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CORPSE MANAGEMENT STRATEGIES IN SOCIAL INSECTS

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ABSTRACT

Social insects are arthropods that lives in a community with other members of the same species. Eusocial insects frequently lose colony members as a result of living in big groupings. They perform cooperative corpse management to maintain the hygiene of the nest, exhibiting behavioural and physiological responses that promote disease resistance, nutrient reallocating and colony protection. Undertaking behaviour is most common in social insects belonging to Hymenoptera and Isoptera which adopts various mechanisms of death recognition, convergent and divergent behavioural responses towards dead items. Corpse removal, burial, cannibalism and avoidance are different solutions evolved by social insects, independently towards the problem of corpse management. Genetic studies and gene expression analysis related to social immune systems gives a better knowledge on 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 social insects.

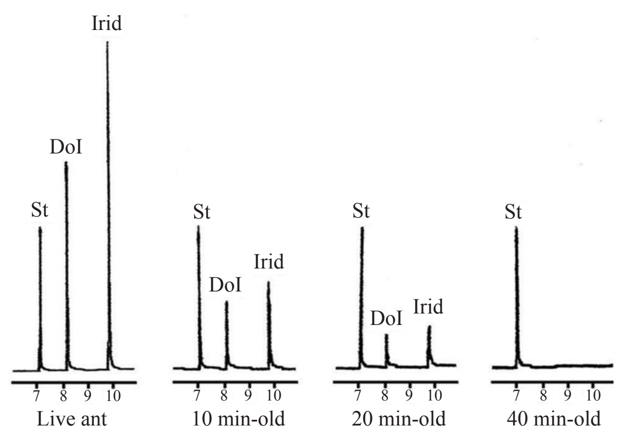
Key words: Social insects, Hymenoptera, Isoptera, necrophoresis, necrophagy, burial behaviour, hygienic behaviour, death cues, CHCs, eusociality, division of labour

Apart from humans, social insects are the only animals having advanced behavioural adaptations for disposing of dead conspecifics that have been recognised since antiquity. Insects that lives in group and manifests colony integration with division of labour is referred as social insects. All ants, termites, some bees and wasps are the true social insects evolved to live in large cooperative colonies. The insects work together in search of food and other resources, to communicate their findings to fellows in the community. When under attack, they mount a vigorous defense of their shelter and resources. Social insects adopt a peculiar behaviour for maintaining the hygiene of their nests as they regularly face death of their group members. Social insects adopt different mechanisms of death identification, convergent and divergent behavioural responses to dispose of dead individuals to prevent further spread between corpses and living members in a colony (Sun and Zhou, 2013). Hymenopterans and Isopterans evolved different solutions such as necrophoresis (bees, wasps, ants), burial (ants, termites), avoidance (ants, termites) and cannibalism (ants, termites) independently towards the corpse management. Anthropomorphically, undertaking behaviour refers to corpse management explaining the innate behaviour of social insects (Neoh et al., 2012). The term necrophoresis was originated from Greek word "necro" means dead and "phoresis" means transport (Renucci et al., 2011) which was described by Wilson and coworkers (Wilson et al., 1958). Necrophoresis is one of the earliest and well described mechanism in social insects, which refers to the removal of dead items from the colony (Wilson et al., 1958). Undertaking behaviour is a sequential array of responses by corpse, targeting the potential health related hazards to well maintain the hygiene of the nest. Necrophoric behaviour is used as synonym with undertaking behaviour in some references. The phenomenon of corpse management was earlier described by naturalists as funerals and cemeteries in honey bees (Visscher, 1983) and ants (Holldobler and Wilson, 2009). Wilson et al. (1958) was first to report the behavioural patterns associated with undertaking behaviour of two ant species, *Pogonomyrmex badius* (Latreille) and *Solenopsis saevissima* (Smith) (Visscher, 1983). Studies on death recognition cue, behavioural process and division of labour were focused till date. 'In the era of genomics' underpinning of corpse management were focused for better understanding and to study the phylogenetic relationship between distant eusocial insects. This review provides new insights and interpretation of corpse management focusing on necrophoretic behaviour of various social and other insects (even though not social), a comparison of undertaking behaviour in different social groups (mainly Hymenoptera and Isoptera) and future aspects of corpse management related to pest control.

Identification of the dead

When an insect dies in a social community, workers of the hive must identify the deceased individuals out of those who live using various signals such as chemical, tactile and possibly visual input before taking any action. In reality, more or less skilled individuals work in bee and ant colonies to promptly remove all the deceased colonists from their nests to be able to stop the chance of disease sources from infecting other members of the society, especially reproductives and young ones (Lopez-Riquelme and Fanjul-Moles, 2013).The crucial initial stage for social insects to induce undertaking behaviour is identification of the dead. Chemical signals are mostly used by eusocial insects to recognise the death. Fordecades, carboxylic acid derived from the decomposition of dead body was persumed to be necromones (pheromones or chemical signals linked to organismal death, which helps to identify and keep away hazards of infection, parasitism and predation) in social insects. However, this hypothesis cannot explain the chemical perception in the nearly instantaneous undertaking, as it takes longer time to have acids (Sun et al., 2018). The recognition of dead mates by the undertakers in a honey bee colony remains unknown (Klett et al., 2021). But the cues from the carcass or dead one, also known as death pheromones or necromones in ants (Qiu et al., 2015), bees (McAfee et al., 2017) or termites (Chouvenc et al., 2011) were discovered to be fatty compounds, particularly linoleic acid and oleic acid. According to Ulyshen and Shelton (2012) the induction of oleic acid which induces necrophoretic behaviour in termites and several species of ants.

Numerous studies have demonstrated the role of chemical signals such as "fatty acid death cue" and "chemical vital sign" in identifying the corpse. The ant species viz., *P. badius* and *S. saevissima*, offered evidence that fatty acids, in particular the oleic acid that builds up in dead carcasses cause aggressive actions. Certain aspects were not explained in this hypothesis (Wilson et al., 1958). Later, Gordon (1989) found that oleic acid is not only released at the time of undertaking but also at foraging time. Choe et al. (2009) demonstrated chemical vital sign hypothesis in argentine ant, *Linepithema humile* (Mayr), in which two cuticular substances present are such as dolichodial (Dol) and iridomyrmecin (Irid). The concentration of these chemicals is high in live ants and decline quickly after death. Within the first 10 minutes after death, there was 50% reduction in the levels of Dol and Irid and the chemicals were absent in the 40-minute-old dead ant samples (Fig. 1). Furthermore,several Hymenopteran species are stimulated to engage in undertaking behaviour by fatty acid olfactory stimuli. In eastern honey bee, *Apis cerana* Fabricius, nasanov glands produce these fattyacids. A bioassay was conducted in dead honey bee where the dummies of *A. cerana* were rinsed with their distinct cuticular chemicals, two doses of oleic acid and a synthetic mixture of nasanov pheromone. Results indicated that oleic acid did not encourage the disposal of carcasses in *A. cerana* whereas removal is stimulated by the synthetic pheromone blend of nasanov pheromone (Klett et al., 2021). The involvement of fattyacids in inducing the undertaking behaviour were also very well documented in the order Isoptera. The corpse of the termite, *Reticulitermes flavipes* (Kollar)release 3-octanol and 3-octanone as dead signals (Sun et al., 2017). Unsaturated fattyacids i.e., oleic acid or linoleic acid are generated by dead arthropods via enzymatic autolysis of cell membranes. Those fattyacids are utilized as a reliable signal of death which highlights the diverse ecological and behavioural interactions among different arthropods. Social aphid, *Tuberaphis styraci* Matsumura uses linoleic acid as corpse recognition signal for corpse management. Dead aphids generate linoleic acid by enzymatic autolysis of cell membrane and seeping out on the body surface of aphid cadavers. This in turn triggers the cleaning behaviour of soldiers (Shibao et al., 2022). In order to understand and improve colony health, honey bee hygienic behaviour studies have grown over the past few years. American foul brood disease was the most dangerous illness affecting



Source: Choe et al. (2009)

Fig. 1. Concentraion of fatty acids in live and 10, 20, 40 minutes old ants after death

honey bees in the 1930s. Researchers and beekeepers noticed that certain colonies resisted the infection and designated these colonies as resistant and observed that larvae that have just died may occasionally be removed and disposed of by bees, removing the evidence (Spivak and Danka, 2021). Social insects have developed some strategies for corpse disposal which are discussed below.

Corpse management strategies

Social insects must handle corpses in order to keep their colonies healthy. They seem to use a variety of undertaking tactics.

Necrophoresis

The term "necrophoric behaviour" is used to describe how the social insects handle corpses differently from other waste products, separating and removing the dead even further to keep the entire community safe from dangerous diseases. Similar hygiene habits were also shown by subsocial insects such as bark beetles, earwigs and grasshoppers wherein they remove the waste and excrement to keep their nest clean (Tallamy and Wood, 1986).

Necrophoresis in bees and wasps: Numerous individuals flock to the nest when corpses are around; many of these not only examine the bodies but also lick, grab and pull them a little distance into the nest using their mandibles. According to Gordon (1996), the series of behavioural characteristics that an undertaker exhibits when she discovers a corpse inside the nest. The visual inspection of the body is followed by movement in the same direction, close up the corpse and then examine the body with antennation. With the help of mandibles they will hold the corpse by its claws or wings. In reality, it has been proven that the corpse appendages are essential for moving them. Although corpses without appendages may stay in the hive for a longer period of time. Legs, wings, antennae, head, and tongue are the appendages that are utilised most frequently, in decreasing order of use. Then they will move the body through the nest and out of the entrance. While performing necrophoresis unlike ants, bees not elevate the corpse; instead, before they reached the colony entrance, bee undertakers pull the bodies backwards by their body parts through the colony. Later they carry the corpse in its mandible from the hive and put the corpse down by returning to the nest.

Worker bee recognizes its alive or dead nestmates by detecting the reduction in cuticular hydrocarbons elicited from the dead bees (Wen, 2020). The body temperature will drop as a bee dies, pertaining to decrease in cuticular hydrocarbons (CHC) like heptacosane and nonacosane. At hive temperatures, heptacosane and nonacosane emissions are life signs. Insects' chemical communication can be adjusted by body temperature by altering the vapour pressure and then the ratio of released chemicals. Extreme weather events are occurring more frequently, which could lead to inaccurate death identification and affect bee health (Wen et al., 2023). In honey bee colonies, when there is reduction in CHC, the undertaker bees can detect this through olfactory senses which helps to identify a dead bee in the colony (Rahman et al., 2016). Necrophoresis has apparently been used by social wasps to dispose of their dead members. Contrastingly, *Vespula rufa* L. have reportedly been observed allowing waste and dead colony members create a garbage dump on the hivebottom (Ross and Matthews, 1991). Hygienic behaviour is one of the main types of necrophoresis in honey bees (Spivak and Gilliam, 1998). When compared to non-hygienic honey bees, hygienic honey bees show greater olfactory sensitivity which is probably due to variations in antennal gene expression (Guarna et al., 2015). The odorant binding protein – OBP 16 and OBP 18 were as antennal biomarkers involved in hygienic behaviour and were shown to be significantly connected with the colony hygienic level. When a brood member dies two odorants, ß-ocimene and oleic acid are produced and cause honeybees to engage in their hygiene-related brood removal behaviour. The odorant ß-ocimene alerts cleaning workers, whereas the death cue that triggers elimination is oleic acid. Both compounds act as strong bind to hygienic behaviour linked odorant binding proteins. Bees with higher levels of hygiene recognise and discard brood containing these odorants faster than bees with low hygeinicity (McAfee et al., 2018).The undertakers of European bee, *Apis mellifera* L. are very efficient, so that the existence of dead bees inside the nest are rare. Like in ants, they do not have any refuse dumps, the corpse carrying workers will fly for short distance around 10-100 m away from the hive. It is a continuous activity that has no daily schedule and continues even at nights. Time required to remove corpse is faster compared to removal of waste material of similar size. It shows that necrophoresis is a distinct behaviour from other nest hygiene practices (Visscher, 1983).

The necrophoric behaviour in stingless bees and bumble bees assume noticeable alterations. In stingless bee, *Melipona favosa* (F.) necrophoric behaviour is observed. The bees will carry corpse in their mandible and move to the garbage bin beneath the entrance of the nest, which is on the ground (Munday and Brown, 2018). Unlike, corpse removal in bumble bees, *Bombus impatiens* Cresson were predicted based on task specialization and body size (Walton et al., 2019).The guard bees in bumble bee hive are involved more in undertaking compared to other duties in the colony like nursing and foraging. Additionally, they were more responsive to alterations in the chemical composition of the nest, making them more inclined to participate in management. The corpse bee was larger than other bees in the colony. Body size of corpse bees displayed a significant remark in corpse management. The largest corpse bees were more successful in removing corpses from nest. Around 31.1%± 6% of *B. impatiens* and 30%± 12.5% *Bombus terrestris* L. colonies were engaged in undertaking behaviour respectively (Walton et al., 2019; Munday and Brown, 2018). Because of this, the group of undertakers in bumble bees may not exist for a distinct purpose; instead, guard bees take up the undertaking task as needed. The behavioural pattern of bees varies with change in load or inoculum of pest or pathogen and was found that corpse removal increases with increase in load of pests and pathogens. When honey bee colonies have significant *Varroa destructor* (Anderson and Trueman) infestation, body removal rises and the reason may be that as time passes there may be chances of more number of bees getting killed. Hence the number of bees removed from the colony remains the same (van Langevelde et al., 2020).

Necrophoresis in ants: Ants are the group of insects whose undertaking behaviour is most studied. Even though ants are known for being obvious garbage dumps, some species does not always act in this way. Ants carry their corpse and dispose them in refuse dumps called ant cemetery (Oi and Pereira, 1993). Individual ants modify their behaviours to the environment, thus the growth and pattern formation of ant cemeteries are affected by the surroundings. Additionally, interactions between worker ants and their nest mates in a colony may enhance or degrade the performance. Whether other ants were present at the cluster location affected each ant's contribution to the cluster building. The development and growth of an ant cemetery may be explained by using this strategy coupled with stigmergy (Sakiyama, 2020). Dumping means transportation of an item outside the nest and dropping it on the ground. Australian desert ant, *Melophorus bagoti* Lubbock focuses on dumping mechanism for removing dead members and other waste items. Ants remove the waste from nests in a stereotypical procedure; they grab the items with their mandibles, position it for lifting and raising above. After raising, they walk with the object for the intended dumping distance and disposed with a stereotypical motion. The dumping distance however varies according to the material type. Low pathogenic risk items dumped in the short distance where as high pathogenic risk items dumped into longer distance. Thus, the dumping distance depends on the potential pathogenic risk (Deeti et al., 2023). In nature, corpse removed from the nest does not remain for long time because soil scavengers will devour them. Pereira et al. (2020) also reported the ability of ants to detect entomopathogenic conidia on waste and strategies taken to fasten the removal of infected individuals. Further, workers population decides the efficiency of waste removal. Thus, low population of worker increases the sanitation risk. They also found the hygienic responses of workers were doubled by the presence of brood in the colony. Maak et al. (2019) reported that the number of queens and the size of the colony have an impact on how aggressively nestmates are treated by non-nestmates, whereas the effectiveness of removal of corpses has a positive correlation with both characteristics in red ant *Myrmica scabrinodis* Nylander. Both the aggression toward non-nestmates and the sanitary behaviours are influenced by the colonies age structure. Sub colonies that have a higher proportion of young individuals tend to be more aggressive and less effective at removing corpses. The number of workers engaged in sanitary behaviours increases when there are many queens in the colony, and the rate of corpse removal is determined more by the age structure of the colony than by its size. In the case of European fire ant, *Myrmica rubra* L., adding more corpses to a cluster causes it to grow in size, which raises the probability of being added again due to their clustering behaviour leading to self-organization of corpse piles or cemeteries. They use the same route as prior journeys due to their spatial short-term memory and biochemical non-preference towards waste piles. There have been reports of distinct garbage dumping and waste burial mounds in other ant species like *Aphaenogaster iberica* Emery, *Camponotus cruentatus* (Latreille), *Camponotus vagus* (Scopoli), *Cataglyphis velox* Suntschi, *Formica lugubris* (Olivier), *Formica sanguinea* Latreille, *Lasius emarginatus* (Olivier) and *Pheidole pallidula* Selenia (Diez et al., 2012). Social insects have to deal with significant risks of exposure to disease and pathogens spreading between group members. To maintain the social immunity of the colony, insect societies contribute several collective hygienic behaviours. Colony size displays a significant role on survival and sanitary strategies in fungus infected ant colonies. Entomopathogenic fungus *Metarhizium brunneum* Petch infected *M. rubra* ant colonies of different size were studied by Leclerc and Detrain (2018) reported largest colonies are less suffered from exposure to life-threatening spores. This is due to fastest removal of infected waste from the nest. However small sized colonies opt for emergency strategy in which workers move out from their nest carrying brood and reintegrate it after sanitization by waste removal, when challenged with fungus-bearing items. This indicates the behavioural plasticity of ant colonies of which colony size determine the efficiency of hygienic management. When bringing carcasses out of the nest, undertakers of the ant species *Solenopsis invicta* Buren and *M. rubra* often move in straight and radial trajectories. If the surface is not even, they move in random direction without any orientation. The undertakers of the fire ant *S. invicta* distribute carcasses around the nest entrance rather than establishing distinct corpse heaps as they wander in random directions away from the colony entrance without displaying preference for orientation. Because of the dispersed placement of corpses around the nest entrance, a boundary known as the corpse boundary has been formed. It is also observed that in *S. invicta*, the corpse carrying workers detect any downward slope and they tend to walk downward very fast with less consumption of energy and releases corpse downward by forming a downhill refuse dump (Howard and Tschinkel, 1976). Workers of *S. invicta* responded differently to corpses from various origins. Particularly, resident workers remove recently deceased non-nestmates more frequently than nestmates. Compared to corpses of their nestmates, resident workers responded more aggressively to those of non-nestmates and removed them from the area more rapidly. Yet, there was no discernible difference between the removal time of bodies of nestmates and non-nestmates (Qiu et al., 2020). Army ants and fungus-growing ants are two examples of ant species that produce significant amounts of garbage and dead bodies in their communities. In close proximity to or just underneath the bivouac, army ants *Eciton burchelli* Cupiens create garbage piles. When the colony occupies in a log or cavity, they will drop off the refuse at the end of the log. Refuse produced by these ants contain remains of prey and carcasses. They will carry corpse and wastes to the refuse dumps by a dense transport row with the participation of many workers. Fungus growing ants like *Atta* sp. colony contain about 2 million workers. They create 500 kg of consolidated garbage and the waste is particularly dangerous as it is exposed to pathogenic inhabitants grown on them. The species, *Atta cephalotes* L. do not undergo necrophoresis where old and site workers act like dump workers while going to die. After few years, it was reported that, here the workers are transporting dead workers and reproductives outside the nest (Hart and Ratnieks, 2002). Altruism in social ants is widely recognised. Some ants sacrifice by removing themselves when they are on the verge of dying. According to Wilson (1983), damaged and lifeless *Pogonomyrmex barbatus* (Smith) and *S. saevissima* workers continue to stand outside the nest or leave it. Before sporulation, *S. invicta* ant corpses are immediately removed from the nest to stop *Beauveria bassiana* (Balsamo) reinfection in the colony. They will also leave the nest hours before their death (Rojas et al., 2018).

Intraspecific necrophagy

Intraspecific necrophagy or cannibalism is wide spread in animal kingdom. It might encourage the spread of diseases and be a significant cause of mortality in certain species. When resources are few, it is feasible to consume the body parts of the corpses and dispose the carcasses by necrophoresis (Maak et al., 2020).

Intraspecific necrophagy in ants: Cannibalism among ants is extremely rare, however it has been observed in a few species. If any adult ant is crushed open exposing the fatty tissue, other ants arrive and eat them. When the queen in *Atta mexicana* Smith has a crushing wound, the workers start eating the tissues instead of discarding the corpses, then the small workers come and lick that carcass and stay within the carcass (Wilson, 1983). Howard and Tschinkel (1976) noticed cannibalism in the garbage heap of *S. invicta* nest. These ants eat the abdomen of dead sexual partners and occasionally, workers would bring the corpse to the nest from the garbage pile. The red wood ant, *Formica polyctena* (Foerster) and honey ant, *Myrmecocystus mimicus* Wheeler, prey on neighbouring colonies of same species for the control and enlargement of its territory, and transport into the nest alive or dead wherein they were consumed by the adults and workers (Mabelis, 1978).

Intraspecific necrophagy in termites: Termites recycle nutrients and viable gut symbionts when they consume new dead bodies, which protects the colony against pathogenic proliferation that might otherwise take place if corpses were left unattended. Highly decayed bodies can be separated from the colony via walling off and burying behaviours to stop the spread of disease and avoid interaction with predators or enemies (Shi et al., 2021). Termites have cellulose-based diet and low in nitrogen and proteins, because of which termites use cannibalism to recycle nitrogen, making them vulnerable to it. It also helps to control disease transmission to nestmates. The subterranean termite, *Reticulitermes lucifugus* Rossifeed apparently healthy nestmates, *Amitermes hastatus* (Haviland) lickqueens with declining fertility and *Coptotermes lacteus* (Froggat) kill and eat the alates (Wilson, 1971). Some termites perform cannibalism for hygienic surrounding. If infected with pathogen, the healthy workers will come and eat the infected ones to eliminate them from the colony. When eastern subterranean termite, *Zootermopsis angusticollis* (Hagen) detects the presence of fungal spore, they will alert others by alarm behaviour and non-exposed nestmates depart from the infectious site (Rosengaus et al., 1999). The vibration acts as the death negative factor in death identification while wounds induce cannibalism. But in the present study of subterranean termite, *Reticulitermes speratus* Kolbe, the longitudinal vibrations produced by the termites have a refusal sign and function against the cannibalising nestmates. The vibrational behaviour against the cannibalistic attack on the thorax can indicate the possibility of another death cue. This can suggest that the key role of phagostimulant activity of the labial gland in *R. speratus* in cannibalism (Yamanaka et al., 2019). Relationship between termites and mites were also documented in corpse management. Weaker termite colonies favour large population size of mites such association is seen between the common mite *Australhypopus* sp. and mound building termite, *Cornitermes cumulans* (Kollar) in relationship with the termite host. Termite mortality had a significant correlation with mite population which indicates the mortality favours for mite growth because it feeds on termite corpses for completing its life cycle (Pisno et al., 2023).

Burial behaviour

It is an important corpse management strategy in social insects to maintain their nest clean. Nests are cleaned by removing foreign objects and covering them with soil or other materials if not removed. Ants cover liquids like water in order to prevent themselves from sticking. In situations where cannibalistic behaviour becomes an ineffective strategy due to the piling up and decaying of the bodies, burying behaviour would then occur (Davis et al., 2018).

Burial behaviour in ants: Most of the ants tend to cover all the unwanted material without burying their dead nest mates. Burial is a group task because many ants participate and arrange building materials and finally bury the corpse by stigmergy (the impulse from the environment changes behaviour of social insects in undertaking behaviour). Around 200 pieces of material can be deposited by 25 workers to bury a body inside the nest (Choe et al., 2009).

Burial behaviour in termites: Termites bury the corpse with soil particles or they construct wall around the corpse with antibiotic secretions. This is done to isolate the spores of pathogens. In *Temnothorax litchensteini* (Bondroit)*,* termites manage their corpse by both burial and necrophoresis. The colonies of *T. litchensteini* exhibit diverse undertaking behaviour, ranging from corpse dumping behaviour to necrophoric attitude (Renucci et al., 2011). In the study, they maintained two colonies of *Temnothorax unifasciatus* (Latreille) and *T. litchensteini* in the laboratory and introduced 6 different types of corpses, new and old corpse coming from the same colony or from another colony of same species or from alien species. These were introduced into the colony and it was observed that different corpse possess different types of behaviour such as burying, necrophoric and mixed (both burial and necrophoric). Out of 38 corpses studied, burying behaviour was observed in 14 corpses, necrophoric behaviour in 16 corpses and mixed behaviour in 8 corpses. Three behavioural patterns were shown by *T. litchensteini* wherein the workers were able to discriminate alien corpse, nestmate corpse, old corpse and new corpse.

The burial behaviour in damp-wood subterranean termite, *Coptotermes intermedius* Silvestri, reveals that they group the corpses as injured and diseased and cover them with soil particles (Park and Raina, 2005). In formosan subterranean termite, *Coptotermes formosanus* Shiraki, when the mortality is low, workers will cannibalize them and, if mortality exceeds the threshold, they will bury them (Yanagawa et al., 2011). Termite graveyards are nutrient-rich soil areas. It is unclear that whether the burial of termite bodies affects the cycling of nutrients. Entombment is the production of graveyards for the disposal of dead bodies in termites. Graveyard sheeting of fungus growing termite, *Macrotermes natalensis* Haviland, characterized by higher carbon content and a slight increase in the C: N ratio compared to normal soil. The presence of organic materials and salt crystals covering termite corpses, as well as calcium carbonate or calcium oxalate crystals in sheeting most likely for preventing the spread of infections. Calcium carbonates and calcium oxalate are indications of the extremely high Ca concentration in termite bodies (Jouquet et al., 2022). Termite workers dispose cadavers of dead nest mates through cannibalism, burial or necrophoresis in order to maintain healthy colonies. However, when numerous reproductives found a new colony by pleometrosis, there are no worker castes to destroy or segregate the corpses in the early stages of the foundation. In the study by Chouvenc et al. (2011), demonstrated that reproductives of the termite *Pseudacanthotermes spiniger* (Maburi) could fulfill this task in early pleometrotic colonies. Because of the claustral settings and the dealates' potential incapacity to eat on their own, their behaviour was limited to the burial of the cadaver within the first chamber. This burial behaviour, previously unknown in the reproductive caste of termites, seems to be caused by chemical signals emitted by corpses during decomposition, the most active of which were different fatty acids, indole and phenol. Finally, the burial resulted in the physical isolation of bodies, lowering the odds of opportunistic pathogens spreading among the remaining individuals. An extensive range of behaviours, including antennation, alarm, retreat, grooming and agonistic behaviours are used in termite corpse management. According to various postmortem times, castes and origin, the Asian subterranean termite, *Coptotermes gestroi* (Wasmann) foragers and soldiers had different corpse handling techniques. Soldiers engaged inspection, alarm, and agony behaviours toward the corpses whereas workers are more involved in managing the corpses which ultimately led to disposal (da Silva et al., 2019).

Avoidance

It is also known as necrophobiaor the fear of the dead, and is seen as a behavioural defence against risks including disease and predation. Animals of many kinds, from arthropods to fish, birds to mammals, including primates, frequently avoid dead people or the stench of death (Swift and Marzluff, 2015). Insects such as collembolans and *Periplaneta Americana* (L.) are frightened by the death. These insects stay away from shelters where conspecifics have been crushed to death, which releases toxins into the surroundings (Rollo et al., 1995). Necrophobic reactions are also seen by tent caterpillars, fall webworms and isopod crustaceans, which have a tendency to avoid body fluids, cadavers, wounded individuals and deceased extracts from conspecifics. Their own body fluids and unsaturated fatty acids also repulse them (Yao, 2009). In Collembola, *Protaphorura armata* (Tullberg), changes their way of movement based on the odour from the colony members in which they repel the area with odours from dead individuals and attract the area with live individuals (Nilsson and Bengtsson, 2004).With social insects that live in permanent nests, avoiding corpses seems like a straightforward method to avoid contact with source of infections, which is not a workable solution.

Avoidance in ants: A significant behaviour that restricts or lowers the spread of diseases may be avoiding sick and dying colony members (Park and Raina, 2005). When the nest becomes uninhabitable or when the colony moves, many ants relocate their nest. When dead bodies, pests and diseases are present or when a new possible nesting site is being assessed for biological safety, some ants avoid certain areas. Colonies of *P. barbatus* frequently move their nests each year following the summer rains (Bulmer et al., 2019). When colonies have nematode (Steinernematidae & Heterorhabditidae) or *B. bassiana* infestations, *S. invicta* moves out of the nest. Even if the diseased ants are eaten or discarded, infestations can occasionally be uncontrollable (Drees et al., 1992). House-hunting ants, *Temnothorax albipennis* (Curtis) hibernate in rock cavities in a variety of habitats. When better accommodation is available, they frequently move in search of it and they may do up to certain distance (Pratt, 2005). In order to stop the spread of illness, they can detect the presence of deceased nestmates and non-nestmate conspecifics and reject even the best new nesting sites and other materials. Consequently, ants have the ability to leave their nests when they become plagued with pests and illnesses and to assess the biological safety of possible new nesting locations (Franks et al., 2005). In *M. rubra* ants, they are able to identify the possibility of infection in a prey body and they will choose to recover food that reduces the colony's overall risk of disease (Pereira and Detrain, 2020). The first line of defense against infection is behavioural avoidance. Immunity at the individual and colony levels are inversely associated and workers in colonies with faster corpse removal have lower individual defences. Individual immunity and social immunity may compete with one another, controlling overall parasite defense. Alternatively, in the absence of pathogen avoidance, enhanced social immunity at the colony level may compensate for disease susceptibility to infection at the individual level and offer a protective benefit in overall colony defense (Cassidy et al., 2021).

Avoidance in termites: Termites often avoid areas where there is a chance of infection or poisoning. They stay away from infectious corpses, polluted nest locations and places where bodies have been deposited or buried (Ulyshen and Shelton, 2012). The subterranean termite *C. formosanus* stays away from both insecticide and non-insecticide killed termites and polluted areas (Song et al., 2006). Termites respond to the presence of entomopathogenic fungi like *Metarhizium anisopliae* (Metchnikoff) (Bulmer et al., 2019). The type of termites and the nature of the corpses have a significant impact on their behaviour when faced with carcasses. Such behavioural reactions are usually connected to the threat that the carcasses provide to the colony, as well as the feeding and nesting ecology of a particular species (Neoh et al., 2012). Qiu and Cheng (2017) found that in red imported fire ants, the chemosensory protein Si-CSP1 gene is linked to necrophoric behaviour. For binding of oleic and linoleic acids, the Si-CSP1 gene is necessary. Based on transcriptomic analysis, it was found that these fattyacids are involved in the necrophoric behaviour of adult workers. Transcriptomic analysis done in different life stages including larval instars 1, 2, 3 and 4, revealed that the mRNA of the protein expressed only in adult stage. On further analysis with different group viz., worker, a late female and male, the expression was seen only in workers group. In case of body parts, the expression is seen only in antenna. So, it is concluded that the Si-CSP1 protein was found only in adult worker at antennal region. Knockdown of this particular gene will lead to lose of the sense, leading to disturbance in the colony which in turn, is a possible way to control ants. Several molecules in eusocial insects are responsible for various behavioural and physiological disease defences to maintain the social immunity in their closely related packed colonies. miRNAs involve in regulation of carbohydrate and energy metabolism, immune response, various life processes in the termite bodies. Down regulation of miRNA had a significant negative effect on the physiological defences of termites. Total antifungal activity was reduced due to reduction in carbohydrate and energy metabolism on dysregulation of the immune genes. Therefore, the susceptibility of termite groups to entomopathogens are influenced by miRNA shaped social immunity, hence miRNAs may be effectively concentrated for the biological control of termites (Liu et al., 2023).

CONCLUSIONS

Corpse management helps the colony by recycling nutrients, maintain nest hygienic and strengthening its defense mechanisms. Necrophoresis, intraspecific necrophagy, burial behaviour and avoidance are the main methods used mainly by social insects to dispose off dead conspecifics. Sometimes two or more of these methods are present in the same species at the same time and the best option depends on how much complex information must be processed by those small social brains. The information has to be examined by chemosensory and tactile organs during the examination of a body. The signals given off by corpses give information needed to make conclusions that have developed to protect the colony's fitness. The mechanisms of corpse detection and recognition are supported by evidence from both points of view, although there are still conflict over the cues and sensory processes that explain behaviour. Behavioural study is an area with enormous scope in pest management. Recently the scientist from South China Agricultural University found that Si-CSP1 gene has important function in corpse management (Qiu and Cheng, 2017). This is a preliminary study in the field which shows the relationship between gene and behavioural responses in insects. Understanding the molecular mechanism is especially important since it opens up a new avenue for controlling pests by influencing their necrophobic behaviour. There are many opportunities to use the findings from these studies in pest management and further research can be done to better understand the behavioural aspects of social insects. It has been demonstrated in numerous studies that RNAi-mediated silencing of target genes can cause insect mortality, offering significant potential for insect pest control. As a result, miRNAs could be thought of as potential new insect control targets (Liu et al., 2023). Corpse management strategies are studied in various social insects individually and one or more combinations of insects. There is a scope to understand the phylogenetic relationship and evolutionary mechanism of this undertaking behaviour when these insects are studied simultaneously. Studying the genes and their expression profiles helps us to modify the genetic background of the insects for the better pest management. Further studies can be carried out for better understanding the behavioural aspects of social and other pestiferous insects and there are much more possibilities in utilizing results from these studies in pest management.

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