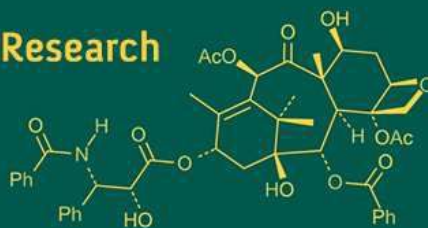
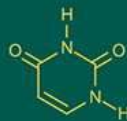


International Journal of Advanced Biochemistry Research



ISSN Print: 2617-4693
ISSN Online: 2617-4707
IJABR 2024; SP-8(8): 1315-1325
www.biochemjournal.com
Received: 09-06-2024
Accepted: 14-07-2024

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Corpse management in eusocial insects

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DOI: <https://doi.org/10.33545/26174693.2024.v8.i8Sq.2050>

Abstract

Arthropods that live in communities with other members of their own species are known as social insects. Because they live in large groups, eusocial insects regularly lose members of their colonies. As part of their cooperative corpse management to keep the nest clean, they display physiological and behavioral reactions to the dead that support food reallocation, disease resistance, and colony protection. We review mechanisms of death recognition, convergent and divergent behavioral responses toward dead individuals, and undertaking task allocation from the perspective of division of labor, focusing on three groups of eusocial insects (bees, ants, and termites) in two phylogenetically distant orders (Hymenoptera and Isoptera). In the hemimetabolous isopterans and holometabolous hymenopterans, separately, distinctly different solutions (such as corpse removal, burial, and cannibalism) have evolved toward the same problem of corpse management. Genetic studies and gene expression analysis related to social immune systems give a better knowledge of behavioural and physiological disease defense in insects which could be considered a novel access to biological pest control. This article provides a comprehensive understanding of corpse management in eusocial insects.

Keywords: Corpse management, eusocial insects, own

Introduction

When a species' individuals interact, it's considered sociable; eusociality is defined by cooperative brood care, reproductive division of labor, and overlapping generation. Presocial insects are separated into subsocial and parasocial groups based on the absence of these three characteristics. Parent-child interactions are referred to as subsociality, whereas interactions between members of the same generation are called parasociality. Other traits that can be seen include building communal nests, being kind, swarming, defending their territory, managing corpses, making group decisions, and communicating within their group. With anatomical disparities found in mature eusocial species, the division of labor that results creates discrete behavioral groupings known as castes. Eusociality is more commonly seen in the phylum Arthropoda. The remarkable eusociality of leafcutter ants (*Atta*) is demonstrated by their ability to grow fungus from broken leaves. Only a small number of species in the orders Hemiptera and Coleoptera have eusocial tendencies, whereas the whole arthropod order Isoptera is eusocial. The Formicidae family of ants, which belongs to the Hymenoptera order, is known to exhibit eusocial behavior. Eusocial behavior is also exhibited by wasps (Vespidae family) and bees (Apidae family).

Apart from humans, social insects also face death in the colony due to biotic and abiotic factors and they have complex behavioral adaptations for managing their dead members within the colony. Chemical cues released by the corpse are sensed through antennae by live members of the colony for undertaking behavior. Different strategies have evolved in hymenopterans and isopterans, such as necrophoresis, burial, avoidance, altruism, and cannibalism. The discussion examines the costs and advantages that are involved. When referring to corpse management, the phrase "undertaking behavior" refers to the natural behavior of social insects. This thorough analysis addresses many important topics, including the causes of death, the biological and pharmacological underpinnings of social reactions, undertaking behavior, adaptations in various eusocial communities, and corpse management techniques. In addition to introducing the idea of behavioral plasticity, this review also provides possible directions for further research in various strategies, Chemical Communication, Genetic and Epigenetic Factors, Adaptation to Environmental Conditions, Impact of Colony Size and Structure, Evolutionary Perspectives, Microbial Involvement, Integrating Behavioral and Molecular Approaches, Interaction with Pathogens and Comparative Studies.

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Factors causing death within the colony

Insect mortality is a result of multiple causes working together naturally. A basic process, aging becomes the leading cause of death for reproductive individuals, leading to the collapse of entire colonies in many species. On the other hand, laborers and soldiers, face death from a variety of biotic and abiotic causes other than aging. As 'somatic' support in superorganisms (Wilson and Sober, 1989) [91], workers often face mortality due to their shortened life spans (Jemielity *et al.*, 2005) [26] and dangerous work such as foraging, colony defense, and sanitation (Porter and Jorgensen, 1981) [49]. Because social insects live in groups and have little genetic variety, diseases offer a serious threat to their colonies, making them vulnerable to pathogenic attacks (Schmid-Hempel, 1995; Cremer *et al.*, 2007; Meunier, 2015; Cremer *et al.*, 2017) [68, 10, 35, 11]. Numerous infections and parasites, including helminths, bacteria, viruses, fungi, and protozoa, can infect colony members and spread throughout the colony, gives disastrous results. Developments in social immunity provide light on underlying processes and coping strategies for infected dead and terminally ill members of the colony. Additionally, workers and soldiers frequently lose their lives defending against rivals and predators (Preisser *et al.*, 2005; Tian *et al.*, 2017) [51, 80]. Extreme weather conditions (freezing and heat), problems with water availability (desiccation and drowning), inadequate food (starvation), and physical nest damage from vertebrates or environmental factors are examples of abiotic variables that contribute to mortality. Research on colony behavioral reactions to insecticide-killed individuals has been prompted by the widespread use of synthetic pesticides for the management of social insects that hold economic significance (Su *et al.*, 1982) [74].

While most insects die from the previously listed causes, eusocial species only die from two exclusive causes: self-destructive behavior used for colony defense (Shorter and Rueppell, 2012) [71] and policing behavior used to settle disputes within the colony (Ratnieks *et al.*, 2006) [56]. Examples of selfless devastation include the self-destructive sting of honeybee workers to protect themselves from vertebrate intruders (Hermann, 1971) [22]; elderly termite workers from *Neocapritermes taracua* releasing defensive secretions by rupturing their bodies (Sobotnik J *et al.* 2012) [72]; and Brazilian ant workers from *Forelius pusillus* who regularly close their nest from the outside to prevent nocturnal predators (Tofilski *et al.*, 2008) [81], and sick and dying workers of the ant *Temnothorax unifasciatus* leaving the nest before death to prevent infection of other colony members (Heinze and Walter, 2010) [21]. In social insects, policing behavior takes many forms. These include eating worker-laid eggs, immobilization, biting, and stinging, which can ultimately result in the death of focal individuals (Monnin *et al.*, 2002; Teseo *et al.*, 2013; Loope *et al.*, 2015) [38, 79, 30]. Policing behavior involves coercive actions that reduce direct reproduction by other individuals.

Death cues

The ability of colony members to identify the dead is essential for the prompt and effective handling of deceased individuals within the colony. Chemical cues are commonly credited with facilitating recognition; two primary theories have been put forth to support this idea: the "fatty acid death cue" (Wilson *et al.*, 1958) [93] and the "chemical vital sign" (Choe *et al.*, 2009) [6]. Death cues are post-mortem

alterations in surface chemicals that impact the behavior of living insects. These chemicals are classified as "chemicals produced before death" or "decomposition by-products" depending on when they occur. For example, in living workers of the Argentine ant *Linepithema humile*, dolichodial and iridomyrmecin are actively generated, concealing impulses for corpse clearance. According to Choe *et al.* (2009) [6], workers can quickly identify and remove bodies because of the compounds' rapid drop after death. *Reticulitermes flavipes*, an eastern subterranean termite, releases 3-octonal and 3-octanone volatiles in tandem with death. This helps nest-mates locate and identify dead bodies in time for disposal (Sun *et al.*, 2017) [75]. The honeybee *Apis mellifera* releases b-ocimene, a volatile brood pheromone linked to food begging, even after they die, which attracts workers to remove dead larvae (McAfee *et al.*, 2018) [34].

Decomposition by-products, the second group, includes compounds created after death. Because of their low volatilities, oleic and linoleic acids are identified as the main inducers of corpse disposal in a variety of species, necessitating either direct contact or close detection. Additional volatile death cues in termites such as *Pseudacanthotermes spiniger* and *Reticulitermes flavipes* are phenol and indole, which are byproducts of protein degradation (Chouvenc *et al.*, 2012) [7]. Diverse Crustacea and Hexapoda species exhibit avoidance behavior in response to conserved groups of post-mortem chemical signatures, including fatty acids, which accumulate through autolytic catabolism or bacterial hydrolysis of triglycerides. Although most research on death detection uses olfactory signals, there is some evidence that visual, auditory, or thermal cues also play a part. In termite burial, tactile cues such as glass beads containing potential chemicals cooperate with oleic acid, suggesting non-olfactory contributions to corpse management. Some chemical cues that cause sanitary activity in honeybees have been found in studies on death cues, especially when the brood is sick or dying (Swanson *et al.*, 2009; Nazzi *et al.*, 2004) [76, 41]. Workers in the ant *Lasius neglectus* are prompted to perform destructive disinfection by eliminating both the pathogen and sick individuals according to the altered cuticular hydrocarbon profile of pupae caused by fungal infection (Pull *et al.*, 2018) [52]. Research on honey bee hygiene behavior has increased to better understand and improve colony health, particularly in response to illnesses such as American foulbrood. Social insects have evolved diverse techniques for disposing of dead bodies, which enhances the collective well-being of the group.

Corpses from different castes have chemical markers that differ in quantity and/or quality.

The chemical profiles of termite's post-mortem play a crucial role in revealing the dynamics of colony activity. The study of death cues and decomposition in termites sheds light on the complex sensory signals and behaviors involved in the undertaking process. Here, we delve into the observed differences in chemical cues, sensory mechanisms, and the broader implications for colony resilience. Termites, specifically short-winged bud nymphs (SWBN), long-winged bud nymphs (LWBN), workers, and soldiers, exhibit distinct chemical profiles after death. Notably, differences in early death cues, such as 3-octanone and 3-octanol, were observed between worker and soldier corpses. Additionally,

all castes consistently released the late death cue, oleic acid, with soldiers exhibiting a slower accumulation rate. The unique chemical signatures in different castes suggest qualitative or quantitative disparities, possibly influencing behavioral responses. The absence of detectable early death cues in SWBN and LWB, coupled with variations in oleic acid accumulation rates, highlights the complexity of sensory signals. Nymphs may rely on tactile cues, emphasizing the multi-modal nature of undertaking behaviors. The intricate sensory signals contribute to the efficiency of personnel, particularly in quickly identifying and consuming recently deceased bodies.

The caste-based differences in chemical makeup, physiology, and biochemistry contribute to the observed variations in death cues. Neuter line castes, including workers and soldiers, engaged in riskier tasks, are exposed to disease and predation, making them more prone to turnover. In contrast, the imaginal line, represented by nymphs, likely involves castes with similar social advantages and a lower turnover rate. The signaling system, incorporating both early and late death cues, enables a synchronized response to corpses from the more risk-prone castes. The prolonged decomposition process and the slower accumulation of late death cues in soldier corpses may result from their unique defensive secretions and bodily fluids. The defensive compounds and distinct shape of soldiers contribute to a different disintegration process compared to workers. The presence of volatile chemicals associated with mortality across various conditions, including freezing, indicates the resilience of these cues. The diverse strategies employed by different castes enhance the colony's overall resilience and effectiveness in managing risks associated with death. This comprehensive understanding provides valuable insights into social insect behaviors and contributes to the broader field of collective responses to environmental challenges.

Perception of death cues and gene expression

Olfaction plays a pivotal role in the sensory world of insects, particularly in navigating and assessing their chemical environment. Hansson emphasized the significance of olfaction in social insects, highlighting its critical role in detecting signals associated with death. Social insect species employ a sophisticated array of chemosensory proteins, such as odorant-binding proteins (OBPs) and odorant receptors, to discern various chemical cues.

In the fire ant *Solenopsis invicta*, the gene *Si-CSP1* is crucial for recognizing oleic and linoleic acids, contributing to efficient corpse disposal. Similarly, honeybees (*Apis mellifera*) exhibit hygienic behavior influenced by OBPs, specifically OBP16 and OBP18, which respond to ligands like oleic acid and β -ocimene. These proteins play a role in evacuating sick brood, illustrating the complex interplay between chemosensory proteins and undertaking behaviors. Guarna *et al.*, 2015 [19].

Mechanism of Odorant Sensing

The process of odorant sensing begins with cues detected by insect antennae. Odorant-binding proteins (OBPs) released by support cells reach olfactory receptor neurons (ORNs) through pores. In the ORNs, the chemical signals are transformed into electrical signals, initiating a behavioral response associated with corpse management. Despite these

significant findings, the receptors responsible for species-specific signals or conserved fatty acid death cues remain unidentified. The complex nature of corpse handling, influenced by various processes and social factors, suggests that genes impacting behavioral responses extend beyond those directly linked to death cue detection. Social cues, including pheromones, can influence gene expression, physiology, and behavior, as demonstrated by studies on honeybees (Grozing *et al.*, 2003) [18].

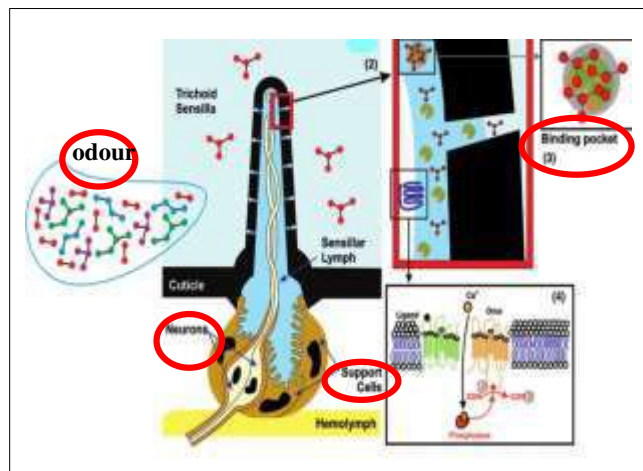


Fig 1: Mechanism of odorant sensing (Sato *et al.*, 2008)

Gene Expression Patterns in Corpse Management:

Examining gene expression patterns in corpse management specialists and non-specialists offers insights into the genetic foundations of this behavior. Research on honeybees has revealed alterations in gene expression associated with sanitary behavior, highlighting the influence of social and environmental cues (Navajas *et al.*, 2008; Le Conte *et al.*, 2011; Boutin *et al.*, 2015) [40, 28, 2]. Undertaker bees, temporarily specialized in corpse removal, exhibit gene expression profiles similar to guards but distinct from comb builders (Cash *et al.*, 2005) [4].

In the eastern subterranean termite *Reticulitermes flavipes*, transcriptome investigations demonstrated rapid alterations in gene expression within half an hour of exposure to death signals. Distinct gene sets were associated with eating versus burying corpses, indicating the complexity of molecular-level corpse management. Advancements in genomics, functional genomics technologies like next-generation sequencing, RNA interference (RNAi), and genome editing are anticipated to propel future research efforts in this field.

Conservation of Fatty Acids as Death Cues:

The identification of fatty acids as conserved death cues in arthropods suggests the involvement of conserved genes or gene networks in their perception. Molecular analysis of oleic acid sensing and the subsequent signaling cascade in social hymenopterans, using publicly available genomes, is a promising avenue for studying corpse management at the mechanistic level. A comprehensive understanding of how corpse management evolved across diverse taxa, from a basic ancestral feature to a sophisticated sequential behavioral response, necessitates studying a wide range of species. In conclusion, the complicated interplay between chemosensory proteins, gene expression patterns, and environmental cues underlies the complex phenomenon of

corpse management in social insects. Continued research using cutting-edge genomic tools will unlock deeper insights into the molecular mechanisms governing these behaviors.

Corpse management Strategies

Due to their similar group living traits, eusocial Hymenoptera and Isoptera are more vulnerable to parasites and diseases. As a result, these animals have evolved unique ways to deal with these challenges as a group, as noted by Cremer *et al.* in 2007^[10]. Different social groupings respond differently to this shared susceptibility in behavior. Social insects react differently to dead members when they are presented with death signs. Undertaking behavior, or corpse management, is a highly fascinating natural activity among social insects. This activity involves the ability to identify dead colony members and use certain chemical cues to move them away from the nest. Corpse removal, or narrowly defined necrophoresis, is a common phenomenon seen in ants and honeybees as reported by Visscher (1983)^[87]. But ants and termites have also been shown to engage in other activities, such as cannibalism, which involves intraspecific necrophagy, and burial, which involves covering the deceased, as mentioned by Driessen *et al.* in 1984.

Avoidance

Necrophobia, or the fear of the dead, is a widespread protective behavior observed across various animal species, ranging from arthropods to mammals, including primates. This instinctual aversion to death serves to minimize potential risks such as illness and predator threats. Insects like collembolans and *Periplaneta americana* actively avoid areas where conspecifics have died, releasing substances to deter their peers. Similarly, tent caterpillars, fall webworms, and isopod crustaceans exhibit necrophobic responses, direct the removal of bodily fluids, cadavers, and injured insects. This avoidance extends even to body fluids and unsaturated fatty acids. For instance, *Protaphorura armata*, a Collembola species, alters its locomotion pattern in response to scents from deceased colony members, gravitating toward living individuals while avoiding areas with the scent of the dead. However, this basic avoidance strategy becomes impractical for social insects inhabiting permanent nests. The eusocial species, living in colonies with fixed nests, cannot feasibly leave the nest to prevent the presence of deceased members. Nest relocation poses increased risks of predation for brood and reproductive adults, necessitating coordinated efforts from the entire colony. While avoiding the dead effectively manages risks for non-eusocial gregarious species, it is not a prevalent strategy in eusocial species with permanent nests.

Avoidance in ants

A key habit that helps prevent the transmission of illness is avoiding unwell or dead colony members (Park and Raina, 2005). Many ant species have been known to move their nests when conditions are adverse or while assessing possible new nesting locations for biological safety, especially when dead bodies, pests, or illnesses are present. When faced with nematode (Steinernematidae & Heterorhabditidae) or *B. bassiana* infections, *Solenopsis invicta* ants flee the nest, while *Pogonomyrmex barbatus* colonies sometimes migrate following summer rains

(Bulmer *et al.*, 2019; Drees *et al.*, 1992)^[3, 14]. Controlling certain infestations can be difficult, even if the diseased ants are eaten or eliminated. *Temnothorax albipennis* is one species of house-hunting ant that frequently relocates in tracking of better living conditions. It assesses potential nesting sites and materials while avoiding locations where non-nestmate conspecifics or deceased nestmates may be present to stop the transmission of disease (Pratt, 2005; Franks *et al.*, 2005)^[50, 15]. This skill enables ants to evaluate the biological safety of possible new nesting sites and abandon colonies beset by pests and illnesses (Franks *et al.*, 2005)^[15]. According to Pereira and Detrain (2020)^[46], *Myrmica rubra* ants can identify possible infections in their prey, which helps them prioritize food retrieval and reduce the total risk of sickness in the colony.

According to Drees (1992)^[14] and for example, the fire ant *Solenopsis invicta* relocates its nest particularly when extensively infested with nematodes or fungal infections. Workers of species that live in simple nests or move around a lot, like the rock ant *Temnothorax albipennis*, display avoidance behavior towards new nest sites containing conspecific corpses, as observed by Franks *et al.* (2005)^[15]. However, it's essential to note that contrary behavior has been documented in certain species, like the pharaoh ant *Monomorium pharaonis* (Pontieri *et al.*, 2014)^[48].

Avoidance of termites

When faced with possible infection or poisoning concerns, termites regularly exhibit avoidance responses. Active avoidance of places with buried or deposited remains, contaminated nesting sites, and contagious corpses are stressed by Ulyshen and Shelton (2012)^[85]. The subterranean termite *Coptotermes formosanus* is attracted to areas where termites have been killed by pesticides as well as those that have not, and that are tainted with pollutants (Song *et al.*, 2006)^[73]. Furthermore, termites respond to entomopathogenic fungi like *Metarhizium anisopliae*, demonstrating their capacity to recognize and avoid possible dangers (Bulmer *et al.*, 2019)^[3]. Termites' unique behavior around carcasses is closely related to the perceived threat these carcasses pose to the colony because of the unique feeding and nesting ecology of each termite species, as discussed by Neoh *et al.* in 2012^[53].

Because of the complex nest structure of subterranean termites, which have colonies of up to millions of members with dynamic tubes and chambers covering hundreds of square meters, moving the entire colony would be prohibitively expensive. As a result, workers bury the dead a practice known as avoidance strategy by closing up the afflicted area to prevent the spread of infections or pesticides. Subterranean termites locally alter the nesting structure, in contrast to species that move their nests; this suggests that termite avoidance is less energy-intensive. To limit the spread of disease, corpse avoidance often entails building or burial; nevertheless, in some situations, avoidance without burial activity is found, as demonstrated by the higher termite *Globitermes sulphureus* in a lab setting (Neoh *et al.*, 2012)^[53].

Necrophoresis

To protect the entire society from any infections, social insects engage in 'necrophoric behavior' uniquely handle corpses, sorting and removing the dead more carefully. Subsocial insects, such as bark beetles, earwigs, and

grasshoppers, are known to follow similar hygienic habits. They carefully clear away garbage and dung to keep their nests clean (Tallamy and Wood, 1986) ^[78].

Necrophoresis in ants

While ants are typically known for their efficient waste management through undertaking behavior, some ant species exhibit unique behaviors, such as establishing ant cemeteries as designated disposal areas. The Australian desert ant, *Melophorus bagoti*, employs a prominent method called dumping for trash and diseased member disposal. The ants follow a structured protocol, using mandibles to capture and transport objects to specific disposal sites. Each material is disposed of differently based on its potential pathogenic risk (Deeti *et al.*, 2023) ^[13]. Ants efficiently handle garbage in natural settings, rapidly removing nest carcasses that are promptly consumed by soil scavengers. Worker ants demonstrate effective removal methods for individuals affected by entomopathogenic conidia, enhancing the colony's overall sanitation. The number of workers plays a crucial role in the efficacy of garbage collection, with fewer workers elevating sanitation risks. Worker reactions to sanitation double when brood is present in the colony. The age structure of the colony influences hygienic practices and aggression toward non-nestmates, with sub-colonies having a higher percentage of young individuals displaying more aggression and less success in corpse elimination. Increased queen numbers correlate with heightened hygienic practices, and colony age distribution has a more significant impact on corpse removal rates than colony size.

European fire ants, like *Myrmica rubra*, exhibit unique behaviors in response to additional corpses, forming larger clusters and displaying enhanced clustering behavior. This leads to the self-organization of corpse mounds or cemeteries, with ants consistently following the same path due to their aversion to garbage mounds and spatial short-term memory. Undertaker ants, such as *M. rubra* and *Solenopsis invicta*, display distinct behaviors while moving carcasses outside their nests. *S. invicta* ants scatter their dead around the nest entrance without building distinct mounds. Workers adeptly identify downward slopes and transfer bodies downwards to create a rubbish dump. Notably, worker ants exhibit more aggression in eliminating non-nestmates than nestmates (Howard and Tschinkel, 1976; Qiu *et al.*, 2020) ^[24-25, 53].

Altruism is evident in social ants, with some ants sacrificing themselves by leaving the nest when near death. Ants like *Pogonomyrmex barbatus* and *S. saevissima* continue to stand outside the nest or leave it when damaged or lifeless. In the case of *S. invicta*, ant corpses are immediately removed from the nest before sporulation to prevent reinfection with *Beauveria bassiana* (Rojas *et al.*, 2018). These complex behaviors contribute to the overall hygiene and health of ant colonies.

Necrophoresis in bees and wasps

In bee colonies, a fascinating behavior called necrophoresis, or the disposal of dead individuals, is observed. When a bee dies, a swarm of worker bees surrounds the diseased, engaging in various actions such as licking, grasping, and dragging the bodies a short distance inside the nest using their mandibles. Gordon (1996) ^[17] outlined a systematic set of actions that "undertaker" bees perform when

encountering a dead body within the nest. This process involves visual examination, coordinated movement, close inspection using antennation, and grasping the body by the wings or claws with their mandibles. Appendages like legs, wings, antennae, head, mouth, and antennae play essential roles in corpse movement, with legs being the most frequently used. The undertaker bees then carry the dead bodies out of the nest. Unlike ants, bees do not lift corpses during necrophoresis instead, undertaker bees draw the bodies backward by their body parts, load them into their mandibles, and carry them out of the hive and back again. Cuticular hydrocarbons (CHCs) released by dying bees serve as important indicators. Undertaker bees can detect reduced CHCs, such as heptacosane and nonacosane, associated with a drop-in body temperature after death, allowing them to identify dead nestmates through their olfactory capabilities (Rahman *et al.*, 2016) ^[55].

Hygienic behavior, a form of necrophoresis in honey bees, is associated with increased olfactory sensitivity in hygienic bees compared to non-hygienic bees, as indicated by differences in antennal gene expression (Guarna *et al.*, 2015) ^[19]. Odorant-binding proteins, specifically OBP 16 and OBP 18, are linked to sanitary behavior. Specific odorants, such as β -ocimene and oleic acid, trigger brood removal activity in honeybees when a brood member dies, and bees with higher hygiene levels can quickly identify and eliminate brood containing these odorants.

The European bee, *Apis mellifera*, efficiently removes dead bees from its colony, preventing the accumulation of corpses inside the nest, as they lack trash cans like ants. Stingless bees, such as *Melipona favosa*, exhibit necrophoric behavior by transporting dead bodies on their mandibles to an underground trash can beneath the nest entrance (Munday and Brown, 2018). In bumblebees like *Bombus impatiens*, corpse clearance varies based on job specialization and body size, with guard bees being particularly sensitive to changes in the nest's chemical composition. Bee behavior in corpse removal responds to factors such as pest and pathogen loads, with an increase in corpse removal observed in response to higher pest and pathogen levels (van Langevelde *et al.*, 2020) ^[86]. This intricate system of necrophoresis contributes to the overall hygiene and health of the bee colony.

Cannibalism/ Intraspecific necrophagy

Cannibalism, the act of consuming one's species, is a widespread behavior observed in various animal species, extending beyond eusocial insects. Serving as a means to acquire essential nutrition and energy, cannibalism takes different forms, including predatory, sexual, and brood cannibalism. Eusocial insects, as highlighted by Rueppell O, Kirkman RW (2005) ^[66] and Schmickl T, Crailsheim K (2001) ^[67], employ cannibalistic activities to control resources, such as consuming live broods or other colony members. In addressing reproductive challenges, they may also consume eggs deposited by workers, termed intraspecific necrophagy, encompassing the consumption of dead, dying, or injured conspecifics. While cannibalism offers nutritional benefits and aids in disease control, there's a potential risk of spreading pathogens among cannibals (Monnin T, Ratnieks FL, 2001; Rudolf VHW, Antonovics J, 2007; Pfennig D, Ho S,) ^[37, 65, 47].

Intraspecific necrophagy in ants

Although uncommon, certain ant species exhibit cannibalistic behavior. In *Atta mexicana* Smith, for instance, when an adult ant is crushed, revealing fatty tissue, fellow ants are attracted to the exposed individual and opt to consume it instead of disposing of the carcass. In the case of a queen sustaining a crushing wound, workers engage in eating the tissues, with smaller workers remaining within the corpse, licking it. Howard and Tschinkel (1976) ^[24-25] observed cannibalism within the *S. invicta* nest debris pile, where ants consume the abdomens of deceased sex partners and occasionally transport bodies from the trash heap to the colony. Notably, red wood ants *Formica polyctena* (Foerster) and honey ants *Myrmecocystus mimicus* Wheeler demonstrate cannibalistic tendencies when consuming individuals from nearby colonies as a means of territorial expansion (Mabelis, 1978) ^[33].

Intraspecific necrophagy in termites:

Termites are essential to the recycling of nutrients and the upkeep of a clean environment in their colonies. By eating fresh corpses, termites can recycle nutrients and healthy gut symbionts, which stops the spread of pathogens that may happen if bodies are left untreated. Termites wall off and bury corpses that are severely decomposed to keep them apart from the colony, stop the spread of illness, and keep them out of the way of predators and other adversaries (Shi *et al.*, 2021) ^[70].

Termites utilize cannibalism to recycle nitrogen because their diet is cellulose-based and deficient in proteins and nitrogen. Additionally, this activity helps to prevent the spread of illness among nestmates. As seen in *Amitermes hastatus* (Haviland), termites in good health will lick decliningly fertile queens; in contrast, termites in *Coptotermes lacteus* (Froggat) would kill and eat alates (Wilson, 1971) ^[92]. To stop the transmission of illness, the eastern subterranean termite, *Zootermopsis angusticollis* (Hagen), for example, reacts alarmingly and leaves the infected place when fungal spores are found (Rosengaus *et al.*, 1999) ^[63]. When it comes to the subterranean termite *Reticulitermes speratus* Kolbe, the termites' vibrations are important. In this termite species, longitudinal vibrations serve as a refusal indicator and deterrent against cannibalistic assaults by nestmates, even though vibrations might be a negative element in death identification. This behavior points to a possible function for the labial gland's phagostimulant action in controlling cannibalism in *R. speratus* (Yamanaka *et al.*, 2019) ^[94].

Burial

Maintaining a clean nest is a critical aspect of social insect corpse management, involving the removal and, if necessary, burial of unwanted items using materials like dirt. For example, ants employ various strategies such as covering liquids like water to prevent them from sticking and burying bodies when cannibalistic activities become inefficient due to an accumulation of corpses. While less common in non-eusocial species, some females, like ambrosia beetles, bury their weak or deceased brood with soil. Burrowing beetles exhibit parental care behavior, unrelated to corpse management when burying small vertebrate carrion as a food source for their larvae.

Ants typically prefer removal over burial for corpses, but burial practices are observed in specific species. For

instance, *M. vindex* buries objects treated with oleic acid, *Temnothorax lichtensteini* buries freshly dead foreign species' corpses, and *S. invicta* covers fungal-infected corpses with soil in artificial nests to prevent disease spread. Co-founding queens of the black garden ant, *Lasius niger*, may bite and bury deceased co-foundresses in closed nests to increase survival chances when removal is not feasible (Pull CD, Cremer S, 2017) ^[11]. Beekeepers, although less common, use propolis, a plant-made glue, to seal nests and entomb large insects or dead mice challenging to remove, including nest intruders like parasitic beetles.

Termites, despite cannibalism providing sustenance, resort to burial when dealing with a high number of dead, severely decomposed remains, highly diseased individuals, or those killed by pesticides or rivals (Sun *et al.*, 2017) ^[75]. Although burial demands more effort and energy than removal, it proves to be the most effective collective behavior for preventing disease transmission within the nest. According to Sun *et al.* (2017) ^[75], burial physically isolates bodies, slows decomposition, and acts as a protective measure against potential invaders by blocking entrances and deterring further assaults.

Burial behavior in ants

Instead of burying their dead nest mates, ants typically cover up unwanted objects. Several ants work together to arrange the building materials and, in the end, stigmergy a process where environmental signals affect social insects' behavior while they complete tasks to interconnect the corpse. According to Choe *et al.* (2009) ^[6], burying a person within the nest requires the contributions of up to 25 workers, who can provide 180 pieces of material.

Burial behavior in termites

Termites employ diverse strategies for managing dead bodies within their colonies. A common technique involves surrounding deceased individuals with walls made of antibiotic secretions or burying them with dirt particles to prevent the spread of diseases. *Temnothorax lichtensteini* colonies exhibit various behavioral responses, including necrophoresis and burial. When different types of bodies were introduced into lab colonies, the termites displayed unique behaviors such as burying, engaging in necrophoric activity, or a combination of both. Workers exhibited specific burial patterns and necrophoric behaviors, allowing them to distinguish between foreign, nestmate, old, and fresh corpses (Renucci *et al.*, 2011) ^[57].

In the case of damp-wood subterranean termites like *Coptotermes intermedius* Silvestri, dead bodies are buried by grouping them according to apparent illnesses or wounds and covering them with soil particles (Park and Raina, 2005) ^[45]. Formosan subterranean termites (*Coptotermes formosanus* Shiraki) resort to cannibalism when worker mortality is minimal. However, if worker mortality surpasses a certain threshold, burial becomes the preferred course of action. The impact of termite graveyards, and nutrient-rich soil patches resulting from entombment, on nutrient cycles remains unclear.

Task allocation of undertaking behavior

Eusociality in social insects is marked by the reproductive division of labor and subsequent task allocation among colony members, particularly evident in non-reproductive worker castes. This division is based on physical polymorphism and age polyethism, involving morphological

variations and age-related functions (Traniello JFA, Rosengaus RB, 1997) ^[83]. Task allocation flexibility is crucial for colony survival, expansion, defense, and disease control (Gordon DM, 1996) ^[17]. Undertaking behavior is a notable aspect of worker castes, involving the recognition of bodies, as seen in species like the leaf-cutter ant *Atta mexicana* (Smith), where caste-specific sensitivity to the breakdown product oleic acid is observed (López-Riquelme *et al.*, 2006) ^[31]. In honey bee colonies, undertaker bees exhibit task specialization, with a small percentage of workers dedicated to corpse disposal. Age polyethism and genetic diversity influence this specialization, and genetic factors shape behavior choices, indicating limited flexibility at the colony level (Trumbo *et al.*, 1997; Robinson *et al.*, 1995) ^[84, 59].

Ant colonies also display task specialization in undertaking behaviors, influenced by genetic variation in species like the desert leaf-cutter ant *Acromyrmex versicolor*. Learning and memory in undertaking behavior vary among species, with honey bee undertakers showing no improvement with experience, while common red ants (*Myrmica rubra*) exhibit spatial memory guiding them to specific places for corpse disposal (Trumbo *et al.*, 1997) ^[84].

In Hymenoptera, colony size affects polyethism, with larger groups exhibiting better assignment of individuals to different tasks (Gautrais *et al.*, 2002; Holbrook *et al.*, 2011) ^[16, 23]. However, task specialization in undertaking behaviors has not been observed in hemimetabolous termites. Pleometrotic termite species, such as *Pseudocanthotermes spiniger*, exhibit corpse-burial behavior, demonstrating intercaste adaptability. Termites use various tactics, including removal, burial, cannibalism, and corpse avoidance, making it challenging to identify individual "undertakers." In termites with higher ranks, evidence of age polyethism exists (Miura T, Matsumoto, 1995) ^[36], but whether undertaking behavior is age-related remains undetermined. Overall, task allocation and specialization play crucial roles in the functioning and survival of eusocial insect colonies.

Conclusions

Death in social insect colonies results from various causes, presenting both advantages and hazards for the colony. Successful corpse management involves distinguishing between alive and dead bodies, identifying mates or non-mates, and assessing the state of the body. Social insects deploy specialized behaviors, such as burying, cannibalism, corpse disposal, or avoidance, to enhance disease resistance by minimizing pathogen transmission. These strategies also contribute to colony defense against outsiders and nutrient recycling. While research has mainly focused on economically significant species like invasive ants, honeybees, and subterranean termites, less-explored species, such as wasps, ants in simpler societies, and primitive termites, present a research gap. Corpse management techniques like necrophoresis, intraspecific necrophagy, burying behavior, and avoidance coexist within species, influenced by information processing in social insect brains. Chemosensory and tactile organs play a crucial role in analyzing data from corpse signals and supporting decision-making mechanisms that safeguard colony fitness. Recent investigations, such as the Si-CSP1 gene study, offer insights into the genetic foundation of necrophobic behavior. Understanding these pathways opens avenues for

novel pest management approaches, including genetic manipulation to influence necrophobic behavior.

Behavioral studies provide promise in pest control, with RNAi-mediated silencing of target genes and miRNAs showing potential as effective strategies. Analyzing collective corpse management tactics across social insects helps decipher evolutionary mechanisms and phylogenetic links underlying these behaviors. Studying genes and their expression patterns facilitates the alteration of insect genetic makeup, offering new possibilities for pest control. Future research should delve into the behavioral aspects of various social and pestiferous insects, leveraging findings to enhance pest control tactics.

Perspectives and Future Research

Recently, undertaking behavior has attracted more attention, especially in the definition of behavioral reactions [Chouvenc T, Su NY, 2012] and in the investigation of sensory cues [Chouvenc *et al.*, 2012; Ulyshen *et al.*, 2012]. However, there is still a lack of knowledge on the distribution of tasks during the undertaking activity and More research is necessary to understand the genetic basis of undertaking responses in hemimetabolous termites and holometabolous hymenopterans. Since eusocial groups all engage in undertaking behavior, comparative research using integrative methods such as chemical ecology, behavioral observation, and genomic analyses across a range of eusocial lineages holds the potential to reveal the closest mechanisms underlying eusociality.

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