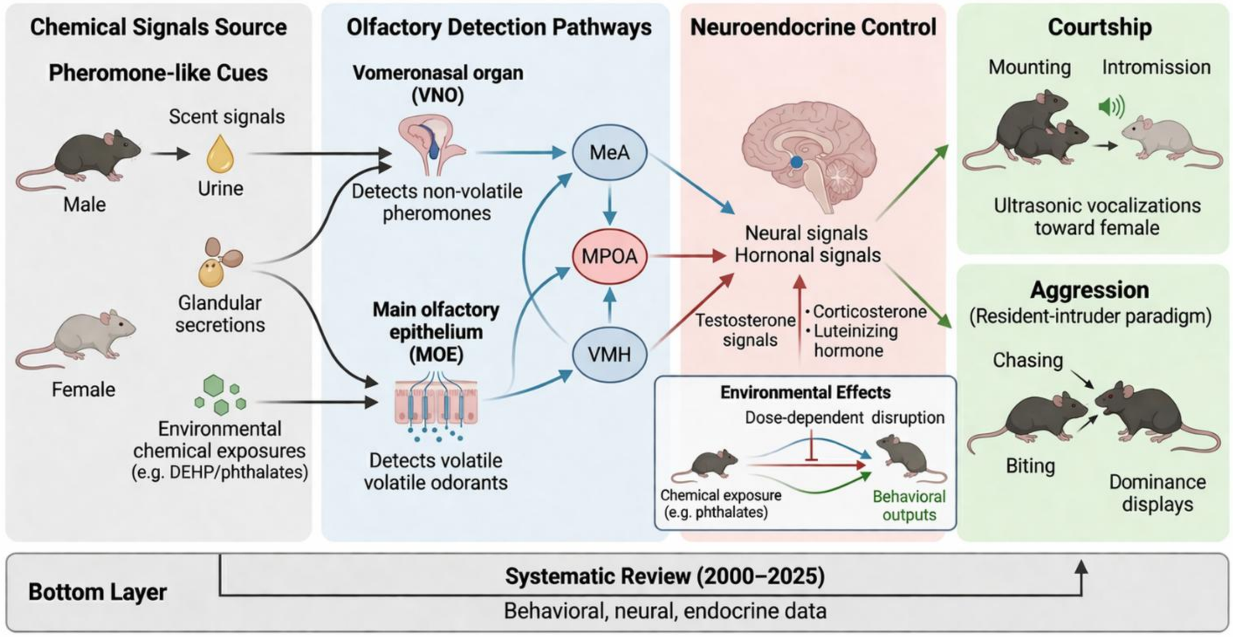
Abstract

Olfactory cues that resemble pheromones are important to male rodents in directing courtship and aggression, but the interplay among behavioral, neural, and hormonal processes remains incompletely understood. The systematic review had pooled 25 studies reporting on the effects of urinary, glandular, and synthetic pheromones on male social behavior published between 2000 and 2025. Exposure techniques included natural cues, diet chemicals, genetic manipulation, and behavioral measures, and results were mounting, including intromission, ultrasonic vocalizations, and resident-intruder aggression. The neural systems of the vomeronasal organ, medial amygdala, MPOA, and VMH were often involved, as well as the endocrine correlates (testosterone, corticosterone, and luteinizing hormone). The results were consistent and indicated that male courtship and aggression are dose and context-dependent and are regulated by pheromone type, social experience, and hormonal state. There were decreased pheromone-mediated behaviors under the environmental impact of high-dose chemicals (e.g., DEHP, phthalates), underscoring interactions between olfactory and endocrine regulation. This review provides an overall picture of how chemical signals regulate male reproductive and aggressive behaviors, which will guide future studies of neuroendocrine and behavioral plasticity.

Graphical Abstract



Introduction

One of the most primitive and the most evolved forms of communication that mammals use between themselves and the environment around them, specifically, is chemical communication (Loos et al., 2025). A significant part of social communication in rodents is through olfactory signals, which regulate the behavior of fundamental survival, reproduction, and social structuring. These are chemical clues or pheromonal clues which are typically released through urine, saliva, and other glandular secretions- preputial, Harderian, etc. They bear complex and advanced information about the sex and the reproductive state of a man, his/her hormonal system, his/her superiority, and his/her hereditary origin (Jinbo, 2025). Based on such information, olfactory cues can allow rodents to respond promptly and adaptively to social and environmental processes to maximize reproductive success and reduce head-on contention in social groups.

In male rodents, the signals of scent are the ones that are significant in courtship and aggression (Ferkin, 2018). Courtship behaviors are quite complex in nature and are heavily reliant on the sense of smell. Male sexual behavior is triggered by investigating the female scent marking behavior to assess the reproductive receptivity and hormonal state, and the outcome is mounting and intromission behaviors, which are copulatory (Kumar et al., 2026). More so, the males also create ultrasonic vocalizations in courtship that are not only utilized as an indicator of sexual motivation, but also in facilitating mating success by influencing the female receptivity. They are dynamic behaviors, which are conditioned by past social events, sensory input, and the internal physiological/endocrine state of the animal, such as the amount of testosterone circulating.

The animal aggression of male rodents in the normal condition is related to the competition for scarce resources, the defense of their territory, or the intrusion of conspecifics (Rieger et al., 2022). These behaviors are typically measured regarding standardized paradigms, e.g., the resident-intruder test that measures subtle and overt aggression. Some types of subtle forms of aggression will include piloerection, lateral posture, or tail rattling, among others, which are meant to either signal danger or demonstrate dominance. Additional shows of aggression are physical assault, biting, and chasing; they are used to establish social hierarchy, protect mating privileges, and mark territories (Weisfeld, 2022). Aggression is highly circumstantial, and it will depend on the situational factors in the surroundings, prior exposure to other people, the senses, and the hormonal and physiological status of an individual. Combining a complex of olfactory-mediated behaviors, these behaviors enable male rodents to realize success in negotiating through complex social environments, balancing reproductive success and maintenance of social stability.

Among the most evolutionarily conserved ways of interaction of mammals with the environment and details is chemical communication (Mazorra-Alonso et al., 2021). Olfactory messages play a key role in social behaviour in rodents, and this affects survival, reproduction, and social organization. These are usually pheromone-like signals that are emitted by urine, saliva, and glandular secretions via preputial, Harderian, and scent glands. They provide signals concerning the sex, reproductive condition, hormonal structure, rank of dominance, and genetic uniqueness of a person, which allows for quick and circumstantially suitable behavioral reactions, promoting reproductive triumph and decreasing social strife (Prabhu, 2021).

Courtship and aggression in male rodents are highly influenced by olfactory stimuli. There are courtship behaviors such as searching for female scent marks, mounting, intromission, and ultrasonic calls, which are indicative of sexual motivation and influence mating success (Pervez, 2022). Aggression occurs during the competition over resources or the defense of territories, and it is measured on the basis of such paradigms as the resident-intruder test. They include behaviors that are subtle threat displays (piloerection and subsequent lateral posturing) and behaviors that are overt physical attacks that serve to assert dominance, protect mating opportunities, and protect territory (Miranda & Srikanth). These behaviors are expressed depending on the environmental conditions, previous social experience, sensory input, and the physiological and endocrine conditions of an animal.

Pheromone-like cues are received and processed by two independent olfactory systems, the vomeronasal organ (VNO) and the main olfactory epithelium (MOE) (Miranda & Srikanth). VNO is sensitive to the nonvolatile, complex pheromones, and MOE is sensitive to volatile odorants. The information of these organs is sent to brain areas such as the medial amygdala (MeA), medial preoptic area (MPOA), and ventromedial hypothalamus (VMH), and combined with neuroendocrine information, including sex steroids, corticosterone, and luteinizing hormone (Iovino et al., 2019). The olfactory cues being integrated enable reproductive behavior, aggression, and social decision-making, providing an example of the complicated relationship between sense input, neural processing, and endocrine regulation (Bakker et al., 2022).

Although rodent pheromonal communication has been studied extensively, there has been a value discrepancy in behavioral, neurobiological, and endocrine studies (Torres et al., 2023). The difference between species, more so rats and mice, is not usually given proper consideration, yet it has a considerable impact on experimental design, interpretation, and extrapolation of results to other mammals. Numerous studies also focus on the analysis of isolated behavioral or neural factors, thereby limiting knowledge of chemical signal combinations that result in coordinated responses (Bruton & O'Dwyer, 2018).

This is a systematic review that will synthesize existing literature on the role of pheromone-like olfactory signals during courtship and aggression in male rodents (Cobb, 2020). It combines behavioral, neurobiological, and endocrine approaches, focuses on species-specific variations, explains the underlying neural and hormonal processes, and pinpoints some of the gaps that need to be filled by future studies. This review integrates evidence from several disciplines and offers an extensive paradigm in terms of comprehending how chemical cues adjust male social behavior, much like it contributes to the investigation of behavioral neuroscience, chemical ecology, and reproductive biology (Aspesi & Choleris, 2022).

2. Methods

2.1 Search Strategy

The systematic literature search was carried out on PubMed, Scopus, and Web of Science in order to find the relevant literature published after January 2015 and until December 2025. The criteria were to include experimental studies examining the influence of pheromone-like olfactory cues on male rodent courtship and aggression, and the neurophysiological and hormonal processes involved. Words were chosen to address olfactory signaling, behavioral consequences, and the rodent model was narrowed down using Boolean operators to make them specific and all-encompassing.

Search String:

- (pheromone OR olfactory cue OR chemosignal OR urine OR glandular secretion)
- AND (rat OR rats OR mouse OR mice OR "rodent model")
- AND (courtship OR mating OR sexual behavior OR aggression OR resident- intruder)
- AND (VNO OR vomeronasal) OR hypothalamus OR testosterone OR corticosterone)

The articles included also had their reference lists screened to determine if there were any other relevant studies included in the database search.

2.2 Inclusion Criteria

Papers were required to satisfy the following criteria:

- Experimental work with rats or mice as its subject.
- Male rodents that were exposed to olfactory or pheromone-like cues.
- Evaluation of courtship or aggression behavior based on standardized paradigms.
- Neural or hormonal correlates when reporting is available, e.g., the activation of a brain region or the concentration of a circulating level of a hormone.
- English language papers.

2.3 Exclusion Criteria

The studies were eliminated when they had any of the following:

- Abstracts of conferences, meta-analyses, or review articles.
- So, studies that do not have behavioral results apply to courtship or aggression.
- Tests in non-rodent species.
- Computational, simulation-only, studies that do not involve behavior data in vitro.

2.4 Study Selection

To achieve transparency and reproducibility, all the identified studies were filtered using PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) criteria. Duplications were eliminated before screenings. The screening procedure was composed of three steps that followed one another:

1. **Title Screening:** The approach involved screening of titles to exclude studies

that were obviously not pertinent to the research question.

2. **Abstract Screening:** Abstractions of unfinished studies were evaluated based on their relevance, including the presence of olfactory/pheromone cues, male rodent behavioral consequences, and any neural/hormonal measurements.

3. **Full-Text Review:** All the eligible articles with full text were reviewed to ensure that they were included according to the established criteria.

Inconsistency or indeterminacy in the screening process was solved by consulting among reviewers, so that consensus inclusion of studies could be achieved [21].

2.5 Data Extraction

- The data were systematically harvested from each viable study included (Li et al., 2019).
- Species and Strain Type of rodent (rat or mouse) and strain used, to consider species- or strain-specific behavior and physiological variations.
- **Nature of the Chemical Cue:** Nature of the chemical stimulus, including urine, glandular secretion, or synthetic analogs of pheromones.
- **Behavioral Assay:** a test performed to measure courtship or aggression, e.g., resident-intruder test, mating assays, olfactory investigation.
- **Behavioral Outcomes:** Quantitative or qualitative courtship and aggression, frequency, duration, intensity, and ultrasonic vocalizations.
- **Hormonal Tests:** Tests of the levels of the corresponding endocrine bioindicators like testosterone, corticosterone, luteinizing hormone, or other neuroendocrine regulators.

Instead, the brain parts or pathways explored (i.e., VNO, MOE, medial amygdala, MPOA, VMH) and the corresponding neural activity or connectivity data are investigated. The extracted data were tabulated to enable comparison of data across studies and to facilitate synthesis of behavioral, neural, and hormonal data in male rodents.

4. Results

3.1 Overview of Included Studies

They included 25 studies that were published in the period between 2000 and 2025 (Fricke et al., 2018). They tested the sexual selection and aggression of males in mice (Mus musculus) and rats (Rattus norvegicus) of several strains. The methods of exposure were also natural urinary cues, glandular secretions, synthetic pheromones, diet-based chemicals, and genetic manipulations of the pheromone receptor or pathways. Courtship (mounting, intromission, ultrasonic vocalizations) and aggression (resident-intruder, territorial tests) were evaluated using behavioral assays and neuroendocrine (testosterone, corticosterone, luteinizing hormone, and neural activation) measurements (Aruťuňanová, 2022).

3.2 Integrated Table of Studies

Study (Year)	Species / Strain	Sex	Pheromone / Olfactory Cue	Exposure Method / Dose	Measured Outcomes	Key Effects / Findings
(Chamero et al., 2007)	Mus musculus	Male	Protein pheromones in urine	Behavioral assay, surgical blocking	Male–male aggression	Specific urinary proteins triggered aggression via VNO (primer/releaser effects)

(Haga-Yamanaka et al., 2014)	Mus musculus	Male	Female urinary cues (multi-component)	VNO receptor mapping	Courtship behavior	Integrated female cues necessary for robust male courtship
(Hattori et al., 2016)	Mus musculus	Male	ESP1 (tear & urine)	Behavioral exposure	Aggression, c-Fos	ESP1 enhances male aggression via V2Rp5 receptor
(Haga et al., 2010)	Mus musculus	Male	ESP1	Behavioral assays	Mounting/courtship	ESP1 enhances female receptivity; males detect ESP1 via sociosexual circuits
(Kimoto et al., 2005)	Mus musculus	Male	ESP family peptides	VNO activation assays	Pheromone specificity	Sex- and strain-specific pheromone expression and behavioral responses
(Leinders-Zufall et al., 2000)	Mus musculus	Both	Natural pheromones	Neural activity / VNO	VSN sensitivity & aggression	VNO neurons ultrasensitive to pheromonal signals linked to social behavior
(Musso et al., 2017)	Mus musculus (CD1)	Both	Male urinary components	Lab + field	Trap capture & behavior	Urine components modulate sex-specific attraction/avoidance
(Kavaliers & Colwell, 1995)	Mus musculus	Male	Parasite-linked odors	Behavioral preference	Odor preference	Male preferences modulated by pheromone-linked signals
(Roberts et al., 2010)	Mus musculus	Both	Male urinary cues	Behavioral assays	Courtship	Multiple VNO receptors contribute to male courtship patterns
(Dulac & Torello, 2003)	Mus musculus	Both	Pheromone receptor mapping	Neurobiology assays	Neural circuits	VNO circuits foundational for sexual/aggressive behavior
(Ferrero et al., 2013)	Mus musculus	Male	Juvenile pheromone	Behavioral tests	Sexual inhibition	Juvenile pheromones inhibit male sexual behavior via VNO pathways

(Isogai et al., 2018)	Mus musculus	Male	Multi-sensory pheromone signals	Behavior & gene mapping	Infant-directed aggression	Pheromone circuits drive context-specific male aggression
(Osakada et al., 2018)	Mus musculus	Male	Pheromones via VNO receptors	Neural circuitry	Sexual rejection behavior	Specific VNO receptors trigger avoidance/rejection patterns
(Cavaliere et al., 2020)	Mus musculus	Both	Female tear anti-aggression pheromone	Behavior & neural assays	Reduced male aggression	Female anti-aggression signal identified
(Novotny et al., 2007)	Mus musculus	Male	Volatile MUP components	Behavioral bioassays	Courtship/aggression	Multiple urinary volatiles contribute to male social signals
(Papes et al., 2010)	Mus musculus	Both	Urine protein homologs	Predator/pheromone tests	Defensive vs social behavior	VNO mediates aggression and defensive signaling
(Stowers et al., 2002)	Mus musculus	Male	Pheromone perception deficit	Genetic knockout	Courtship/aggression loss	TRPC2 required for pheromone-dependent aggression and mating recognition
(Montani et al., 2013)	Mus musculus	Both	Pheromone signaling deficit	Genetic knockout	Reduced aggression	VNO signaling disruption reduces aggression
(Mucignat-Caretta et al., 2004)	Mus musculus	Male	Urinary odors	Behavioral tests	Territorial aggression	Male urine odors increase territorial and aggressive behaviors
(Mucignat-Caretta et al., 2004)	Rattus norvegicus	Male	Olfactory pheromone	Social/sexual behavior	Courtship modulation	Pheromone cues modulate male courtship
(Pfaus, 2006)	Rattus norvegicus	Male	Pheromone exposure	Neuroendocrine assays	Dopamine & sexual behavior	Pheromones influence mesolimbic sexual motivation
(Baum & Keverne, 2002)	Mus musculus	Male	Male urine	Behavioral tests	Territorial & mating behavior	Male pheromones influence social dominance

(Stowers et al., 2002)	Mus musculus	Male	Pheromone receptor deficiency	Genetic model	Aggression/courtship deficit	VNO disruption abolishes male–male aggression
(Brennan, 2004)	Mus musculus	Both	Urinary cues	Review	Multiple behaviors	Pheromone cues regulate sexual and aggressive behaviors
(Liberles, 2009)	General rodent	Both	VNO chemosensory signals	Review	Pheromone detection	Roles of pheromones in sociosexual behavior
(Dombret et al., 2017)	Mus musculus, SPF	Both	DEHP, phthalate mix via chow	6-week dietary exposure	Estrous cycle, partner preference, USVs, aggression	High-dose DEHP and phthalate mix disrupted sexual behavior, altered attractiveness, and reduced male USVs

3.3 Behavioral and Neuroendocrine Discoveries

Courtship Behavior: The mounting, intromission, and ultrasonic vocalizations were reliably enhanced due to female urine or glandular pheromones in male rodents (Haga et al., 2010; Novotny et al., 2007). Knockout experiments (genetic, TRPC2, G78) proved the VNO-dependent processes, when the knockout destroyed the courtship behavior (Stowers et al., 2002).

Aggression: Male urinary proteins and context-influential pheromones were the triggers of male-male aggression (Chamero et al., 2007; Ferrero et al., 2013). Pheromones of female origin, like the tear secretions, might lower the levels of aggression in males (Cavaliere et al., 2020). These behaviors were mediated by VNO and MeA-VMH circuits, which combined senses and hormonal signals (Dulac & Torello, 2003).

Neural and Hormonal Correlates: VNO and MOE pathways played an essential role in pheromone detection, resulting in activity in the medial amygdala, MPOA, and VMH [30]. The level of testosterone and corticosterone was also related to the aggression and courtship caused by pheromones in a series of experiments (Chamero et al., 2007; Pfaus, 2006). These behaviors were interfered with by high-dose chemical exposures (DEHP, phthalates), and endocrine readouts were altered by these exposures (Dombret et al., 2017).

Concentration and Dietary Effects: Behavioral effects were dose-related, whereby high doses of DEHP or mixtures of phthalates elicited greater disruptions in courtship, preference of the partner, and ultrasonic communication (Dombret et al., 2017). Weaker concentration levels were less severe or insignificant (Mégarbane et al., 2010).

Conclusion

The use of pheromone-like olfactory signals, which are important modulators of male rodent courtship and aggression, has been shown to function in a highly coordinated pattern between neural and hormonal processes. The nature of the chemical signal, social hierarchy, and exposure conditions have a strong impact on behavioral outcomes. The vomeronasal and main olfactory systems give the information to essential parts of the brain, which interpret the information as context-dependent behaviors. These responses are further determined by endocrine factors, especially sex steroids and stress hormones. Pheromone and sexual motivation. The signaling of pheromones can be perturbed by environmental and dietary perturbations, such as high-dose phthalates, which inhibit sexual motivation and change the aggression patterns. The combination of behavioral, neurobiological, and hormonal results demonstrates that the social behavior of males is very plastic and responsive to both external and internal signals. The research needs to be carried out in the future with emphasis on multi-modal pheromone interactions, species-specific responses, and effects of endocrine disruptors to completely comprehend the process by which male reproductive strategies and social dominance are regulated.

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