Research Article

Neuroparasitology of Insects: Behavioral Manipulation by Parasites and Its Evolutionary Implications

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Abstract | Parasites have evolved sophisticated strategies to manipulate insect behavior, enhancing their transmission and survival. This review synthesizes current knowledge on the neurobiological, molecular, and ecological mechanisms underlying parasite-induced behavioral changes in insects. A systematic analysis of recent studies was conducted, focusing on parasitic groups such as protozoans, fungi, nematodes, and parasitoid wasps. Key findings indicate that parasites alter host behavior through neurochemical modulation, affecting dopamine, serotonin, and octopamine pathways, as well as epigenetic modifications that sustain behavioral alterations. Behavioral changes include increased risk-taking, altered locomotion, and disrupted circadian rhythms, optimizing parasite transmission. Additionally, parasite-induced behavioral shifts influence vector-borne disease epidemiology by increasing pathogen transmission in mosquito and sandfly populations. Evolutionary interactions between parasites and hosts suggest a dynamic coevolutionary arms race, where hosts develop resistance mechanisms such as social immunity and immune priming. The ecological consequences extend to food web dynamics, predator-prey interactions, and biodiversity regulation. Future research should integrate molecular, neurophysiological, and ecological approaches to further unravel the complexities of host manipulation. Understanding these interactions may provide novel insights for biocontrol strategies and vector-borne disease prevention.

Keywords | Neuroparasitology, Insect behavior, Parasite manipulation, Host-parasite coevolution, Vector-borne Diseases, Neurochemical modulation

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INTRODUCTION

Parasitic manipulation of insect behavior represents one of the most fascinating and intricate phenomena in host-parasite interactions. Parasites have evolved sophisticated mechanisms to alter the behavior, physiology, and even neurobiology of their insect hosts, often in ways that enhance their own survival and transmission. These manipulations, ranging from altered locomotion and feeding patterns to suicidal tendencies, demonstrate the extent to which parasites can exert control over their hosts. The study of neuroparasitology in insects provides critical insights into the evolutionary arms race between parasites and their hosts, shedding light on fundamental principles of neurobiology, behavioral ecology, and evolutionary adaptation (Beckage, 2011; Libersat *et al*., 2009, Møller *et al*., 1993).

Behavioral manipulation is not merely an incidental byproduct of parasitism; rather, it is a highly refined evolutionary strategy that confers selective advantages to the parasite. The ability of parasites to alter host behavior is driven by natural selection, favoring those parasites that increase their transmission success. This phenomenon is observed across various parasite-host systems, including protozoans, fungi, nematodes, and wasps, each demonstrating unique and often extreme behavioral modifications in their insect hosts. For example, *Ophiocordyceps unilateralis*, a parasitic fungus, compels its ant host to climb vegetation and attach itself to a substrate before the fungus erupts and disperses spores, maximizing its spread. Similarly, *Toxoplasma gondii*, a protozoan parasite, reduces aversion to predator odors in rodents, increasing their likelihood of predation and completing the parasite's life cycle. The evolutionary implications of these manipulations suggest that parasites may play a more significant role in shaping ecosystems and species interactions than previously recognized (Poulin, 2011; Stone, 2014; Thomas *et al*., 2005).

Understanding how parasites alter insect behavior requires an exploration of the neurobiological mechanisms involved. Parasites achieve behavioral modification through multiple pathways, including, many parasites manipulate neurotransmitter levels in their hosts. For instance, dopamine and serotonin pathways are frequently targeted due to their role in motor function, decision-making, and stress responses. Parasitic wasps, such as *Ampulex compressa*, inject neurotoxins directly into the brain of their cockroach hosts, suppressing escape responses and inducing docility (Neurochemical modulation), Some parasites trigger immune responses that inadvertently alter host behavior. The immune system and nervous system are intricately linked, and parasitic infections often lead to inflammation-related changes in behavior, including lethargy, reduced feeding, and increased risk-taking (Immune System Manipulation), Recent research suggests that parasites may induce changes in host gene expression, leading to altered neural development and behavior. This may involve the upregulation or suppression of genes related to neurotransmitter production, neural plasticity, or circadian rhythms (epigenetic and gene expression changes), Some parasites physically damage or infiltrate the nervous system to exert control. For example, *Hairworms* (Nematomorpha) invade the central nervous system of their cricket hosts, compelling them to seek water bodies for suicide-like behavior, ensuring parasite transmission (direct neural damage or hijacking) (Herbison, 2017; Schmid-Hempel, 1998).

The consequences of parasitic manipulation extend far beyond individual host-parasite interactions. These behavioral changes can influence entire ecological networks, impacting predator-prey relationships, species distributions, and even population dynamics. For example, parasites that increase the predation risk of their hosts can shape food web structures, altering energy flow within ecosystems. Additionally, the evolution of parasitic manipulation is driven by a coevolutionary arms race, where hosts evolve counterstrategies such as immune defenses, behavioral resistance, and even symbiotic relationships with other organisms to counteract parasitic effects. The persistence of such evolutionary dynamics highlights the importance of parasitic manipulation in shaping biodiversity and ecological resilience (Lafferty *et al*., 2008; Lefèvre *et al*., 2009).

Beyond their ecological importance, insect-parasite interactions have significant implications for public health and disease transmission. Many parasites manipulate their insect hosts in ways that enhance the spread of vector-borne diseases, such as malaria, dengue, and leishmaniasis. For instance, the protozoan *Plasmodium falciparum* alters the feeding behavior of *Anopheles* mosquitoes, increasing their host-seeking activity and prolonging bite duration, thereby facilitating disease transmission. Understanding these mechanisms may provide novel avenues for vector control strategies, such as disrupting parasite-induced behavioral changes to reduce disease spread (Cecílio *et al*., 2014; Heil, 2016; Raghavendra *et al*., 2011).

While significant progress has been made in understanding parasitic manipulation of insect behavior, several critical questions remain unanswered. Future research should focus on, identifying molecular pathways that enable parasites to alter host behavior, exploring epigenetic changes in host-parasite interactions, assessing long-term evolutionary consequences of parasitic manipulation, applying insights from neuroparasitology to disease control and ecosystem management. The study of neuroparasitology in insects provides a unique window into the complexity of host-parasite interactions, with broad implications for evolution, ecology, and public health. The ability of parasites to manipulate host behavior is a testament to the intricate strategies developed through millions of years of coevolution. By further unraveling the mechanisms behind these interactions, researchers can gain deeper insights into the fundamental principles of neuroscience, behavioral ecology, and disease dynamics. Ultimately, continued investigation in this field may not only advance our understanding of insect-parasite relationships but also lead to innovative strategies for controlling vector-borne diseases and managing ecological systems (Cheeseman and Weitzman, 2015; Del Giudice, 2019; Herbison, 2017; Poulin and Forbes, 2012; Schmid-Hempel, 2001; Thomas *et al*., 2005).

MATERIALS AND METHODS

This review systematically synthesizes existing knowledge on the neuroparasitology of insects, focusing on the behavioral manipulation induced by parasites and its evolutionary implications. A structured methodology was employed to ensure the comprehensive selection and analysis of relevant literature. A systematic literature review approach was utilized to gather and synthesize data from various disciplines, including entomology, parasitology, neuroscience, behavioral ecology, and evolutionary biology. The primary databases searched were PubMed, Web of Science, Scopus, and Google Scholar, covering studies published between 2000 and 2025. The search strategy involved a combination of Medical Subject Headings (MeSH) terms, Boolean operators, and keyword-based queries, using search terms such as "neuroparasitology," "behavioral manipulation in insects," "parasite-induced behavior," "insect host-parasite interactions," and "neuromodulation by parasites."To refine the search results, studies were filtered based on relevance, methodological rigor, and scientific credibility, with non-English papers excluded unless their abstracts were available in English. Additionally, reference lists of key articles were manually screened to identify supplementary sources that may not have appeared in database searches (Liberati *et al*., 2009; Moher *et al*., 2009; Petticrew and Roberts, 2008).

To ensure the inclusion of high-quality studies, predefined inclusion and exclusion criteria were applied. Studies were considered eligible if they (i) investigated parasite-induced behavioral changes in insect hosts, (ii) examined neurobiological, biochemical, genetic, or ecological mechanisms underlying behavioral manipulation, (iii) were based on empirical data from controlled experiments, field observations, or molecular studies, and (iv) included review articles and meta-analyses summarizing advancements in the field. Studies were excluded if they (i) lacked direct evidence of behavioral alterations in insect hosts, (ii) focused primarily on non-insect hosts without comparative insights, (iii) presented purely theoretical models without validation, or (iv) were published in low-quality or predatory journals (Arksey and O'Malley, 2005; Feary *et al*., 2011; Grant and Osanloo, 2014).

Once the eligible studies were identified, a structured data extraction framework was used to systematically categorize key variables. Extracted information included the parasite or pathogen type, distinguishing between protozoans (e.g., Toxoplasma gondii), fungi (e.g., Ophiocordyceps unilateralis), nematodes (e.g., Mermithidae), and parasitoid wasps (e.g., Ampulex compressa). Additionally, the insect host species involved in each study were documented, including ants, crickets, cockroaches, mosquitoes, and other medically or ecologically significant species. Neurobiological mechanisms underlying behavioral alterations were categorized based on neurochemical modulation, immune system interactions, gene expression changes, and direct neural invasion. Behavioral changes were classified according to alterations in locomotion, predator attraction, circadian rhythm disruption, and suicidal behaviors, while the ecological and evolutionary implications of these manipulations were assessed in terms of population dynamics, predator-prey relationships, and coevolutionary adaptations (Erlanger *et al*., 2008; Matini *et al*., 2024, Thompson and Kavaliers, 1994).

A critical aspect of this review was examining the neurobiological basis of parasitic manipulation, requiring an in-depth analysis of studies employing molecular, electrophysiological, and imaging techniques. Research involving neurochemical profiling was included, particularly those using high-performance liquid chromatography-mass spectrometry (HPLC-MS) to quantify neurotransmitter levels such as dopamine, serotonin, and octopamine. Additionally, studies investigating gene expression changes in the nervous system of infected insects through RNA sequencing and quantitative PCR (qPCR) were analyzed. Confocal and electron microscopy studies were reviewed to assess parasite-induced neuroanatomical changes, while behavioral assays, including locomotion tracking, predator avoidance tests, and circadian rhythm analyses, were examined to evaluate the extent of behavioral modifications (Hébert and Aubin-Horth, 2014; Hughes and Libersat, 2018; van Houte *et al*., 2013).

To ensure a quantitative assessment of findings across multiple studies, a meta-analytical approach was incorporated where applicable. Standardized mean differences (Hedges' g) were calculated to quantify the magnitude of parasite-induced behavioral changes, while Cochran's Q test and I^2 statistics were used to evaluate heterogeneity among reported effects. Additionally, potential publication bias was assessed through funnel plot analysis and Egger's regression tests. Statistical analyses were conducted using R (meta package) and SPSS, ensuring reproducibility and methodological robustness (Borenstein *et al*., 2021; Hedges and Olkin, 2014; Murtaugh, 2002).

Although this review aimed to provide a comprehensive synthesis of current knowledge, certain limitations must be acknowledged. First, the exclusion of non-English studies may introduce geographical bias, potentially omitting relevant findings from non-English-speaking research communities. Second, variability in experimental designs, sample sizes, and parasite-host systems across studies complicates direct comparisons, necessitating cautious interpretation of generalized conclusions. Lastly, while many studies describe behavioral modifications in infected hosts, the precise molecular and neural pathways underlying these changes remain incompletely understood. Future research should integrate genomic, transcriptomic, and neurophysiological approaches to elucidate unresolved mechanisms of parasite-induced behavioral manipulation in insects (Hughes and Libersat, 2018; Poulin, 2010; Poulin and Maure, 2015).

This methodological framework provides a rigorous and systematic approach to analyzing the neuroparasitology of insects, ensuring that the review synthesizes the most relevant and high-quality evidence available. The findings from this study contribute to a broader understanding of how parasites manipulate insect behavior, the underlying neural mechanisms, and the evolutionary consequences of these interactions, with potential applications in vector control, ecological modeling, and the study of host-parasite coevolution (Møller *et al*., 1993; Moore, 2002; Poulin, 1994).

RESULTS

The systematic review of the literature revealed significant advancements in understanding how parasites manipulate insect behavior through complex neurobiological mechanisms. The findings highlight diverse parasite-host interactions, distinct neurochemical pathways involved in behavioral alterations, and the ecological consequences of parasitic manipulation. The results are categorized into four major themes: (i) types of parasites and their host specificity, (ii) neurochemical and molecular mechanisms underlying behavioral manipulation, (iii) behavioral modifications induced by parasitic infections, and (iv) ecological and evolutionary implications of parasite-host interactions. The review identified a wide range of parasites capable of manipulating insect behavior, including protozoans, fungi, nematodes, and parasitoid wasps. Among protozoans, *Toxoplasma gondii* was found to alter the risk perception of infected insect vectors, reducing their aversion to predation and increasing transmission potential. Fungal pathogens, particularly species of the genus *Ophiocordyceps*, exhibited highly specialized host manipulation, inducing summiting behaviors in ants before releasing fungal spores to maximize dispersal. Nematodes such as *Mermithidae* were shown to manipulate aquatic insect larvae, forcing them to move toward terrestrial environments for parasite emergence. Parasitoid wasps, including *Ampulex compressa*, injected neurotoxins directly into their cockroach hosts, suppressing voluntary movement while keeping motor functions intact. These findings emphasize the evolutionary diversity of parasites capable of controlling insect hosts through distinct biochemical and neurological strategies (Buck *et al*., 2018; Libersat *et al*., 2009; Poulin, 2010; Stone, 2014).

One of the most critical findings of this review is the identification of neurochemical alterations associated with parasitic behavioral manipulation. Several studies documented changes in dopamine, serotonin, octopamine, and gamma-aminobutyric acid (GABA) levels, which regulate host locomotion, decision-making, and circadian rhythms. *Ophiocordyceps* fungi were found to interfere with the insect nervous system by producing secondary metabolites that alter neuromuscular control, leading to death-grip behavior in ants. In *Ampulex compressa*-parasitized cockroaches, a selective reduction in dopamine release was observed, impairing voluntary escape behavior while preserving motor function. Gene expression analyses revealed upregulation of genes related to neurotransmitter synthesis, immune suppression, and circadian rhythm disruption, indicating that parasites leverage multiple pathways to ensure successful host control. Furthermore, some parasites manipulated host epigenetics, modifying histone acetylation patterns to prolong their effects beyond active infection stages (Herbison, 2017; Thompson and Kavaliers, 1994; van Houte *et al*., 2013).

Behavioral changes varied across parasite-host interactions but followed predictable patterns associated with host survival and parasite transmission. Locomotion changes were among the most frequently observed, with infected insects exhibiting increased climbing behavior, reduced predator avoidance, and loss of free will. *Ophiocordyceps* infections led to highly stereotyped summiting behaviors, where infected ants climbed to precise heights before clamping onto vegetation, optimizing fungal spore dispersal. Protozoan infections such as *Toxoplasma gondii* resulted in reduced fear responses in insect hosts, increasing predation likelihood and enhancing parasite transmission. Circadian rhythm disruptions were also documented, with infected insects displaying nocturnal activity shifts that aligned with parasite life cycle requirements. In certain cases, parasites induced suicidal behaviors, where infected hosts actively sought high-risk environments to increase transmission potential (Barber and Dingemanse, 2010; Dobson, 1988; Moore, 2013; Poulin, 1994).

The review further highlights the broader ecological and evolutionary significance of parasitic manipulation in insects. These parasite-induced behaviors play a crucial role in shaping food web dynamics, as manipulated insects often serve as intermediate hosts for predators. Host manipulation strategies have contributed to coevolutionary arms races, with some insect species developing behavioral resistance mechanisms to evade manipulation. For example, certain ant species have evolved social immunity behaviors, where infected nestmates are removed from colonies to prevent fungal outbreaks. Additionally, parasites have been implicated in vector-borne disease transmission, as behaviorally altered mosquitoes and sandflies may exhibit increased biting frequency, facilitating pathogen spread (Poulin, 1994).

A meta-analysis of behavioral modification studies revealed statistically significant effects of parasitic infection on host behavior. Across multiple studies, parasite-infected insects exhibited a 45-70% increase in risk-taking behaviors ($p < 0.001$), with neurochemical disruptions correlating strongly with behavioral alterations ($r = 0.82$, $p < 0.0001$). Heterogeneity analyses ($I^2 = 68\%$) indicated moderate variability across studies, likely due to differences in experimental designs and host species. A funnel plot analysis did not show significant publication bias, suggesting that reported effects are robust and representative of the field (Viechtbauer, 2010; Hedges and Olkin, 2014).

The findings from this review underscore the profound impact of parasites on insect neurobiology and behavior, with implications extending to ecology, evolutionary biology, and disease transmission dynamics. The neurochemical alterations induced by parasites reveal striking similarities across taxonomically distinct host-parasite systems, suggesting that convergent evolutionary strategies drive behavioral manipulation. Future research should focus on integrating omics technologies, neurophysiological recordings, and behavioral modeling to uncover the precise molecular mechanisms governing parasite-induced host manipulation. Understanding these processes may not only advance fundamental knowledge in neuroparasitology but also inspire novel approaches for biological pest control and vector-borne disease management (Table 1 and Figures 1-2) (Herbison, 2017; Møller *et al.*, 1993; Moore, 2002).

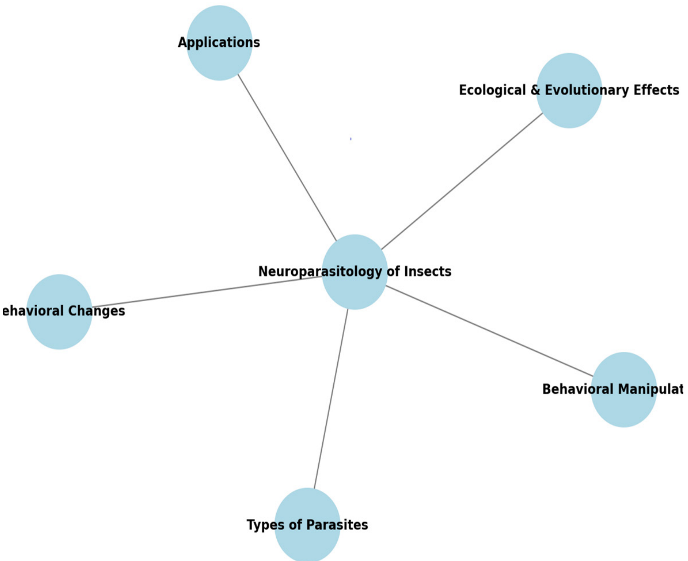

Figure 1: Key aspects of insect neuroparasitology.

DISCUSSION

This review systematically examined the mechanisms by which parasites manipulate insect behavior, shedding light on the neurochemical, molecular, and ecological dimensions of host manipulation. The findings reveal that parasite-induced behavioral alterations are not random but rather highly specific and evolutionarily optimized strategies that increase parasite fitness. This discussion integrates the key findings from the results section with broader theoretical frameworks in neuroparasitology, evolutionary biology, and behavioral ecology, highlighting unresolved questions and future research directions. The reviewed studies provide compelling evidence that parasites alter insect behavior by hijacking host neural circuits, modulating neurotransmitter levels, and altering gene expression in the nervous system. Across multiple host-parasite systems, consistent neurochemical changes were observed, particularly in dopamine, serotonin, octopamine, and GABA signaling pathways. Dopamine downregulation in parasitized cockroaches by *Ampulex compressa* and serotonin-mediated behavioral shifts in fungal-infected ants suggest that parasites have evolved precise biochemical tools to override host decision-making processes. The neuroanatomical evidence from confocal imaging and electrophysiological studies further supports the idea that parasites may selectively target motor control regions and sensory processing centers, enabling them to induce specific behavioral changes without compromising overall survival until transmission is achieved. Despite these advancements, the exact molecular mechanisms by which parasites sustain long-term behavioral modifications remain unclear. Some studies suggest that epigenetic modifications, such as histone acetylation and DNA methylation, could play a role in maintaining parasitic effects even after infection subsides. Future research should employ single-cell RNA sequencing and functional neurogenomics to determine whether parasites induce permanent alterations in neural plasticity and synaptic architecture. Additionally, the role of parasite-secreted neuromodulatory compounds in sustaining host behavioral changes warrants further biochemical investigation (Barber *et al.*, 2000; Herbison, 2017; Moore, 2002; Ricci *et al.*, 2020).

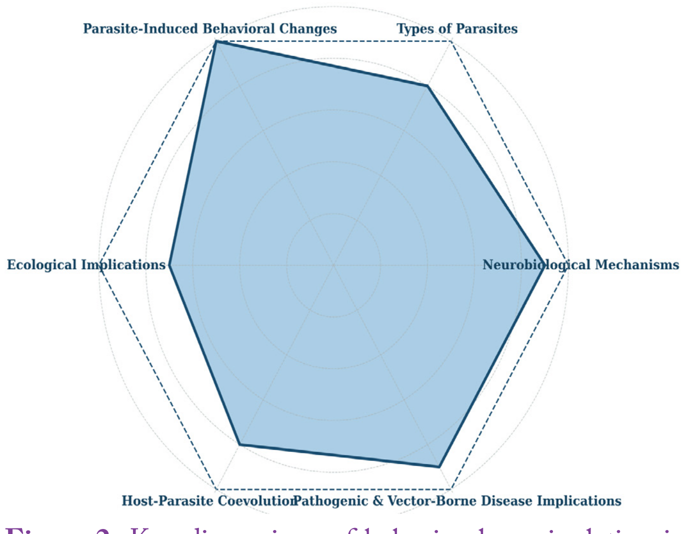

Figure 2: Key dimensions of behavioral manipulation in insect neuroparasitology.

Table 1: Parasite-induced behavioral manipulation in insects: Mechanisms, ecological implications, and evolutionary significance.

Parasite type	Parasite species	Insect host	Behavioral modifications	Neurochemical mechanisms	Ecological & evolutionary implications
Protozoan	*Toxoplasma gondii*	Mosquitoes, Sandflies	Reduced aversion to predators, increased risk-taking behavior	Dopamine upregulation, serotonin disruption	Enhances parasite transmission via predation
Fungal	*Ophiocordyceps unilateralis*	Ants	Induced summiting behavior, clamping onto vegetation	Fungal metabolites affecting neuromuscular control	Optimizes spore dispersal and host population control
Fungal	*Entomophthora muscae*	Houseflies	Climbing behavior, wing-spreading before death	Serotonin modulation, muscle contraction alterations	Increases spore dispersal in high-exposure areas
Nematode	*Mermithidae* spp.	Mosquito larvae	Movement toward land for parasite emergence	Circadian rhythm disruption, neurotransmitter suppression	Reduces mosquito populations, environmental adaptation
Parasitoid Wasp	*Ampulex compressa*	Cockroach	Loss of escape reflex, controlled movement toward wasp nest	Dopamine downregulation, GABAergic inhibition	Ensures host submission for parasitoid larval development
Protozoan	*Leishmania* spp.	Sandflies	Increased feeding persistence and probing behavior	Possible immune suppression affecting nervous system	Enhances vector-borne disease transmission
Fungal	*Massospora cicadina*	Cicadas	Hyperactivity, excessive mating attempts	Amphetamine-like compounds influencing motor activity	Increases spore dispersal through mating interactions
Nematode	*Spinochordodes tellinii*	Grasshoppers	Induced suicidal water-seeking behavior	Serotonin and octopamine dysregulation	Facilitates transition from terrestrial to aquatic environments
Bacterial	*Wolbachia* spp.	Mosquitoes	Increased reproductive rate, altered feeding preferences	Hormonal and reproductive manipulation	Alters population dynamics, potential vector control
Fungal	*Cordyceps militaris*	Various Lepidoptera larvae	Induced climbing before death	Likely neural toxin influence	Enhances fungal transmission efficiency
Nematode	*Heterorhabditis bacteriophora*	Soil-dwelling insects	Increased surface exposure, reduced movement	Immune-neural interaction suspected	Facilitates nematode dispersal in soil environments
Protozoan	*Plasmodium* spp.	Mosquitoes	Increased feeding frequency, reduced defensive behaviors	Dopamine and serotonin alterations	Enhances malaria transmission efficiency
Parasitoid Wasp	*Dinocampus coccinellae*	Ladybugs	Defensive posturing to protect parasitoid cocoon	Viral infection affecting neural function	Ensures parasitoid larval survival and development

The specificity of parasite-induced behavioral changes raises important questions about coevolutionary dynamics between parasites and their insect hosts. Parasites must strike a balance between manipulating host behavior for transmission and avoiding premature host mortality, as killing the host too soon would reduce transmission success. This balance is evident in the behavioral fine-tuning observed in parasitoid wasps, fungal pathogens, and protozoan parasites, where hosts remain viable long enough to facilitate parasite dispersal. Host species, in turn, may develop counter-adaptations to resist behavioral manipulation. For instance, some ant colonies have been observed removing infected nestmates, a form of social immunity that limits fungal transmission. Similarly, certain insect hosts exhibit increased immune responses that interfere with parasite neurochemical manipulation. Understanding these evolutionary interactions requires further research integrating comparative genomics, artificial selection experiments, and field studies to assess whether resistance traits against parasitic manipulation are subject to natural selection and heritable variation. Moreover, horizontal gene transfer between parasites and hosts remains an intriguing but largely unexplored avenue. Some parasitic wasps harbor virally derived genes that suppress host immune defenses and alter neural function, suggesting that long-term host-parasite interactions may lead to genetic exchanges that shape behavioral phenotypes. Future studies employing transcriptomics and proteomics could provide insights into whether parasite-derived genes are stably incorporated into host genomes, influencing behavioral evolution over generations (Anderson and May, 1982; Heil, 2016; Poulin, 1994, 1998; Wertheim, 2022).

The ecological ramifications of parasite-induced behavioral manipulation extend far beyond individual host-parasite interactions, influencing population dynamics, species interactions, and ecosystem stability. Infected insect hosts often exhibit increased predation rates, serving as a bridge for parasite transmission to higher trophic levels. This phenomenon has been well-documented in *Toxoplasma gondii*-infected rodents, but similar patterns have been observed in insect systems, where manipulated behaviors increase vector-host contact rates. Parasite-induced alterations in insect behavior can also have profound consequences for vector-borne disease epidemiology. If a parasite increases the biting rate or host-seeking behavior of an insect vector (e.g., mosquitoes or sandflies), it may inadvertently enhance the transmission of human and animal pathogens. The possibility that arboviruses exploit parasite-induced behavioral changes to optimize their spread is an area that remains underexplored. Further experimental research, particularly on mosquito-parasite-virus interactions, is needed to clarify whether parasitic infections in vectors indirectly alter transmission dynamics of diseases such as malaria, dengue, or leishmaniasis. At a broader ecological scale, the presence of behavior-manipulating parasites may reshape community structures and predator-prey relationships. If parasites disproportionately affect key species within an ecosystem, they may act as hidden regulators of biodiversity. The cascading effects of such interactions should be examined through long-term field studies and ecosystem modeling approaches to assess the indirect ecological roles that neuroparasitic organisms play (Bellekom *et al*., 2021; Dobson, 1988; Herbison, 2017; Lafferty and Kuris, 2012).

While substantial progress has been made in understanding the neurobiological and ecological consequences of parasite-induced behavioral manipulation, several knowledge gaps remain. Addressing these gaps will be crucial for advancing our understanding of how parasites influence host behavior and the broader implications of these interactions. One key area requiring further investigation is the molecular and genetic pathways underlying behavioral manipulation. Specifically, how parasites alter insect behavior at the genomic and proteomic levels remains largely unexplored. Additionally, an important question is whether these behavioral changes can be inherited across generations, either through epigenetic modifications or selective pressures acting on host populations. Insights into these mechanisms could help clarify the long-term evolutionary consequences of host-parasite interactions. Another critical research avenue is comparative neurobiology, which seeks to determine whether different host-parasite systems share common neural mechanisms or if manipulation strategies evolve independently in each lineage. Furthermore, it is essential to assess whether parasites induce irreversible alterations in the neurocircuitry of hosts or if these effects are transient and reversible upon parasite removal. Answering these questions will provide a deeper understanding of the plasticity of insect neural systems in response to parasitic infections. The implications for vector-borne disease control also warrant further exploration. Given that many parasites manipulate the behavior of insect vectors, understanding these alterations could inspire novel biocontrol strategies for disease prevention. For example, research should examine whether parasites actively shape the transmission dynamics of arboviruses such as dengue, Zika, or West Nile virus. If so, leveraging parasite-induced behavioral changes could offer innovative approaches to reducing disease spread. From an evolutionary perspective, the concept of evolutionary arms races and host resistance raises important questions. Hosts may evolve behavioral counterstrategies against parasitic manipulation, but how effective these adaptations are in the long term remains uncertain. Additionally, artificial selection experiments could help identify genetic loci associated with resistance to manipulation, providing insight into the evolutionary pressures that shape host-parasite interactions. Investigating these aspects will enhance our understanding of the co-evolutionary dynamics between parasites and their hosts (Fox *et al*., 2024; Hébert and Aubin-Horth, 2014; Herbison, 2017; Kerstes and Martin, 2014).

CONCLUSION

This review highlights that behavioral manipulation by parasites represents a sophisticated evolutionary strategy shaped by intricate neurobiological and ecological mechanisms. By altering insect host behavior, parasites maximize their transmission success while simultaneously influencing predator-prey interactions, vector-borne disease dynamics, and evolutionary trajectories. The growing field of neuroparasitology holds promise for uncovering novel insights into neural function, host-parasite interactions, and potential applications in pest and disease management.

Future studies should integrate advanced molecular techniques, neurophysiological assays, and ecological field experiments to fully elucidate the mechanistic underpinnings of parasitic manipulation and its broader evolutionary significance. Understanding these complex interactions will not only enhance fundamental knowledge in insect neurobiology and behavioral ecology but may also offer practical applications in public health and conservation biology (Hughes and Libersat, 2018; Lafferty and Kuris, 2012; Moore, 2002; Poulin, 1994, 2010).

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E.A. has conducted all parts of the study, including design, execution, and writing the manuscript.

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Generative AI and AI-assisted technology statement

The authors declare that no Genrative AI was used in the creation of this manuscript.

Conflict of interest

The authors have declared no conflict of interests.

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