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Recent Advances on the Effects of Intraspecific and Interspecific Pheromones on Host Seeking Behavior of Entomopathogenic Nematodes[A]

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Abstract: Recent studies have advanced our understanding of how intraspecific and interspecific pheromones influence the host-seeking behaviour of entomopathogenic nematodes (EPNs), a crucial component of biological pest control. EPNs rely on some chemical cues in the soil environment, including ascaroside, CO_2 emissions, and organic compounds, to locate and infect their hosts. EPNs exhibit species-specific foraging strategies, with ambushers such as *Steinernema carpocapsae* (Rhabditida: Steinernematidae) remaining stationary while cruisers like *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) actively search for potential hosts. Pheromonal communication enhances group movement, aggregation, and infection efficiency. Some studies indicate that pheromone-exposed EPNs demonstrate improved dispersal and pathogenicity, with implications for enhancing their biocontrol potential. However, learned and innate preferences in host selection further refine their efficacy. Researches suggest that pheromone-based treatments could optimize EPN applications by increasing host-targeting precision and reducing environmental variability. Understanding these mechanisms is essential for improving EPN-based pest management strategies. Future research should explore the integration of pheromones in mass-release programs, assess the impact of interspecific interactions, and evaluate how environmental factors such as pesticides influence pheromone efficacy. These findings highlight the potential of

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pheromone-mediated behavioral adaptations to enhance sustainable and efficient biological control methods in agriculture.

Keywords: Biological control, EPN, Host searching, Semiochemicals.

Entomopatojen Nematodların Tür İçi ve Türler Arası Feromonlarının Konukçu Arama Davranışı Üzerindeki Etkilerine İlişkin Son Gelişmeler

Öz: Son çalışmalar, biyolojik mücadelinin önemli bir bileşeni olan entomopatojen nematodların (EPN'ler) konukçu arama davranışını tür içi ve türler arası feromonların nasıl etkilediğine dair anlayışımızı ilerletmiştir. EPN'ler, toprak içerisinde konukçularını bulmak ve enfekte etmek için askarositler, CO_2 emisyonları ve organik bileşikler dahil olmak üzere bazı kimyasallarını kullanır. EPN'ler, türe özgü beslenme stratejileri sergilemektedirler; *Steinernema carpocapsae* (Rhabditida: Steinernematidae) gibi ambusher türler hareketsiz kalırken, *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae) gibi cruiser türlerde aktif olarak konukçu aramaktadırlar. Feromonlar, grup hareketini, kümelenmeyi ve enfeksiyon verimliliğini artırır. Bazı çalışmalar, feromon etkisinde kalan EPN'lerin, biyolojik kontrol potansiyellerini artırmaya yönelik çıkarımlarla birlikte gelişmiş dağılım ve patojenite gösterdiğini belirlemiştir. Ayrıca, konukçu seçimindeki öğrenilmiş ve doğuştan gelen tercihler, etkinliklerini daha da iyileştirmektedir. Araştırmalar, feromon bazlı uygulamaların konukçu bulma hassasiyetini artırarak ve çevresel değişkenliği azaltarak EPN uygulamalarını optimize edebileceğini öne sürmektedir. Bu mekanizmaların anlaşılması, EPN temelli zararlı yönetimi stratejilerini geliştirmek için önemlidir. Gelecekteki araştırmalar, feromonların toplu salınım programlarına entegrasyonunu araştırmalı, türler arası etkileşimlerin etkisini ve pestisitler gibi çevresel faktörlerin feromon etkinliğini nasıl etkilediğini değerlendirmelidir. Bu bulgular, feromon aracılı davranışsal adaptasyonların tarımda sürdürülebilir ve etkili biyolojik kontrol yöntemlerini geliştirme potansiyelini vurgulamaktadır.

Anahtar Kelimeler: Biyolojik mücadele, EPN, Konukçu arama, Semiyokimyasallar.

Introduction

Biological control is a method that uses natural enemies to regulate the populations of pests as well as other living things in the ecosystem (Waage and Greathead, 1988; Simberloff, 2012; Lacey et al., 2015; Nchu, 2024). This approach commonly involves the utilize of parasitoids, predators, and pathogens to maintain pest populations below the economic damage threshold (Flinn and Schöller, 2012; Ballal and Verghese, 2015; Aksoy and Kovanci, 2016; Flick et al., 2016; Dabsu and Kovancı, 2022; Yaraşır et al., 2024). By reducing pest populations, natural enemies increase mortality rates or decrease fertility rates of the target pests (Flick et al., 2016; Dabsu and Kovancı, 2022; Dede et al., 2022). Also, biological control provides an effective means of pest management without causing environmental harm or leaving chemical residues. This method offers a sustainable solution for agricultural pest management, delivering long-term economic and ecological benefits (He et al., 2021; Dede et al., 2022; Frank, 2024; Susurluk and Bütüner, 2024).

Among the biological control agents frequently employed in biological control, entomopathogenic nematodes (EPNs) are among the most significant (Boemare et al., 1996; Burnell and Stock, 2000). EPNs are obligate endoparasitic organisms that spend almost their entire lifecycle in the soil. These organisms belong to the class Secernentea, order Rhabditida, and the families Heterorhabditidae and Steinernematidae (Caroli et al., 1996; Gaugler et al., 1997; Grewal, 1998; Koppenhofer et al., 2007; Bütüner and Susurluk, 2023a). EPNs possess the remarkable ability to search for hosts without feeding for months (Akı et al., 2023) and actively seek and infect hosts during their infective juvenile (IJ) stage, also known as juvenile 3 (J3) (Gaugler et al., 1997; Lewis et al., 2006; Bütüner and Susurluk, 2023b; Zhang et al., 2021; Bütüner et al., 2024; Rakubu et al., 2024). These nematodes have demonstrated high efficacy in controlling numerous pests and exist in a symbiotic relationship with gram-negative bacteria from the Enterobacteriaceae family. These bacteria are specialized at the family level, with *Photorhabdus* spp. associated with *Heterorhabditis* species and *Xenorhabdus* spp. with *Steinernema* species (Ciche et al., 2006; Susurluk and Ehlers, 2008; Susurluk, 2008; Bütüner and Susurluk, 2023a).

These organisms are particularly effective in controlling pests that spend at least one stage of their life cycle in the soil. Adaptic factors such as temperature, soil moisture, and pH significantly influence the infection mechanisms of EPNs (Puža and Mráček, 2005; Stuart et al., 2015; Matuska-Łyżwa et al., 2024; Susurluk and Bütüner, 2024). Additionally, EPNs exhibit species-specific host-seeking behaviours. Ambusher EPNs, such as *Steinernema carpocapsae* (Rhabditida: Steinernematidae), remain passively positioned near the soil surface, waiting for active hosts to pass by. These nematodes employ a "jumping" behaviour to capture moving hosts, a behaviour facilitated by their sensitivity to environmental cues such as CO_2 emissions, vibrations, and temperature changes (Wilson et al., 2012; Lortkipanidze et al., 2016; Zhang et al., 2021; Ramakrishnan et al., 2022; Rakubu et al., 2024). In contrast, cruising EPNs, such as *Heterorhabditis bacteriophora* (Rhabditida: Heterorhabditidae), actively move through the soil in search of hosts. These nematodes utilize chemical signals (chemotaxis), thermal cues (thermotaxis), and moisture gradients to locate potential hosts. This strategy is particularly effective against less mobile or soil-buried hosts. Although the factors influencing EPN host-seeking behaviour are not yet fully understood, research has revealed that EPNs are influenced by volatile compounds emitted by their hosts, plant volatiles released as a reaction to herbivorous pests, and conspecific and heterospecific pheromones, as demonstrated in recent studies (Kaplan et al., 2020; Erdogan et al., 2021; Stevens et al., 2023; Stevens et al., 2024). The host-seeking mechanisms of EPNs, coupled with their environmental adaptability and behavioural strategies, make them a valuable tool in biological control. The integration of chemical, physical, and environmental signals determines their success in pest management. Research into these mechanisms provides a critical foundation for enhancing the effectiveness of biological control methods.

This review highlights recent studies focusing on the role of pheromones in the host-seeking behaviours of EPNs, emphasising their potential to improve pest management strategies.

Pheromones effects on EPN and Host-Seeking Behaviour

Pheromones are crucial chemical signals that influence the collective movement and host-searching behaviour of EPNs. The structure and function of ascarosides in entomopathogenic nematodes represent an intriguing area of research, primarily due to their role as signalling molecules that influence a variety of biological processes. Ascarosides are glycosides derived from the dideoxysugar ascarylose, which is covalently attached to fatty acid-like side chains. This structural configuration enables them to function as pheromones, mediating interactions both within nematode populations and with other organisms, including plants and fungi (Hsueh et al., 2013; Yang et al., 2023; Choe et al., 2012). Recent studies have emphasised the diversity of ascarosides and their specific roles in the life cycles of entomopathogenic nematodes, such as *H. bacteriophora*. For example, a novel ascaroside, asc C11 EA, has been identified as essential for regulating the parasitic life cycle of this nematode, particularly in inhibiting the recovery of infective juveniles (IJs) under certain population densities (Noguez et al., 2012). This suggests that ascarosides not only facilitate communication among nematodes but also play a significant role in their ecological interactions and life history strategies. The biosynthesis of ascarosides is influenced by a range of factors, including diet and developmental stage, as demonstrated in *Caenorhabditis elegans*. The production of these signalling molecules is tightly regulated, allowing nematodes to adjust their behaviours in response to environmental cues (Kaplan et al., 2011; Hollister et al., 2013). Moreover, the structural diversity of ascarosides is achieved through modular assembly, in which various metabolic building blocks are combined to generate a wide array of signalling molecules (Panda et al., 2017). This modularity is vital for the nematodes capacity to communicate effectively and respond to their surroundings. In addition to their roles in nematode behaviour, ascarosides have been shown to influence interactions with other organisms. For instance, they can mediate plant-nematode interactions, with specific ascaroside blends inducing either attraction or avoidance behaviours in plants (Manohar et al., 2020; Manosalva et al., 2015). This underscores the ecological significance of ascarosides beyond the nematodes themselves, as they can affect plant defences and pathogen resistance mechanisms (Manosalva et al., 2015). The signalling capabilities of ascarosides extend to their involvement in the dispersal behaviour of nematodes. Studies have demonstrated that certain ascarosides, such as ascr#9, are released into the environment and can influence the movement and aggregation of nematodes, thereby enhancing their survival and reproductive success (Hartley et al., 2019; Kaplan et al., 2012). This highlights the importance of understanding the chemical ecology of ascarosides in the context of entomopathogenic nematodes and their interactions with both biotic and abiotic factors in their environments.

For example, a study on *Steinernema glaseri* (Rhabditida: Steinernematidae) found that the tendency of this species to move towards conspecific groups increased when the group had previously encountered a host. Additionally, the likelihood of joining heterospecific groups was greater in those that had previously encountered a host (Stevens et al., 2023). Similarly, Stevens et al. (2024) found that the aggregation behavior of the three EPN species (*S. carpocapsae*, *S. feltiae*, and *S. glaseri*) was significantly influenced by both conspecific signaling and species interactions. When isolated, each species showed strong aggregation, indicating the importance of species-specific signals in maintaining population structure. However, in mixed-species environments, aggregation was reduced when nematodes were placed together in the center, likely due to interference between species-specific signals. Interestingly, when placed in separate corners, aggregation increased, suggesting that spatial separation may preserve species-specific behaviors. These results imply that while mixed-species environments may reduce competition, they could also disrupt signaling mechanisms critical for effective host search behavior, with implications for the formulation of biocontrol products. Further research is needed to explore the impact of these interactions in natural settings and optimize pest control strategies.This demonstrates that pheromones play a role in both intraspecific and interspecific interactions of EPNs. On another note, it has been shown that species such as *S. carpocapsae* exhibit leader-following behaviour, which is supported by pheromones (Erdogan et al., 2021). The presence of a host-exposed leader nematode increased the likelihood of following. These findings reveal that EPNs develop collective movement strategies through pheromone-based communication mechanisms. A study by Oliveira-Hofman et al. (2019) emphasizes the role of pheromone extracts in enhancing the efficacy of EPNs. In this study, extracts from infected hosts were found to increase the movement and dispersal of species such as *S. carpocapsae* and *S. feltiae*. In soil column experiments, pheromone extracts guided more IJs towards *Tenebrio molitor* (Coleoptera: Tenebrionidae) larvae and increased infection rates. Additionally, in greenhouse tests, nematodes treated with pheromone extracts were observed to more effectively kill economically important pests, particularly *Curculio caryae* (Coleoptera: Curculionidae) and *Hermetia illucens* (Diptera: Stratiomyidae) larvae. These results suggest that the biological control potential of EPNs can be enhanced by treating them with pheromones prior to field application. Yang et al. (2023) examined the role of innate and learned preferences in the process of EPNs recognizing and infecting insect hosts. EPNs are used in agriculture for biological control of insect pests and have the ability to orient themselves towards suitable hosts for successful reproduction. In the study, *Steinernema diaprepesi* (Rhabditida: Steinernematidae) were reared on different insect hosts, and preferences were recorded for each. These nematodes were then 'imprinted' with plant terpenoids of agricultural significance. The results showed that exposure to plant volatiles increased nematode infection rates, although some host-compound combinations were found to be repellent. These findings reveal that the effects of learned and innate preferences on biological control efficacy are complex and context-dependent. Kaplan et al. (2020) investigated the behaviour of EPNs by examining how askarozid pheromones influenced their dispersal and food-seeking behaviours. The study compared the dispersal behaviour of *S. feltiae* and *S. carpocapsae* species in the absence of host pheromones. *S. feltiae* stopped dispersing without host pheromones, while *S. carpocapsae* continued dispersing but exhibited a temperature-dependent resting period. This resting period could be overcome by specific pheromones and temperature conditions. The study provides valuable insights into new molecular mechanisms for enhancing EPNs host-searching, pathogenicity, and effectiveness in biological control.

The host-searching behaviour of EPNs primarily occurs through chemical signals. Signals such as ascaroside pheromones, CO_2 and organic compounds released by damaged roots have been effective in helping these organisms detect their target hosts (Trejo-Meléndez and Contreras-Garduño, 2024). Zhang et al. (2021) reported how CO_2 and plant and insect-derived signals shape the host-searching and recognition behaviours of EPNs. While the responses of EPNs to environmental stimuli vary by species, it has been emphasised that they hierarchically integrate chemical signals. Additionally, the effects of selective pressure, age, and experience on the sensitivity of EPNs to chemical cues have been examined. These findings suggest that the chemical ecology of EPNs can be transformed into sustainable pest control strategies in agriculture. Furthermore, understanding the host-searching behaviour of EPNs on an individual level also illuminates the reasons behind their community-level movements. For instance, group movements can lead to higher infection rates, potentially enhancing the effectiveness of symbiotic bacteria and bypassing the host's immune system.

Conclusion

The influence of pheromones on the behaviour of EPNs is crucial for enhancing their use in biological control. Pheromone-supported collective movement strategies could facilitate more effective mass-release planning. Additionally, more detailed research into interspecific interactions between heterospecific species could provide valuable insights into which EPN species should be used together in biological control. Future research should focus on pheromone-based methods to help EPNs find their target hosts more efficiently. Furthermore, exploring the impact of pheromones on EPNs would contribute significantly to advancing knowledge in this field.

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