Neuroethology of Corpse-Directed Behaviors in Bees

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Acknowledgements

This work is funded by the University of Washington Department of Psychology, Department of Biology, and the Royalty Research Fund. We would like to sincerely thank Nastacia Goodwin, Sama Ahmed, Laura Quinche, and Andrea Durant for their thoughtful comments on our manuscript.

Abstract

Across taxa, social animals inevitably encounter dying or dead conspecifics and respond in patterned ways, yet the mechanisms underlying these behaviors remain understudied. Bees offer a powerful comparative system for exploring the neuroethology of corpse-directed behaviors. Across the bee phylogeny, sociality has been gained and lost multiple times, resulting in species that range from solitary to highly eusocial. As nesting became increasingly communal, bees evolved diverse corpse-directed behaviors including avoidance, transport and removal, cannibalism, and burial. These behaviors are thought to mitigate pathogen and predation risks, influence resource allocation, and shape colony functioning. In this review, we synthesize findings on corpse-directed behaviors across bee species and social systems. We examine the emerging neurobiological, sensory, endocrine, molecular, and social mechanisms that support corpse detection and behavioral specialization. Lastly, we highlight key gaps in existing research and priorities for future work on the neurobiological and evolutionary foundations of corpse-directed behaviors.

Introduction

Group-living animals, from social insects to mammals, are among the most evolutionarily successful organisms on Earth, exhibiting remarkable ecological dominance, cognitive complexity, and long lifespans [1–3]. Social behaviors are critical for the health and functioning of animal and human societies [4–8]. Yet nearly all mechanistic studies of social behaviors focus on interactions between living conspecifics. In reality, social animals regularly encounter dying or dead conspecifics, and respond in strikingly patterned ways [9,10]. For example, humans and mice readily engage in prosocial physical contact with unconscious individuals, promoting recovery from unresponsiveness [11,12]. Many mammals, including non-human primates, elephants, and aquatic mammals, transport, groom, and protect deceased infants [9,13–17]. Corvids aggregate around deceased conspecifics and perform alarm calls to share information about potential threats [18–20]. Rodents and termites bury aged corpses, which reduces pathogen spread and predator threats [21,22]. Thus, interacting with the dead is a fundamental component of social living.

Despite the prevalence of corpse-directed behaviors across taxa, the mechanisms by which animals detect and respond to dead conspecifics remain poorly understood. Bees (Clade: Apoidea) are an ideal system to address this gap. Across bee lineages, multiple independent gains and losses of sociality have resulted in species that span the full spectrum from solitary to highly eusocial (Figure 1A) [23,24]. As group living evolved, social insects developed strategies for active corpse management, otherwise known as undertaking behaviors [22,25–30]. Bees exhibit diverse undertaking behaviors, including necrophobia (corpse avoidance), necrophoresis (corpse transport and removal), cannibalism, and burial [26,28,29,31–34]. These behaviors enhance colony fitness by minimizing pathogen spread, reducing potential predator threats, and recycling nutrients [22,27,35,36]. In this review, we first summarize corpse-directed behaviors across bee lineages and modes of sociality, then discuss the underlying mechanisms, including chemosensation, hormonal profiles, gut microbiota, gene expression, and behavioral specialization.

Corpse-directed behavior across bees

Honey bees

Honey bees are advanced eusocial insects characterized by age-based division of labor and sophisticated social communication [37]. Honey bee colonies comprise nestmates at multiple life stages [38]. Workers exhibit undertaking behaviors toward both dead adults and dead brood containing larvae or pupae [28,39–41].

Honey bee behavioral responses to dead adult nestmates have been most well-studied in the western honey bee (*Apis mellifera*). Workers display a wide range of responses to adult corpses, including antennal and proboscis contact, grasping, pulling, and removal from the nest, which can involve multiple workers transporting the corpse around the nest (Figure 1B) [28]. Interestingly, removal follows an indirect path to the nest entrance, which is not expected if the primary function of undertaking is to minimize pathogen spread [28].

Honey bee responses to dead brood are widely regarded as hygienic behaviors [42]. *A. mellifera* and *Apis cerana* workers uncap brood cells to remove dead or diseased larvae and pupae from the nest (Figure 1B) [40,41,43,44]. *A. cerana* removes dead brood faster than *A. mellifera*, though both reach the same percentage of removal after 48 hours [43,45,46]. In some cases, *A. mellifera* partially cannibalizes *Varroa* mite-infected pupae [32]. Beyond cavity-nesting species, migratory, open-air nesting honey bees also show brood undertaking behaviors [47,48]. The dwarf honey bee, *Apis florea*, removes dead brood from both sealed and unsealed cells [48]. The giant honey bees, *Apis dorsata* and *Apis laboriosa*, only remove dead brood from already-damaged cells, leaving dead brood in intact cells alone [47]. This distinction is likely associated with their different migratory patterns: *A. florea* migrates short distances based on resource availability, making the prompt removal of any dead brood beneficial, while *A. dorsata* migrate seasonally for long distances, making it adaptive to leave sealed dead brood behind [49,50].

Research on honey bee undertaking has established key observational and experimental approaches applicable to other bee species. Both adult and brood removal demonstrate colonies' rapid response to parasite and disease threats. Future studies should investigate adult removal across species and quantify the full behavioral sequence of brood removal to enable direct comparisons and elucidate how complex social behaviors are organized and regulated.

Bumblebees

Compared to honey bees, bumblebees are annually eusocial and exhibit weak task specialization [51]. In the common eastern bumblebee (*Bombus impatiens*) and the buff-tailed bumblebee (*Bombus terrestris*), workers make antennal contact, pick up, and drag both larval and adult corpses (Figure 1C) [26,29]. Undertakers pick up larvae quickly but spend more time antennating and biting adult corpses [26]. A higher percentage of larvae are successfully removed than adults, which may reflect physical constraints of corpse type: larvae can be removed by flight or dragging, while adults can only be dragged out of the nest [26]. These differences lead to the question of how bumblebees respond to dead pupae, which is completely unknown. Pupae, being the intermediate life stage, may carry different values to the colony and may result in different undertaking strategies.

Findings from bumblebees demonstrate that even species with annual colonies and limited task specialization exhibit adaptive undertaking strategies. Compared to honey bees, bumblebees have lower rates of removing corpses from the nest and exhibit greater behavioral variability, including occasional burial and midden deposition [26,28,29]. The behavioral differences may reflect reduced pressure for long-term nest hygiene in their annual colonies. However, with few detailed studies to date, key aspects, such as the spatial trajectories of undertakers and corpses, remain unknown.

Quantifying these features can reveal how nest structure, colony organization, and social complexity shape removal strategies.

Other bees

In other bee species, studies of corpse-directed behavior differ in scope and detail. Experimental protocols vary greatly, and for many species, corpse-directed behaviors are described only by brief observations, making cross-species comparisons difficult. However, existing data reveal a broad pattern consistent with kin selection: solitary species manage their own dead offspring, whereas social species gain indirect fitness by managing the corpses of closely related nestmates.

Solitary but gregarious species manage dead offspring and tolerate dead conspecifics. The alkali bee *Nomia melanderi*, which nests solitarily in dense aggregations, uncaps and fills diseased or dead brood cells with compacted soil, which resembles burial (Figure 1E) [33,34]. When nest sharing occurs, dead female conspecifics are either buried within or outside of the nest [52]. The red mason bee *Osmia bicornis*, another solitary species, tolerates conspecific corpses and continues to nest nearby [53].

Semi-social and facultatively eusocial bees also manage dead offspring. The allodapine bee *Braunsapis foveata* pushes dead larvae and pupae out of the nest with its head or abdomen, similar to nest waste removal (Figure 1D), and the sweat bee *Megalopta genalis* pulls dead larvae out of brood cells and removes them from the nest [54,55]. These behaviors suggest that brood removal may have emerged from general nest-cleaning strategies [54].

Other eusocial species show undertaking behaviors similar to honey bees and bumblebees. Annually eusocial sweat bees (*Lasioglossum lineare*, *Lasioglossum malachurum*) remove or bury dead brood [56,57]. Advanced eusocial stingless bees (*Melipona spp.*) uncap and remove dead brood [58–60]. Across eusocial bees, corpse removal is consistent, but burial within the nest only occurs in some species, which may reflect ecological constraints, such as the availability of movable substrate in the nest.

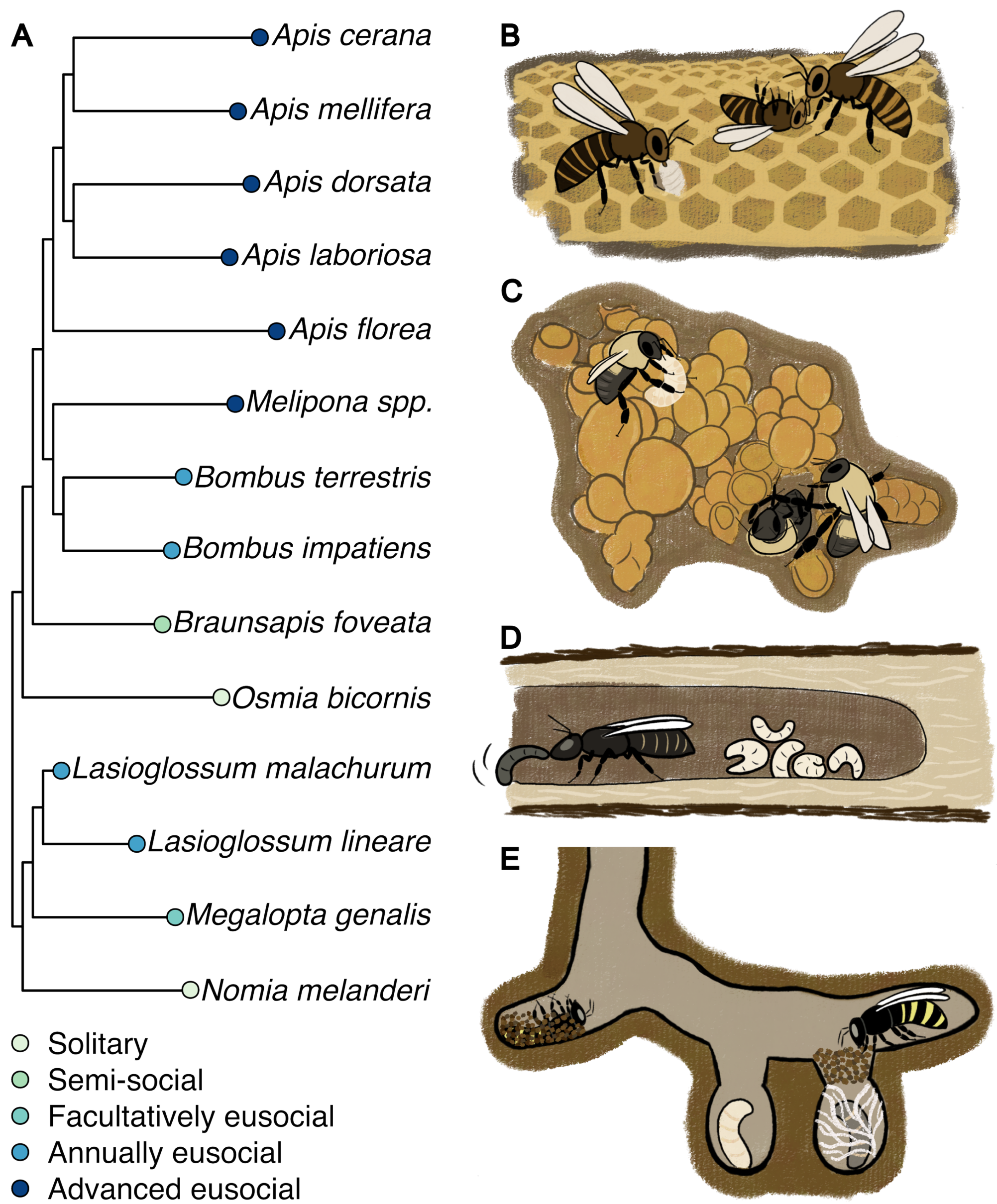

Figure 1. Diverse bee lineages exhibit a wide range of corpse-directed behaviors. **A**. Phylogeny of bee lineages with documented corpse-directed behaviors discussed in this paper [24]. Colors represent degree of sociality. **B**. Honey bees (*Apis spp.*) remove dead larvae, pupae, and adult corpses [28,40,41]. **C.** Bumblebees (*Bombus spp.*) remove dead larvae and adult corpses [26,29]. **D**. Allodapine bee (*Braunsapis foveata*) pushes dead larvae out of the nest [54]. **E**. Alkali bee (*Nomia melanderi*) buries dead larvae in the brood cell and adult corpses at the end of a burrow [34].

Neurobiological mechanisms and social influences

Across bee species, corpse-directed behaviors vary in form and complexity, yet they all mitigate risks associated with death. Their prevalence across species raises important questions about the sensory and neural adaptations that enable prompt detection and response to death. Here, we explore emerging insights on how sensory systems, ecological context, and social organization may contribute to corpse-directed behaviors. Although most of the known mechanisms are from the western honey bee (*A. mellifera*), these results provide a framework for what may be possible and shared across bees.

Chemosensation

Many bee species nest in dark cavities or subterranean environments, making chemical signaling the primary mode of communication [52,61]. Chemical cues are critical for the initiation of undertaking behaviors [22,28,62–64]. Two main classes of death cues have been identified in honey bees: fatty acids that are highly conserved across taxa and volatiles that are species-specific [22,62,65–68]. While other death cues may also be involved, existing research has focused on how oleic acid, a fatty acid, and the volatile pheromone β-ocimene impact removal of brood and adult corpses.

Dead honey bee (*A. mellifera*) brood release both oleic acid and β-ocimene, and application of either or both compounds to healthy brood triggers brood rejection and removal [62,68]. Interestingly, β-ocimene is a brood pheromone associated with larval food-begging, initiation of foraging, and inhibition of worker reproduction, but dead brood release significantly higher amounts of β-ocimene than live brood [68–72]. Thus, β-ocimene may function broadly as an urgency signal, recruiting workers to care for brood at low concentrations and prompting the disposal of dead brood at high concentrations, while oleic acid acts as a death cue in parallel. Sharing chemical cues and sensory pathways across contexts may be efficient for integrating different in-nest behaviors.

In contrast, death cues from adult honey bee corpses remain largely unknown. β-ocimene is not present on live workers, but whether it is released upon death is unknown [73]. Oleic acid is a more plausible death cue from adults. It is a highly conserved death cue across insects and elicits removal in ants and burial in termites, even when applied to inanimate objects [22,25,30,65,66,74]. Oleic acid alone does not elicit adult corpse removal in *A. cerana*, but the Nasonov gland extract, which contains oleic acid and other fatty acids, does [63]. This may be because oleic acid is not exclusively a death cue in honey bees, as it also exists in body tissues and pollen [75–77]. Oleic acid may contribute to adult death signaling, and its capacity to induce undertaking behaviors could depend on its concentration, the presence of other chemicals, the life stage of the corpse, and species-specific sensory tuning.

Workers likely detect death cues through multiple sensory modalities. In *A. mellifera*, electroantennogram recordings show that both β-ocimene and a blend of β-ocimene and oleic acid elicit significant antennal depolarization, while oleic acid alone does not (Figure 2A) [62]. Therefore, β-ocimene is likely an olfactory signal, whereas oleic acid may be detected through a combination of olfaction and contact-based chemoreception, though its exact sensory pathway is unclear. Beyond antennal responses, undertakers are molecularly tuned to death cues. In *A. mellifera*, brood-removing undertakers show upregulation of two antennal odorant binding proteins (OBPs) with high affinity to oleic acid and β-ocimene [62]. In *A. cerana*, highly hygienic colonies show upregulation of several OBPs [78]. These findings suggest that undertakers experience increased sensitivity to death cues, along with other physiological specializations that we explore below.

Hormonal profiles and gut microbiota

Honey bee undertakers differ from other workers in their hormonal profiles and gut microbiota, potentially supporting their specialization. Under age-based division of labor, workers transition from nursing to foraging as they age, and a subset of middle-aged bees start undertaking while their age-matched peers remain in nursing roles [64]. Adult corpse undertakers show higher levels of juvenile hormone in their corpora allata-corpora cardiaca complex than in-nest workers, comparable to those of foragers [79]. Juvenile hormone is associated with division of labor, and elevated levels may facilitate the shift to undertaking [80]. Brood undertakers show strong octopamine activity in neurons in the deutocerebrum [81]. Octopamine treatment in non-undertakers enhances antennal sensitivity to diseased brood odors, demonstrating a modulatory effect on sensory tuning [81]. Moreover, brood undertakers have distinct gut microbiota, with greater microbial diversity and higher abundance of immunity-associated bacterial species than non-undertakers (Figure 2C) [82]. These physiological differences may predispose some workers to take on undertaking tasks while mitigating risks of contacting corpses, raising the question of whether these traits evolved prior to the emergence of undertaking or developed through exposure to corpses.

Gene expression

Honey bees' specialization in undertaking is accompanied by differences in gene expression [83]. Transcriptomic data show that adult corpse undertakers' brain gene expression more closely resembles that of guard bees than that of nurses or foragers (Figure 2B) [84]. The *foraging (for)* gene, linked to distance traveled and activities outside of the nest, is expressed at higher levels in undertakers and foragers and lower levels in in-nest workers [85,86]. These findings suggest that undertaking shares molecular pathways with other highly active and high-risk tasks such as guarding or foraging. Future comparative work across species will be essential for identifying evolutionary conservation of molecular mechanisms underlying undertaking.

Behavioral specialization

While physiological and molecular mechanisms may influence which workers are more likely to engage in undertaking, the expression of social behaviors is strongly shaped by social context. Interactions with nestmates, task allocation, and other colony-level cues can determine when and how undertaking is performed.

Colony life history shapes how undertaking is distributed among workers. Honey bees exhibit highly structured division of labor in their perennial colonies, with only 1-2% of workers participating in undertaking at a time and up to 10% ever participating [28,38,87]. Bumblebees are more behaviorally flexible in their annual colonies, with 31.1% of workers participating in undertaking [29,51]. Among undertakers, different behavioral phenotypes exist, some individuals repeatedly perform undertaking while others do so only once [29,39]. Repeat undertakers are more successful at completing corpse removals [29,39].

Spatial patterns provide additional evidence that undertaking is a specialized task. In honey bees, adult corpse undertakers preferentially occupy the lower hive near the entrance, similar to guard bees [64]. The spatial distribution of brood undertakers is currently unknown, though they do not differ in colony integration or centrality from other bees [88]. In bumblebees, foragers and nurses show different spatial distributions while in the nest, but the spatial preferences of undertakers have not yet been documented [89]. Understanding where undertakers operate in the nest could reveal overlaps with other colony tasks and provide insights into task allocation.

Morphological differences may also contribute to undertaking specialization, particularly in bumblebees. Bumblebee workers' body size varies considerably and is linked to their division of labor [89,90]. In *B. impatiens*, adult corpse undertakers are larger than non-undertakers [29]. In *B. terrestris*, undertakers and non-undertakers do not differ in body size, but larval undertakers are larger than adult corpse undertakers [26]. Interestingly, depleting large workers did not impair the colony's undertaking performance [91]. Therefore, body size may influence the likelihood of undertaking, but behavioral flexibility compensates for changing availability of workers. Future work on biomechanics and muscle physiology of corpse handling could help us understand the demands of performing this task.

Together, these findings demonstrate that undertaking is a specialized yet flexible task performed by a subset of workers. Honey bee workers that specialize in brood removal are also more likely to remove adult corpses from the nest, but these two behaviors have largely been studied in isolation [92]. Future work integrating both forms of undertaking using consistent assays will be crucial for understanding specialization and flexibility in undertaking subgroups.

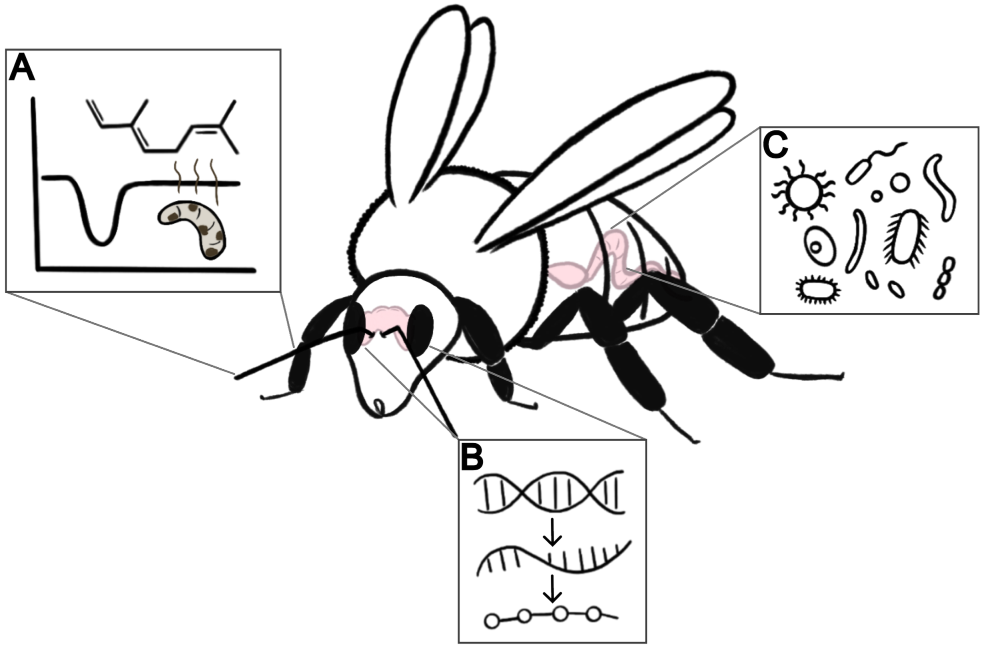

Figure 2. Sensory, molecular, and physiological mechanisms underlying corpse-directed behaviors. **A**. The antenna senses chemical signals (e.g. β-ocimene) from a corpse and results in depolarization [62]. **B**. Differential brain gene expressions distinguish undertakers from in-nest workers [84–86]. **C**. Undertakers exhibit distinct gut microbiota composition with greater microbial diversity and higher abundance of immunity-associated bacteria [82].

Conclusion

Corpse-directed behaviors are a fundamental component of social living, and the diverse phenotypes across bee lineages provide excellent opportunities for comparative analyses. Corpse-directed behaviors are deeply implicated in the traits that characterize eusociality: 1) they are a specialized task within division of labor; 2) removal of diseased and dead brood directly supports cooperative brood care; 3) removal of dead nestmates maintains the health of a colony with overlapping generations. Beyond their implications on social evolution, understanding corpse-directed behaviors also sheds light on how animals respond adaptively across dynamic, complex social environments. Future mechanistic experiments to further elucidate behaviors, sensory pathways, and neural circuits in other bee species will inform us how evolution has shaped the neurobiological underpinnings of this critical behavior.

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