

CHEMOSENSORY GENOMICS AND CHEMICAL ECOLOGY OF *GALLERIA MELLONELLA* AND ITS MOLECULAR PROSPECTS FOR SUSTAINABLE WAX MOTH MANAGEMENT

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ABSTRACT

Molecular studies on odorant receptors (OR), odorant-binding proteins (OBP) and the functioning of the receptor and pheromone signal transduction in wax moth *Galleria mellonella* have expanded exponentially during the past few decades. The olfactory system of *G. mellonella* relies on the coordinated action of odorant-binding proteins (OBPs), chemosensory proteins (CSPs), odorant receptors (ORs), ionotropic receptors (IRs), gustatory receptors (GRs), sensory neuron membrane proteins (SNMPs), odorant-degrading enzymes (ODEs), and neuropeptide signaling pathways that mediate the detection and processing of volatile semiochemicals derived from bees, beeswax, brood combs, propolis, pollen, and pheromonal cues. Recent transcriptomic, genomic, and peptidomic investigations have considerably expanded the repertoire of chemosensory genes in *G. mellonella*, revealing molecular components involved in odor discrimination, pheromone perception, behavioral plasticity, and environmental adaptation. Functional characterization of these gene families has further identified conserved and species-specific molecular pathways that may serve as promising targets for behavioural manipulation and molecular pest control. The integration of chemical ecology with functional genomics, RNA interference (RNAi), genome editing, ligand–receptor interaction studies, and semiochemical-based technologies is creating new opportunities for species-specific and environmentally compatible wax moth management. This review synthesizes current knowledge on the chemical ecology and chemosensory genomics of *G. mellonella*, highlights recent advances in molecular mechanisms underlying insect–host interactions, and discusses emerging prospects for developing precision, sustainable, and bee-safe management strategies for protecting apicultural systems.

KEYWORDS: *Galleria mellonella*; chemical ecology; chemosensory genomics; odorant receptors; semiochemicals; sustainable pest management.

INTRODUCTION

The honeybee is a prominent member of the order Hymenoptera and plays an essential role not only in pollination but also in the production of various economically and medicinally valuable products, such as honey, wax, propolis, royal jelly, and bee venom. These products are highly esteemed for their nutritional and therapeutic benefits, rendering honeybees vital from both ecological and economic perspectives. It is estimated that honey bees contribute nearly 90% of insect pollination necessary for the cultivation of the most widely consumed food crops globally (Klein et al., 2006) (Plettner, Eliash, Singh, Pinnelli, & Soroker, 2017). The economic worth of this pollination service is approximated at around €138 billion each year, while the potential global decline in food crop production without insect pollinators could amount to €191 to €310 billion (Gallai, Salles, Settele, & Vaissière, 2009) (Plettner et al., 2017). However, the existence of this crucial key pollinator is becoming more vulnerable due to a range of pests and diseases. Among these threats, wax moths are regarded as one of the most destructive enemies, causing serious hindrance to honey bee populations.

The greater wax moth *Galleria mellonella* (Linnaeus, 1758), also known as the bee moth, wax worm (Hayes et al. 1936), the wax (or bee) miller (Ellis, Graham, & Mortensen, 2013) and the lesser wax moth *Achroia grisella* (Fabricius, 1794) (Lepidoptera: Pyralidae) are common pests of *Apis mellifera* colonies worldwide (Ellis et al., 2013). *G. mellonella* appears to be the most damaging of these species, significantly affecting colonies of *A. mellifera* and *A. cerana* (Sterling et al., 2025). Only the larval stage is harmful (Charriere & Imdorf, 1999). The growth and survival of *G. mellonella* are significantly affected by the species of host bees, the properties of the comb, and climatic conditions (Warren & Huddleston, 1962). The growing concerns about resistance and the limitations of chemical fumigants have led to a heightened interest in environmentally friendly alternatives.

Essential oils like clove, cinnamon, garlic, camphor, mint, and *Moringa oleifera* demonstrate significant larvicidal and adulticidal properties (Said, Naglaa, & Dina, 2022); (Helaly, Ali, & Ghazala, 2022). Conventional wax moth control methods are well documented; however, molecular mechanisms underlying wax moth behaviour and survival remain comparatively underexplored.

Additionally, understanding the molecular foundations of olfaction elucidates how the wax moth perceives and reacts to environmental signals, creating possibilities for focused pest control (Zhao et al., 2019) (Yang et al., 2021). *G. mellonella* possesses a specialized olfactory system for detecting sex pheromones; however, the genes and molecular pathways underlying its chemoreception remain insufficiently characterized. Advancing molecular investigations of the olfactory organs in *G. mellonella* will enhance the understanding of pheromone detection mechanisms in this species and support the development of behaviour-based pest management strategies (Zhao et al., 2019).

Despite considerable research on the biology and ecology of wax moths, the molecular processes underlying chemical perception and behavioural responses are still not fully understood. Recent advances in genomic and transcriptomic technologies have begun to reveal the diversity of chemosensory genes involved in odour detection and signal transduction. However, the functional roles of many of these genes in mediating host recognition and habitat selection remain largely unexplored. A comprehensive understanding of these mechanisms is essential for linking chemical ecology with behavioural regulation and for identifying novel targets for sustainable pest management.

Biology and Seasonal Population Dynamics of *Galleria mellonella*

G. mellonella is a typical holometabolous insect, signifying that its life cycle encompasses four developmental stages namely egg, larva, pupa, and adult (Smith, 1965) (Fasasi & Malaka, 2006) (Swamy, 2008) (Ellis et al., 2013) (Hosamani, Hanumantha Swamy, Kattimani, & Kalibavi, 2017) (Kwadha et al., 2019) (Desai, Siddhapara, Patel, & Prajapati, 2019) (Wojda, Staniec, Sulek, & Kordaczuk, 2020). Every step of the life cycle will be influenced by both warm and cold temperatures. At temperatures below 5°C, larvae may go completely dormant. Developmental activity is significantly decreased at moderately low temperatures (8–18°C). Furthermore, temperatures below 18°C and above 38°C prevent eggs from hatching (NSW Department of Primary Industries [NSW DPI], 2023). Within four to ten days of emerging, the female begins to lay eggs, producing between 300 and 600 eggs, while individual moths may lay up to 1,800 eggs. Seven successive instars are endured by the larvae. The newly hatched larvae move more quickly, appear wedge-shaped, and are pale white in colour (Desai et al., 2019). Whereas the later instars appear spindle-shaped and dirty grey. In addition to being slow feeders in their first instar, later instar larvae are prolific eaters and form silken cocoons around themselves when starving (Desai et al., 2019). When fully formed larvae reach the seventh instar, they begin to move in search of an ideal pupation place and begin to scrape the surface just before pupation. The larvae usually pupate in the apiary by entering the hive's cracks (Hosamani et al., 2017). When the temperature becomes ideal, the larvae begin to pupate after spinning the cocoon; this process typically takes 14–16 days. In the last phases of pupation, light brown pupae turn darker (Vijayakumar et al., 2019). In the case of adults, both males and females are identical in terms of size and colour, with the exception of the female's robust abdomen (169mg) (Fasasi & Malaka, 2006). There is remarkable sexual dimorphism in the adult greater wax moth. (Williams, 1997) (Ellis et al., 2013) (Paddock, 1918) (Kwadha, Ong'Amo, Ndegwa, Raina, & Fombong, 2017). Compared to the females, the male is significantly smaller and less black in colour (Williams, 1997) (Ellis et al., 2013); (Paddock, 1918); (Kwadha et al., 2017). The population dynamics and survival of wax moths are greatly influenced by their ability to exploit weak colonies (Nielsen & Brister, 1979); in case of strong colonies, it attacks when the colonies population is declining (Bhatnagar, Suman, Sharma, & Sankhla, 2020) as workers in strong colonies eliminate most larvae shortly after the infestation (Nielsen & Brister, 1979)

G. mellonella has been observed to exhibit a seasonal occurrence, with population onset in April. Subsequently, the population increases steadily and reaches its peak in July, after which it gradually declines until March. Notably, March has the lowest number of Greater wax moth larvae, pupae, and adults (Lalita & Yadav, 2018). Therefore, it is essential to keep the colony of the hive to be strong and healthy to avoid infestation of wax moth by providing proper seasonal colony management practices (Ambaw, Teklehaimannot, & Workye, 2020). In addition to having a severe impact on weak or stressed colonies, the larvae of both wax moth species cause significant damage to stored beekeeping equipments (Kwadha et al., 2017).

Comb preference

The increased susceptibility of older honey bee combs to *G. mellonella*'s infestation is closely linked to the pest's enhanced development and reproductive success. According to (Lalita & Yadav, 2018) as comb age increased, the developmental duration of immature stages decreased, while the body size of eggs, larvae, and pupae increased. Adult Moths that emerged from older combs showed increased longevity, faster wing development, and significantly enhanced fecundity. The results imply that the aged combs of *A. mellifera*, which are enriched with residual pollen, larval cocoons, and organic matter, provide a nutritionally superior substrate and have a significant impact on *G. mellonella*'s preference for combs. Besides comb age, the species of the comb is vital in determining the pest's developmental biology. The species of honey bee comb on which *G. mellonella* was reared has a significant impact on its developmental performance. Egg and prepupal durations remained relatively consistent, but notable differences were seen during the larval and pupal stages. Specifically,

individuals raised on *Apis mellifera* comb showed extended larval and pupal periods when compared to those raised on *A. cerana*, *A. dorsata*, and *A. florea* (Hosamani et al., 2017). In addition to species-specific differences, the age of the comb also affects the degree of infestation and damage intensity. (Darwish, 2022) reported that the extent of damage caused by *G. mellonella* larvae increased progressively with comb age and infestation duration. At 30 days of infestation, five-year-old combs recorded the highest damage, whereas one-year-old combs exhibited comparatively lower damage. The overall mean damage percentage increased from 28.14% in one-year-old combs to 44.92% in five-year-old combs, indicating a marked rise in susceptibility with advancing comb age (Darwish, 2022).

Hive Interaction and Mating

Adult female *G. mellonella* enter hives at night and lay eggs in cracks and crevices of the bottom board and hive walls. After hatching, larvae begin feeding on the combs (Vijayakumar et al., 2019). (Nielsen & Brister, 1979) observed that adult wax moths often leave the hive entrance quickly and fly to trees or other high points at night to mate. Individuals are most active during the first three days and become less active as they age.

Wax moth behavior is strongly influenced by pheromones, including sex pheromones produced by males (Finn & Payne, 1977); (Svensson et al., 2014); (Y. Li et al., 2019). The hive environment also contains pheromones such as nonanal, decanal, and undecanal, which can modulate wax moth cognitive and behavioral responses (Farina, Grüter, Acosta, & Mc Cabe, 2007); (Dupuy et al., 2017) ; (Rouyar et al., 2015); (Y. Li et al., 2019). Moths primarily approach hives at night when bees are less vigilant. Around two hours after nightfall, newly hatched moths may leave the hive to mate before selecting a hive to invade. They can infiltrate hives effectively, multiply in bee combs, and evade honeybee defences, suggesting that bees are unable to fully prevent wax moth infestation. Interestingly, *G. mellonella* can detect but appears to ignore honeybee alarm pheromones (Y. Li et al., 2019). In natural settings, sex attractants prompt females to locate males, guided further by acoustic cues (Flint & Merkle, 1983). Bee combs emit a complex mixture of volatile and non-volatile compounds that strongly influence the behaviour of *Galleria mellonella*. These chemical signals guide host recognition, oviposition behaviour, and larval feeding activities within hive environments. Such interactions highlight the ecological significance of semiochemical communication in wax moth - honeybee associations. Understanding these chemical cues provides valuable insights for developing behavioural and semiochemical-based pest management strategies.

Acoustic Communication in Mate Selection

Male mating calls with higher acoustic intensity or power are generally preferred by females, as demonstrated in studies of female choice (Ryan & Keddy-Hector, 1992). In *A. grisella*, female preference favours males that produce energetically costly calls, thereby selecting males capable of sustained energy investment in communication. Because larger males inherently possess higher net metabolic rates, females often prefer them (Reinhold, Greenfield, Jang, & Broce, 1998). However, although attractive males typically exhibit higher metabolic rates, some unattractive males also show similarly elevated rates. This indicates that female choice is not based solely on energetic expenditure (Reinhold et al., 1998).

Consequently, females also rely on non-energetic signal characteristics such as peak amplitude, asynchrony interval, and single-pulse rate to assess male quality (Reinhold et al., 1998). Female preference for energetically expensive signals may arise either through arbitrary (Fisherian) sexual selection or as a mechanism to obtain direct benefits, such as selecting parasite-free mates or facilitating efficient mate localization (Reinhold et al., 1998). In this context, female *A. grisella* can distinguish male moth signals from bat echolocation calls due to the much faster pulse repetition rate of moth calls (Greenfield & Weber, 2000); (Jones, Barabas, Elliott, & Parsons, 2002).

In contrast, *G. mellonella* moths are considered tone-deaf because their auditory system consists of four sensory cells with similar frequency tuning but different response thresholds (Skals & Surlykke, 2000); (Jones et al., 2002). As a result, frequency differences alone cannot be used to discriminate moth signals from bat calls. In *G. mellonella*, the threshold for flight cessation, an antipredator response, decreases as pulse repetition rate increases, but repetition rate has little effect when the duty cycle remains constant (Skals & Surlykke, 2000); (Jones et al., 2002). These findings suggest that *G. mellonella* responds primarily to signal power rather than pulse repetition rate per second. Therefore, it has been proposed that *G. mellonella* may differentiate between bat echolocation and moth communication signals based on pulse duration rather than frequency or repetition rate (Jones et al., 2002).

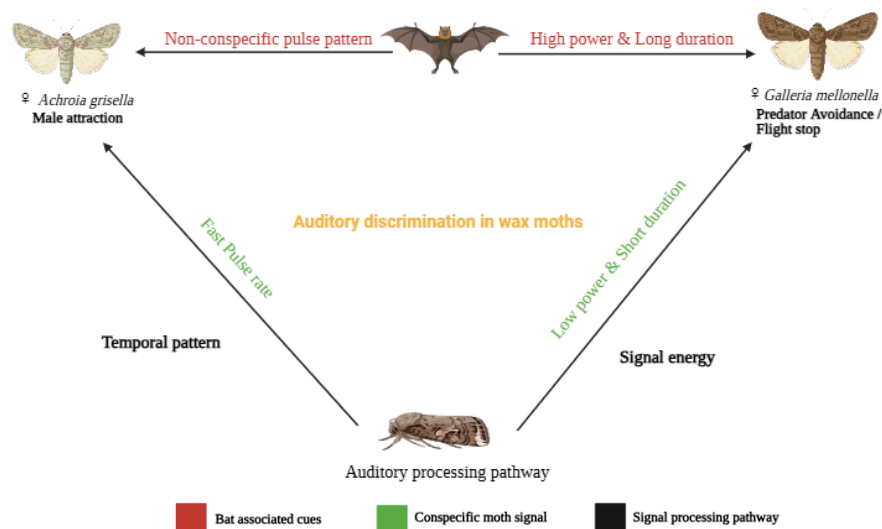


Figure 1:. Schematic representation of ultrasonic sound production and perception involved in courtship behaviour and mate recognition

Multimodal Pheromone Signalling

In most lepidopterans, females produce and emit sex pheromones to attract males. In contrast, in *G. mellonella*, males produce and release sex pheromones to attract females during mating. This is contrary to the widespread belief that female moths are the primary pheromone emitters (Zhao et al., 2019).

In addition to chemical cues, mechanical and auditory stimuli also influence pheromone signaling in *G. mellonella*. (Spangler, 1985) demonstrated that pheromone release in males is strongly affected by acoustic and vibrational stimuli. Exposure of males outside beehives to airborne vibrations around 50 Hz led to a marked increase in pheromone emission, suggesting that release is dynamically regulated rather than constant. Pheromone production varies among males based on factors such as body size, age, and prior exposure to females (Spangler, 1987); (Y. Li et al., 2019).

Male wax moths are particularly sensitive to substrate-borne vibrations in the frequency range of female wing beats. Behavioural observations indicate that pheromone release is associated with wing fluttering, which is closely linked to vibrational communication (Spangler, 1987). Sensory responses decline substantially above ~116 Hz, corresponding to the frequency of honeybee wing fanning, indicating a filtering mechanism that prevents unnecessary pheromone release in the presence of bees. This selective responsiveness likely allows males to conserve pheromone resources while maintaining effective mating communication, particularly in weak colonies that are preferentially invaded by wax moths (Spangler, 1987).

Host-Plant Volatile Pathways in Pheromone Communication

Many male-produced pheromones are structurally similar to host plant volatiles; for instance, nonanal and undecanal function as the principal pheromone components in *G. mellonella* (P Lizana et al., 2020). These aldehydes are widely recognised volatile compounds released by plants or flowers that are also found in the volatile profile of beehives (Brambilla et al., 2022); (Edziri, Mastouri, Cheraif, & Aouni, 2010); (Godoy, Arias, Venthur, Quiroz, & Mutis, 2022); (Jørgensen, Hansen, Christensen, Jensen, & Kaack, 2000); (Bin & ZHANG, 2019); (Paula Lizana et al., 2023). In addition to the minor pheromone component 5,11-dimethylpentacosane, aldehydes appear to be central to the moth's chemical communication (Svensson et al., 2014).

It has been proposed that males have co-opted chemosensory proteins that were originally involved in female host-seeking behaviour (Phelan, 1992); (Conner & Iyengar, 2016); (P Lizana et al., 2020). Notably, *G. mellonella* males also emit aldehydes that are natural components of beehives (Torto, Suazo, Alborno, Tumlinson, & Teal, 2005); (Schmitt, Herzner, Weckerle, Schreier, & Strohm, 2007); (Kwadha et al., 2017); (Manyi-Loh, Ndip, & Clarke, 2011); (P Lizana et al., 2020).

The male forewings of *G. mellonella* are said to contain pheromone glands (Romel, Scott-Dupree, & Carter, 1992); (P Lizana et al., 2020). The presence of GOBP1 and OBP1.2 in the male abdomen and antennae, together with PBP2 and GOBP2 in all tissues of both sexes, suggests that they may have a chemosensory role and are likely tuned to sex pheromone components (P Lizana et al., 2020).

Molecular Basis of Host Colony Recognition

Transcriptome analysis of *G. mellonella* larvae has uncovered a small yet functionally significant group of chemosensory genes. Comprehensive transcriptome investigations of chemosensory genes in *G. mellonella* have demonstrated considerable variation across different tissues and developmental stages. (Zhao et al., 2019) Discovered 22 Odorant Binding Proteins (OBPs), 20 Chemosensory Proteins (CSPs), 46 Odorant Receptors (ORs), 17 Ionotropic Receptors (IRs), and 2 Sensory Neuron Membrane Proteins (SNMPs) in adult antennae,

whereas (Jiang et al., 2021) reported 21 OBPs, 18 CSPs, 43 ORs, 18 IRs, and 2 SNMPs in the same tissue. In contrast, the larval datasets identified by (Xie et al., 2025) included 25 chemosensory-related genes, comprising 9 OBPs, 1 CSP, 5 ORs, 4 GRs, 4 IRs, and 2 SNMPs, along with several genes (1 OBP, 1 IR, 1 SNMP, and 4 GRs) that had not been previously identified in studies of adult antennae (Xie et al., 2025). Two novel genes, GmelOBP22 and GmelSNMP3, exhibited strong expression in larval heads, suggesting important roles in chemosensory function, development, and survival. These findings will provide molecular evidence for the olfactory mechanisms underlying host-seeking and feeding behaviour in wax moth larvae and form a foundation for future functional characterisation (Xie et al., 2025). The greater variety and number of chemosensory genes in adult antennae indicates that olfaction is crucial for detecting host colonies from a distance, while the reduced and distinct set of chemosensory genes in larvae represents a specialization for short-range contact chemoreception in the hive.

Role of Sex-Biased Odorant Receptors

Overall gene expression indicates that females exhibit higher levels of GmelORs than males (Paula Lizana et al., 2023). Notably, the sensitivity of GmelOR4 to nonanal suggests a unique role among plant volatile odorant receptors, specifically in detecting the moth's primary sex pheromone component (Paula Lizana et al., 2023). GmelOR4 likely plays a critical role in retaining *G. mellonella* near beehives. Ecological studies by (Flint & Merkle, 1983), (Kwadha et al., 2019), and (Spangler, 1985) showed that males approach nearby plants to release pheromones and attract females for mating. Therefore, GmelOR4 may be important for both males and females in identifying key volatiles in their chemical ecology (Paula Lizana et al., 2023).

The expression of OR-encoding unigenes, including GmelOR5, 6, 7, 8, and 9, is biased toward females. Female-specific OR unigenes may detect male sex pheromones. Alternatively, these female-biased OR genes may govern other female-specific behaviors, such as locating bee-comb hosts for oviposition (Zhao et al., 2019).

Digestive Adaptations

Larval instars of the greater wax moth (*G. mellonella*) exhibit stage-specific differences in food consumption, digestion, and nutrient utilization that reflect adaptive digestive strategies. Earlier instars consume less food but show higher approximate digestibility (AD), indicating efficient nutrient extraction possibly due to longer gut retention time (Rath, Prasad, & Sinha, 2003); (Sohail, Aqueel, Ellis, Raza, & Ullah, 2020). In contrast, later instars show increased consumption rates and metabolic activity (Bailey & Singh, 1977); (Mackey, 1978); (Vats & Kaushal, 1980); (Kerkut, 2013); (Sohail et al., 2020), but decreased AD and efficiency of conversion of digested food (ECD), indicating a shift toward bulk feeding and rapid biomass accumulation in advance to moulting (Arendt, 1997); (Gotthard, 2004); (Sohail et al., 2020). Overall, early instars of *G. mellonella* seem to digest wax substrates more effectively, whereas later instars focus on increased consumption and biomass deposition. This ontogenetic modulation of digestive efficiency constitutes the foundation to wax degradation capacity and offers insights into stage-specific feeding damage and potential physiological targets for sustainable management (Sohail et al., 2020).

The GWM consumes beeswax, a complex polymer made up of saturated and unsaturated monoesters and hydrocarbons. This remarkable ability suggests it has specialized digestive adaptations. Given that the dominant ethene ($-\text{CH}_2-\text{CH}_2-$) connections in beeswax tend to be very similar to those found in polyethylene, it has been hypothesized that the processes involved in wax degradation could be comparable to those in plastic biodegradation (Saikia, Borah, Baruah, Rokozeno, & Deka, 2022).

G. mellonella larvae's capacity to break down polyethylene (PE) has gained considerable interest because of the chemical resemblance between synthetic polymers and beeswax (Das et al., 2024).

Detoxification–Behavior Interactions

Exposure of *G. mellonella* larvae to plant-derived alkaloids significantly alters feeding behavior, nutritional intake, and developmental patterns. During the initial days of berberine exposure, larvae showed faster pupation and consumed approximately 5% less food, suggesting that chemical stress accelerates developmental decisions while suppressing feeding activity (Venthur & Zhou, 2018). Berberine acts as a behavioural deterrent, consistent with studies showing antifeedant effects in larvae of *Lymantria dispar*. Alkaloids generally elicit aversive behavioural responses in insects (Shields et al., 2008); (Venthur & Zhou, 2018). Alkaloid exposure also impacts detoxification enzyme systems. Following berberine treatment, glutathione S-transferase (GST) activity increased substantially, peaking at 48 hours, indicating an inducible detoxification response (Venthur & Zhou, 2018). Similar GST upregulation was observed in larvae exposed to polyethene, suggesting a generalised detoxification response to chemically complex substrates (Peydaei, Bagheri, Gurevich, de Jonge, & Nielsen, 2020); (Venthur & Zhou, 2018). Transcriptome analysis identified 22 GST-related transcripts ranging from 174 to 1,386 nt, including several full-length open reading frames. Differential expression analysis revealed that most GSTs were overexpressed upon berberine exposure, with GmelGST8 and GmelGST20 showing particularly high expression, indicating critical roles in alkaloid detoxification. Molecular modelling further suggested that GST8 may have a higher affinity for berberine metabolism than GST20 (Venthur & Zhou, 2018). Phylogenetic analysis connected several wax moth GSTs with detoxification enzymes in other lepidopterans. Insecticide-detoxifying GSTs involved in metabolizing organophosphates, pyrethroids, and phytochemicals, such as BmGSTu2, CpGSTe3, and SlGSTe1, clustered with GmelGSTs (Yamamoto & Yamada, 2016); (Zou et al., 2016); (Hu et al., 2020); (Venthur & Zhou, 2018). Other GSTs were associated with pheromone or odorant-degrading enzymes, including GmelGSTD1, which metabolizes host plant volatiles and sex pheromone

components, suggesting a link between detoxification capacity and chemical signal processing (G. W. Li, Chen, Xu, & Wu, 2018); (Venthur & Zhou, 2018). Together, these findings suggest that GST-mediated detoxification enables *G. mellonella* larvae to survive in alkaloid-rich and chemically complex environments by converting toxic compounds into less harmful conjugates, indirectly influencing larval behaviour and development (Venthur & Zhou, 2018)

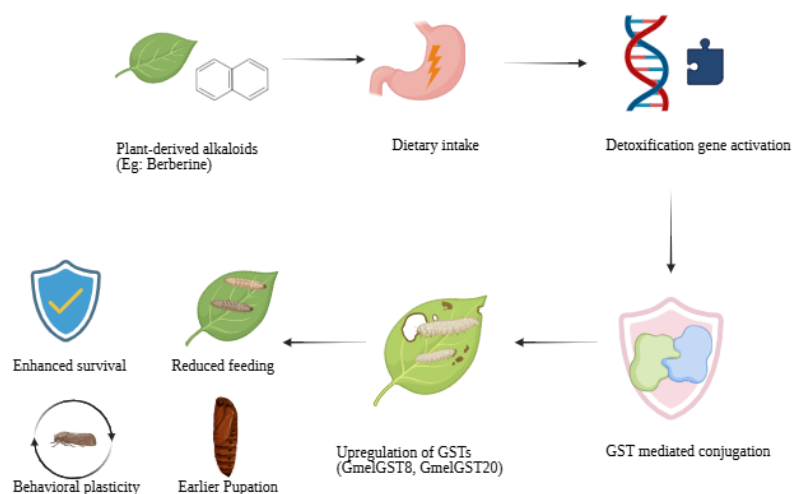


Figure 2: Conceptual diagram illustrating the role of detoxification pathways in modulating larval feeding activity and developmental patterns

Conventional measures

A variety of chemical, fumigant, and physical strategies, including phosphine, CO₂, sulfur fumigation, and light-based traps, have been employed to manage *G. mellonella* infestations in hives (Abrol & Kakroo, 1996); (Tremblay, 1978); (Kondrateva et al., 2020). While effective in reducing moth populations, these approaches are largely non-specific, often fail to prevent re-infestation, and do not target the underlying molecular pathways that govern larval survival, detoxification, and chemosensory-mediated behaviour. Moreover, the repeated use of chemical fumigants may pose risks to honeybee colonies and contaminate hive products. These limitations highlight the importance of developing eco-friendly and molecularly targeted strategies for wax moth management, including strategies that exploit GST-mediated detoxification, chemosensory receptor function, and neuropeptide signalling, to develop more precise and sustainable pest-management tools.

Control method	Dose/ concentration	Exposure conditions	Target stages	Efficacy	Reference
Aluminum phosphide	2.0 g/m ²		All stages	Effective; no effect on bee behavior	(Abrol & Kakroo, 1996)
Sulphur (SO ₂)	Burning sulphur strips / SO ₂ spray	Repeat after 2 weeks	Larvae, pupae, adults	Highly effective; ineffective against eggs	(Charriere & Imdorf, 1999)
Carbon dioxide (CO ₂)	60%	26°C	All stages	Effective in sealed cupboards	(Contessi, 1996)
CO ₂ under polythene			All stages	Not satisfactory due to gas permeability	(Contessi, 1996)
Phosphine	Variable doses		All stages	Did not repel bees or affect brood	(Dominguez & Bande, 1992)

Sulphur vapour			Larvae, pupae	Effective	(Dominguez & Bande, 1992)
Naphthalene vapour			Larvae	Ineffective against 20-day larvae	(Dominguez & Bande, 1992)
Phosphine	0.6 g pellet/super	Sealed stacks	Eggs, larvae, pupae	Highly effective only under gas-tight sealing	(Goodman, Williams, Oldroyd, & Hoffman, 1990)
Carbon dioxide (CO ₂)	8 L/min	3 min, sealed chamber	Larvae, pupae (<i>G. mellonella</i> , <i>A. grisella</i>)	Effective control	(Greatti & D'Agrao, 1992)
Sulphur	200 g/m ²	48 h	All stages	80–90% mortality	(Jhajj, Gatoria, & Bakhetia, 1996)
Aluminum phosphide	0.7–1.0 g/m ²	48 h	All stages	80–90% mortality	(Jhajj et al., 1996)
Ethylene dibromide		48 h	All stages	Only 18–65% mortality	(Jhajj et al., 1996)
Aluminum phosphide (ALP)	6 g/m ²	4 days	Eggs, larvae, pupae, adults	100% control; residues <0.01 ppm	(Lee, Choi, & Choi, 1991)
Formic acid	85% formic acid; 10 ml/comb (90 ml per box of 9 combs)	Applied on absorbent cardboard plates placed over top bars; exposure for 3 months	All stages	Used as a long-term fumigant for protection of stored combs against wax moth infestation	(Mansour, Sanad, & Saad, 2010)
SO ₂ , acetic acid			All stages	SO ₂ more effective than acetic acid	(Ritter, Perschil, & Vogel, 1992)
Para-dichlorobenzene (PDB)	89 g/breeding box	Crystals sprinkled on top of combs	Larvae and adults	Commonly used to kill and repel lesser and greater wax moths	(Mansour, 2003); (Mansour et al., 2010)
Oxfendazole	1.5% incorporated in diet	Continuous exposure through treated diet	Larvae → adults	Adult emergence reduced to 35% compared to untreated control, indicating strong developmental inhibition	(Sugeçti, Büyükgüznel, & Büyükgüznel, 2016)
Oxfendazole	0.0015–1.5%	Larvae reared to 7th instar on treated artificial diet	Larvae	cellular damage and physiological stress; suggests insecticidal	(Sugeçti & Büyükgüznel, 2018)

				potential at optimized concentrations	
Oxyclozanide (anthelmintic)	0.003, 0.03 and 0.3% (diet incorporation)	Larvae reared on treated artificial diet	Larvae, pupae, adults	Caused dose-dependent suppression of larval development, pupation and adult emergence ($R^2 = 0.95-0.97$).	(Çelik, Büyükgüzel, & Büyükgüzel, 2019)
Triclabendazole (benzimidazole anthelmintic)	0.001, 0.01 and 0.1 g/100 g diet	Larvae reared on treated artificial diet	Larvae, pupae, adults	Induced strong oxidative stress; significantly increased MDA levels and GST activity across all developmental stages and midgut tissue, indicating toxic and detoxification responses	(Büyükgüzel & Büyükgüzel, 2021)
Cd 4-formylbenzoate pyrazine complex		in silico docking followed by in vivo hemolymph analysis	Larvae	Showed strong juvenile hormone binding (-8.1 kcal/mol) and induced metabolic enzyme disruption and cellular damage in larvae.	(Harmankaya et al., 2025)
Colony strengthening through feeding	1 kg sugar solution (1:1 sugar:water) per colony per month	Applied during dearth season; monthly feeding	Larvae	Improved colony strength, increased brood, pollen, nectar stores, and reduced wax moth infestation compared to control	(Gela, Negera, Bezabh, & Begna, 2017)
Reducing supers	Removal of excess supers	Supers removed when colonies dwindled; stored in well-aerated areas	Larvae and adults	Significantly reduced number of infected combs	(Gela et al., 2017)

Removal of unoccupied frames	Complete removal of empty frames	Applied when colonies clustered to one side of hive	Larvae	Reduced infestation by eliminating breeding sites	(Gela et al., 2017)
Wax moth trapping (fermented bait)	1 cup water + 1 cup sugar + 1 banana peel + ½ cup vinegar	Fermented for several days; trap hung near colonies in 2-L bottle with 1-inch hole	Adult	Significantly reduced adult moth population	(Gela et al., 2017)
LED light wavelength attraction	RGB LEDs (SMD 5050); wavelengths 577, 546, 490, 435 nm	15-min exposure at 23:00 hr for 5 days	Adult	45% of adults attracted to 435 nm (blue-violet light); shortest wavelength acted as strong attractant	(Kondrateva et al., 2020)
LED light wavelength - prolonged exposure	RGB LEDs; 7 h exposure (23:00–06:00)	Continuous nightly exposure for 7 days	Adult	Prolonged exposure at 435 nm caused adult mortality, indicating potential for light-based control	(Kondrateva et al., 2020)
LED radiation effect on biomass production	RGB LEDs (435–577 nm)	7 h nightly exposure for 7 days	Eggs, larvae, pupae, adults	Light spectrum influenced total biomass accumulation; wavelength-dependent effects on productivity	(Kondrateva et al., 2020)
Table 1: Summary of conventional control methods, doses, and efficacy against different life stages of <i>Galleria mellonella</i>					

Chemosensory Organs and Olfactory System in *Galleria mellonella*

G. mellonella employs a finely-tuned olfactory system situated in the sensory hairs (sensilla) on its antennae to identify pheromones and other scents (Carey & Carlson, 2011). The antenna type is filiform in both males and females; however, their number of segments differs, ranging from 40–50 in males and 50–60 in females (Leyrer & Monroe, 1973). According to (Zhao et al., 2019), various olfactory proteins, including chemosensory protein (CSP), ionotropic receptor (IR), odorant-binding protein (OBP), olfactory receptor (OR), and sensory neuron membrane protein (SNMP), are expressed at high levels in the sensillum lymph. Different types of sensilla have been identified in lepidopteran moths and are believed to be present in *G. mellonella*, including sensilla trichodea, basiconica, coeloconica, and chaetica (Keil, 1999). Where, sensilla trichodea is usually elongate and porous, mainly serve to detect sex pheromones especially in males. while sensilla basiconica play a role in the perception of host plant volatiles and environmental odors (Hansson & Stensmyr, 2011).

1. Odorant Receptors (OR)

Five putative odorant receptors (ORs) with full-length proteins of 396–474 amino acids and 5–7 transmembrane domains were found through transcriptome analysis of *G. mellonella* larval heads and bodies. These ORs are compatible with normal insect ORs. With the exception of GmelOR8 and GmelOR39, which had comparatively greater expression levels, the majority of ORs displayed low expression in larval tissues (Xie et al., 2025). 46 of the assembled unigenes were identified as ORs from the seven-transmembrane receptor superfamily. Of them, 34 were full-length open reading frames that encoded proteins with five to ten transmembrane domains, which are typical of insect ORs, and more than 355 amino acids (Xie et al., 2025). The previously described OR

repertoire was expanded by a genome-wide study, which also found 62 OR candidates in *G. mellonella*, including 16 additional genes (Paula Lizana et al., 2023). Among the olfaction-related genes in *G. mellonella*, transcriptomic studies have also discovered 80 odorant receptor genes, demonstrating the variety of ORs involved in odour sensing (Shuang et al., 2019).

2. Ionotropic receptors (IRs)

Ionotropic receptors (IRs) are a class of receptor genes found in the odour-sensitive antennal olfactory sensory neurons (OSNs) that are analogous to ionotropic glutamate receptors (iGluRs). Interestingly, OSNs that exhibit these IRs are different from those that express odorant receptors (ORs) (Benton, Vannice, Gomez-Diaz, & Vosshall, 2009); (Mang, 2025). IRs are implicated in thermosensation and hygrosensation and have been demonstrated to mediate the detection of a variety of odorants, such as phenylacetaldehyde, amines, and acids. Divergent IRs and antennal IRs are the two subfamilies into which IRs can be roughly divided. While antennal IRs are more evolutionarily conserved and probably found in all insect taxa, divergent IRs show low sequence conservation across species, suggesting species-specific roles (Mang, 2025). Several ionotropic receptors (IRs) in *G. mellonella* have been found through transcriptome studies. (Shuang et al., 2019) reported 56 IRs, while (Yang et al., 2021) identified 14 IRs. In addition, (Parepally, Krishnarao, Vyas, Divija, & Jayanthi, 2023), reported 5–7 IRs, and (Xie et al., 2025) identified 18 IRs, showing variance in IR counts across several transcriptome analysis data.

3. Odorant-Binding Protein (OBP)

Odorant-binding proteins (OBPs) are small soluble proteins that are important to the initial phases of insect olfactory perception by transporting hydrophobic odorant molecules through the sensillum lymph to odorant receptors (ORs) on the dendritic membrane of olfactory sensory neurons and initiating signal transduction pathways (Kordaczuk & Wojda, 2026). OBPs are essential for identifying pheromones, host-related semiochemicals, and other environmental signals and are believed to be the first molecular components involved in insect odour recognition. Transcriptome analysis indicates that *G. mellonella* has a large repertoire of OBP genes associated with chemosensory processes. In the antennal transcriptome, 44 unigenes with transcript lengths ranging from 308 to 3794 bp were identified as OBPs, including general odorant-binding proteins (GOBPs), pheromone-binding proteins (PBPs), and antennal binding proteins (ABPs). In the same dataset, 62 odorant receptor (OR) genes with nearly full sequences ranging from 347 to 3649 bp were identified (Parepally et al., 2023). Nine OBP genes, including a novel gene named GmelOBP22, were identified through transcriptome analysis of larval heads and bodies. All identified OBPs contain full-length open reading frames encoding proteins of 133–196 amino acids. GmelOBP22, possessing four cysteines, belongs to the Minus-C OBP subfamily, while eight OBPs with six conserved cysteine residues were classified as classic OBPs based on conserved cysteine patterns. Pairwise amino acid identities among the identified larval OBPs ranged from 4.79% to 67.86%, indicating sequence variability within the OBP family in *G. mellonella* (Xie et al., 2025).

4. Chemosensory protein (CSP)

Chemosensory Proteins (CSPs) are named for their high levels of expression in the chemosensory organs of insects; they are a family of small soluble polypeptides. CSP proteins are identified by four highly conserved cysteine residues, characteristic of typical insect CSPs (Zhao et al., 2019). In insect chemoreception, they may serve functions similar to those of OBPs (Odorant-binding Proteins), another group of soluble polypeptides that can bind pheromones and odorants. It is reported that both families of proteins are involved in the detection and release of semiochemicals, with specific functions depending on the insect species (Zhu, Iovinella, Dani, Pelosi, & Wang, 2019). Several CSP genes in *G. mellonella* have been found by transcriptome analysis. According to a study by (Yang et al., 2021), 35 unigenes with full-length open reading frames (ORFs) encoding proteins with 97–147 amino acids were identified as possible CSPs. All of these unigenes were anticipated to have the usual four cysteine residues. Twenty CSP-encoding unigenes were found in another investigation by (Zhao et al., 2019), of which 17 were full-length sequences. All full-length proteins had a signal peptide, which indicates that these are secreted proteins. Additional transcriptome analysis identified 18 CSP genes, all of which had full ORFs and projected protein lengths between 97 and 131 amino acids. The majority of CSPs had significant amino acid identity (61–85%) with lepidopteran orthologs, according to sequence similarity analysis, whereas a small number of members showed lower similarity (33–42%), indicating possible functional diversity (Jiang et al., 2021). Expression analysis revealed that GmelCSP1 is expressed in both larval head and body tissues, with higher transcript levels in the head, supporting a potential role in chemosensory processes (Xie et al., 2025).

5. Sensory neuromembrane proteins (SNMPs)

Insect-specific membrane proteins known as SNMPs were first discovered in Lepidopteran pheromone-sensitive olfactory sensory neurons (OSNs) and are crucial for pheromone detection (Agnihotri, Liu, & Xu, 2021). *G. mellonella* transcriptome investigations have revealed two SNMP genes, GmelSNMP1 and GmelSNMP2, which both encode full-length proteins with two transmembrane domains and open reading frames of more than 520 amino acids (Zhao et al., 2019); (Yang et al., 2021). According to a sequence comparison, GmelSNMP1 of *Eogystia hippophaecolus* share 71% amino acid identity, but GmelSNMP2 and SNMP2 of *Ostrinia nubilalis* share 66% identity (Jiang et al., 2021). Additionally, expression investigations revealed that GmelSNMP2 is expressed in both antennal and non-antennal tissues, while GmelSNMP1 is mostly expressed in the antennae, with higher expression in adult females than in males (Xie et al., 2025). These results imply that SNMPs are crucial for *G. mellonella* olfactory signaling and pheromone detection.

The variation in gene numbers reported across studies likely reflects differences in sequencing depth, developmental stages analysed, and transcriptome assembly strategies. Recent genomic and transcriptomic analyses have revealed a diverse repertoire of chemosensory genes in insects. However, the functional characterization of many of these genes in *G. mellonella* remains limited. Further studies integrating behavioural experiments with gene-expression analyses may provide deeper insights into how these molecular components contribute to host detection and environmental adaptation.

Gene Family	Numbers reported	Key Functions	References
Odorant Binding Proteins (OBPs)	44 OBP unigenes	Transport odor molecules to receptors	(Parepally et al., 2023)
OBPs (larval transcriptome)	9 OBPs	Chemosensory ligand binding	(Xie et al., 2025)
Chemosensory Proteins (CSPs)	36 CSPs	Chemical signal transport	(Shuang et al., 2019)
Odorant Receptors (ORs)	62 ORs	Odor detection	(Parepally et al., 2023)
OR candidates	80 ORs	Olfactory signal perception	(Shuang et al., 2019)
Ionotropic Receptors (IRs)	56 IRs	Detection of acids, amines and volatiles	(Shuang et al., 2019)
IRs	18 IRs	Chemosensory perception	(Xie et al., 2025)
IRs	5–7 IRs	Olfactory signaling	(Parepally et al., 2023)
IRs	14 IRs	Chemical cue detection	(Yang et al., 2021)
SNMPs	2 (SNMP1, SNMP2)	Pheromone detection	(Zhao et al., 2019); (Jiang et al., 2021)

Table 2: Reported chemosensory proteins and receptors involved in odor detection and chemical communication in *Galleria mellonella*

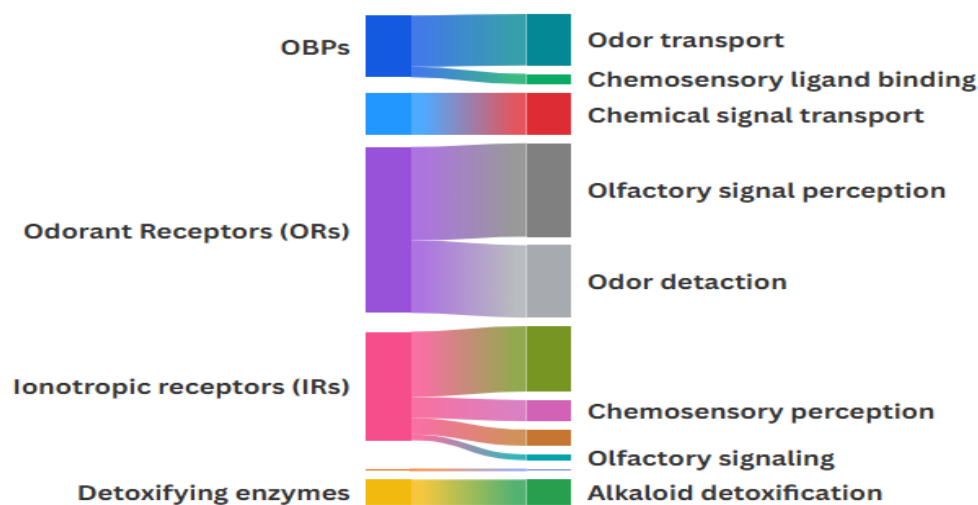


Figure 3 Sankey diagram summarizing reported gene numbers and their roles in odor molecule transport, ligand binding, odor detection, and pheromone-mediated signalling

Future prospects

The molecular framework of chemosensory control in *G. mellonella* have been greatly improved by recent multi-omics research. (Luo et al., 2024) found 72 neuropeptide precursors using an integrated transcriptome and peptidomic method, of which 40 were confirmed experimentally in the peptidome. Notably, twelve neuropeptide precursor genes were distinct to *G. mellonella* and not found in honeybees, indicating possible genetic targets for pest management techniques tailored to individual species. These results show that *G. mellonella* has a highly developed chemosensory network that combines odorant detection with neuropeptide signaling, allowing for effective adaptation to the chemically complicated hive environment. It is anticipated that the identification of important chemosensory genes involved in host detection, pheromone communication, and behavioral regulation would proceed more quickly with the expansion of genomic and transcriptomic resources. Chemosensory proteins (CSPs) are highly expressed in sensory organs like antennae, mouthparts, and tarsi, where they serve as ligand-binding carriers that deliver odor molecules to target receptors, according to research conducted on other lepidopteran insects (Agnihotri et al., 2021). CSPs are involved in host-plant volatile recognition, pheromone detection, and gustatory perception, according to expression analyses in species like *Helicoverpa armigera*, *Plutella xylostella*, *Mythimna separata*, and *Cnaphalocrocis medinalis*, underscoring their significance in insect behavioral responses (Zhang & Lei, 2015); (Younas et al., 2018); (Zeng et al., 2018);

(Qie et al., 2024); (Pelosi, Zhou, Ban, & Calvello, 2006). All of these results pinpoint chemosensory gene families as potential molecular targets for novel pest-management techniques, such as RNAi-mediated functional interference, gene-targeted disruption, and semiochemical-based tactics. The development of sustainable and species-specific management strategies for *G. mellonella* will be aided by future research that incorporates functional genomics, behavioural assays, and genome-editing technologies to better understand the functions of chemosensory pathways (Venthur & Zhou, 2018); (Parepally et al., 2023); (Xie et al., 2025).

CONCLUSION

The chemical ecology and chemosensory genomics of *G. mellonella* provide valuable insights into the mechanisms underlying host recognition, feeding behaviour, and reproductive strategies. Chemical cues derived from bee combs and hive environments play a crucial role in guiding insect behaviour through complex olfactory and gustatory pathways. Advances in transcriptomic and genomic analyses have significantly expanded our understanding of the chemosensory gene families involved in odour detection and signal transduction. Integrating behavioural ecology with molecular studies offers a promising framework for identifying novel targets for pest control. In particular, chemosensory proteins and associated signalling pathways represent potential candidates for innovative management strategies such as semiochemical disruption, behavioural manipulation, and RNAi-based interventions. Continued research combining chemical ecology, functional genomics, and applied pest management approaches will be essential for developing sustainable and environmentally friendly methods to mitigate wax moth infestations in apiculture systems.

Acknowledgement: The authors sincerely acknowledge the Department of Agricultural Entomology, Agricultural College and Research Institute (AC&RI), Madurai, Tamil Nadu Agricultural University, for providing the facilities and academic environment that supported the preparation of this review.

Conflict of interest : The authors declare no potential conflicts of interest with respect to the review, authorship and/or publication of this article

Consent to publish : All authors agree to publish the manuscript in Genetics and Molecular Research.

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