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Review

Corpse Management in Social Insects

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Abstract

Undertaking behavior is an essential adaptation to social life that is critical for colony hygiene in enclosed nests. Social insects dispose of dead individuals in various fashions to prevent further contact between corpses and living members in a colony. Focusing on three groups of eusocial insects (bees, ants, and termites) in two phylogenetically distant orders (Hymenoptera and Isoptera), 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. Distinctly different solutions (e.g., corpse removal, burial and cannibalism) have evolved, independently, in the holometabolous hymenopterans and hemimetabolous isopterans toward the same problem of corpse management. In addition, issues which can lead to a better understanding of the roles that undertaking behavior has played in the evolution of eusociality are discussed.

Key words: undertaking behavior; necrophoresis; eusociality; Hymenoptera; Isoptera.

Introduction

Social animals regularly face death of their group members. Species from diverse taxa recognize corpses and modify their behavior to reduce potential deleterious health effects. For example, the general awareness and prolonged curiosity exhibited toward dead individuals has been observed in elephants [1], and necrophagy of conspecifics occurs in various species of mammals, reptiles, amphibians, fishes and crustaceans [2]. Sanitary issues caused by exposure to corpses are universal, but especially in social organisms living in enclosed nests with dense populations, which make them vulnerable to contagious pathogens and parasites [3]. To maintain healthy colonies, eusocial hymenopterans (bees, wasps, ants) and isopterans (termites) have evolved sophisticated mechanisms to counter the threat of epidemic disease at both the individual and colony level, including active immune responses and behavioral adaptations [3, 4]. Corpse management, also anthropomorphically known as undertaking behavior, is one of the most intriguing innate behaviors in social insects [5-7].

Responses to corpses vary in insects with different level of sociality, including solitary (no shared nesting site, no parental care), gregarious (shared nesting site), and eusocial (overlap of generations, reproductive division of labor, and cooperative brood care). In some solitary or gregarious insect species (e.g. cockroaches, springtails), the response to a dead or injured conspecific is usually avoidance [8, 9]. In social spiders (gregarious) [10] and a social aphid (arguably eusocial), *Pemphigus spyrothecae* Passerini [11], disposing of the dead is simply a part of nest cleaning because it is indistinguishable from dealing with inanimate nest waste. In species of the two extensively-studied eusocial lineages, Hymenoptera (ants, bees, and wasps) and Isoptera (termites), corpse management is distinctive and differs from other nest cleaning behaviors such as disposing of feces and decaying food remains [6, 12, 13]. Facilitated with different behavioral repertoires (e.g., removal, burial, and cannibalism), honey bees, ants, and termites have evolved complex systems of corpse management

dealing with corpses of different ages, origins, and infection status [7, 14-16]. Although the specific components of corpse management are distinctly unique in various taxa of eusocial insects, the evolution of a complex strategy for dealing with the dead is a shared characteristic of eusociality.

In social insects, undertaking behavior is a sequential array of corpse-induced behavioral responses that target potential health-related hazards to maintain colony fitness. Among many responses to corpses, one of the earliest and well described in social insects is necrophoresis, which refers to the removal of dead individuals from the nest. The term necrophoresis was defined by Wilson et al. [5], which originated from Greek (necros refers to the dead and phoresis means transport) [15]. Necrophoric behavior is interchangeable with undertaking behavior in some literature. Here, we use undertaking behavior as a broad term that includes corpse removal from the nest, burial (covering the dead with soil and/or other materials), cannibalism (intraspecific necrophagy), and avoidance (preventing contagion by intentionally avoiding areas where the dead are located), a behavior sometimes considered as necrophobia.

The phenomenon of undertaking behavior resulted in anthropomorphic descriptions by early naturalists, such as “funerals” and “cemeteries” in honey bees [6] and ants [17, 18]. In-depth study of behavioral patterns associated with undertaking did not start until 1958, when Wilson et al. first identified the chemical cue eliciting undertaking behavior in two ant species, *Pogonomyrmex badius* (Latreille) and *Solenopsis saevissima* (Smith) [5]. To date, studies of undertaking behavior have been focused on three aspects: death recognition cue, behavioral process, and division of labor. Recently, there have been renewed interests in undertaking behavior in termites focusing on death cues and behavioral responses [7, 19-21]. Despite studies for over 50 years, the genetic underpinning of undertaking behavior is still not well understood. Some aspects of undertaking behavior are shared by the phylogenetically distant eusocial hymenopterans and isopterans, e.g., recognition/differentiation of the dead from the living. This review provides 1) an overview of undertaking behavior, focusing on death recognition, behavioral responses, and task allocation as they relate to dealing with the dead, 2) a comparison of adaptations in different eusocial groups, specifically, Hymenoptera and Isoptera, and 3) prospects for future studies.

Death recognition and elicitation of undertaking behavior

Once individuals die in the active area of a social

colony, colony members need to distinguish the dead from the living before taking any action. Death recognition depends on diverse cues, including chemical, tactile (e.g., shape and texture), and possibly visual input. Recognition of the dead has been widely shown to be achieved through chemical cues, explained by two primary hypotheses, “fatty acid death cue” [5] and “chemical vital sign” [12].

Pioneering studies on the nature of undertaking stimuli conducted by Wilson and his colleagues [5] in two ant species, *Pogonomyrmex badius* and *S. saevissima*, suggested that fatty acids, particularly oleic acid accumulating in dead bodies, trigger undertaking responses. This conclusion was confirmed later in other ant species [22]. The idea of a “fatty acid death cue” eliciting undertaking responses has been widely accepted for decades [23, 24]. However, certain aspects of undertaking behavior could not be explained by this hypothesis alone. Gordon found that oleic acid released foraging as well as undertaking behavior in *Pogonomyrmex badius*, depending on the social activities of the colony at a given time [25]. The rapid recognition and the subsequent response to corpses (within 1 hour) by nestmates indicate that decision-making time is too brief to allow decomposition and the release of a fatty acid death cue in the red imported fire ant, *Solenopsis invicta* Buren [26] and in honey bee, *Apis mellifera* Linnaeus [6]. Therefore, it was suggested that chemical(s) associated with life might inhibit a pre-existing undertaking releaser [6, 26]; and the “chemical vital sign hypothesis” was first demonstrated by Choe et al. [12] in the Argentine ant *Linepithema humile* (Mayr). Reductions in the quantity of two cuticular chemicals, dolichodial and iridomyrmecin on live workers, plays a more important role in inducing undertaking responses. Triglycerides were identified to be pre-existing chemicals inducing both necrophoresis and aggression [12]. The “chemical vital sign” hypothesis suggests an adaptive response toward freshly dead/killed individuals in insect societies. Instead of waiting for the release of “fatty acid death cue”, social insects living in dense populated colonies rely on the “chemical vital sign” to recognize dead individuals and elicit appropriate undertaking responses before the decomposition of corpses. This adaptation is not uncommon, and it is consistent with what typically happens in many species of vertebrates, in which dead individuals are recognized instantly according to the absence of signals associated with life, such as lack of movement or response to stimuli.

In comparison to ants, neither a “fatty acid death cue” nor a “chemical vital sign” has been determined in honey bees. However, Visscher [6] suggested that a

chemical signature was present immediately after the death. In addition, visual, auditory, and thermal cues were excluded in honey bees due to the facts that undertaking behavior took place in darkness, and removal activity was reduced to minimal when corpses were extracted with solvent or coated with paraffin [6]. In Isoptera, the mechanism of undertaking elicitation has been recently studied in a fungus-growing termite, *Pseudacanthotermes spiniger* (Sjöstedt). The burial behavior in *Pseudacanthotermes spiniger* was triggered by a blend of indole, phenol, and fatty acids [19], which, at least in part, supported the "fatty acid death cue" hypothesis. In the eastern subterranean termite, *Reticulitermes flavipes* (Kollar), however, the "chemical vital sign" hypothesis could not be excluded based on our observation that workers showed an immediate response (< 15min) toward freshly killed nestmates [27]. In a congeneric species, *R. virginicus* (Banks), Ulyshen and Shelton (2012) suggested that fatty acids (e.g., oleic acid) and tactile cues synergistically induce burial behavior. This is the only case in which a tactile cue was implicated; however, tactile cues alone have not been found to be effective. Termite workers are sensitive to light [28, 29], however, the involvement of visual cues is unlikely to be a major factor in the subterranean termites because undertaking behavior is independent of light-dark regime [20, 21, 27].

The term "necromone" has been used to describe death-recognition chemicals [9]. Fatty acids are a common recognition mechanism for death in arthropods. Oleic acid and linoleic acid are the two major unsaturated fatty acid compounds to induce undertaking behavior in ants [5, 22, 26] and avoidance in a wide range of arthropods including terrestrial Isopoda, Collembola, cockroaches, and social caterpillars, and these compounds are considered to be conserved necromones [8, 9]. Fatty acids have limited volatility and are derived from corpses or injured cells by enzymatic or bacterial processes, and serve as reliable cues for risks including predation and disease across wide phylogenetic ranges [9]. Interestingly, American cockroaches, *Periplaneta americana* (Linnaeus), are repelled (necrophobic behavior) by oleic acid [8, 30]. In contrast, termites, regarded as "eusocial cockroaches" [31], perform burial behavior in response to the same chemical [20]. A similar situation occurs in Hymenoptera in that solitary bees avoid foraging sites where dead conspecifics are present [32, 33], whereas honey bees remove corpses out of nests [6]. As fatty acid necromones are associated with injury and death caused by predation or contagion, effective recognition of these chemicals might benefit other non-social insects as well.

In summary, recognition of death through chemical cues is shared by honey bees, and many ant and termite species, but the specific chemical signals remain unclear in most species. Oleic acid is the only known common death signal recognized by some insects, whereas it is unknown whether other chemical signatures of death are shared among eusocial hymenopterans and isopterans. Two hypotheses, "fatty acids death cue" and "chemical vital sign", are not mutually exclusive. In addition to the "fatty acid death cue" and "chemical vital sign" hypotheses, it might well be expected that: 1) recognition of fatty acid death cues is an evolutionary conserved response from non-eusocial ancestors to avoid the dead, whereas undertaking is a derived behavioral trait in eusocial insects; and 2) death recognition through diminished chemical vital sign might be an evolutionary novelty in some eusocial insects, which enables workers to respond rapidly to prevent pathogen transmission. Besides chemical cues, the role of tactile cues needs to be studied in most social insects to fully understand elicitation of undertaking behavior.

Behavioral responses toward corpses

Eusocial Hymenoptera and Isoptera share the common features of group-living that make them vulnerable to pathogens and parasites, and consequently, they have evolved undertaking behaviors, individually, to mitigate hazards [3]. Specific behavioral patterns, however, vary among different social groups. Once death cues are recognized, social insects respond to the dead differently. Corpse removal (necrophoresis in a narrow sense) is prevalent in honey bees [6] and ants [5, 22, 34], although burial (covering the dead) [15] and cannibalism (intraspecific necrophagy) [35] were also documented in ants. In contrast, undertaking responses are more complex in termites than eusocial hymenopterans [7].

Studies of undertaking behavior in bees have traditionally focused on the honey bee, *Apis mellifera* [6, 36]. Honey bees dispose of nestmate corpses in a straightforward manner, i.e., corpse removal (Fig. 1C). This behavior pattern is a part of their behavioral repertoire [6, 37]. An "undertaker" bee typically antennates the dead bee briefly, grasps its appendages with mandibles, transports it outside, and drops it from the hive, while other debris in honey bee colonies is removed less rapidly [6].

The behavioral patterns of ants are extremely diverse, and they are known to keep the interior of their nest meticulously clean. Corpse removal (Fig. 1B), a common undertaking strategy in various ant species, is distinguished from other nest cleaning behaviors as corpses are transported more rapidly and

over greater distances than inanimate objects [5, 25, 38]. Ants transport corpses to certain sites, depending on the species. Carrying dead nestmates outside and discarding them on refuse piles (or kitchen middens) have been observed in the myrmicine ants *Pogonomyrmex badius* and *S. saevissima* [5], bull ants *Myrmecia vindex* Smith [22], red imported fire ant *S. invicta* [26], army ants *Eciton* [39], Argentine ants *L. humile* [12], and common red ant, *Myrmica rubra* (Linnaeus) [40]. Leaf-cutter ants of the genus *Atta*, however, remove them to special refuse chambers [41, 42]. Corpse removal has also been reported in several other ant species such as the desert leaf-cutter ant *Acromyrmex versicolor* (Pergande) [34] and another species *Temnothorax lichtensteini* (Bondroit) [15]. Cannibalism of dead individuals was observed in the myrmicine ants of genera *Pheidole* and *Solenopsis*, the weaver ants *Oecophylla* [17], and the red wood ant *Formica rufa* (Linnaeus) [43]. In the red imported fire ant *S. invicta*, cannibalism was occasionally observed at refuse piles in the field [26]. The red wood ant, *Formica polyctena* Foerster, eat their defeated enemies after intercolony battle, which has been considered to be adaptive as *F. polyctena* practices cannibalism behavior more frequently during period of food shortage [35, 44]. Cannibalism of the dead is not a predominant corpse management strategy in ants, but corpses could elicit foraging behavior and be consumed by neighboring scavenging species [5, 26]. Besides cannibalism, ants are reported to perform burial behaviors using soil and nest material in response to corpses [17] such as in *T. lichtensteini*, but it is less common probably because the energy input of burial activity is higher than corpse removal [15]. Another prophylactic strategy noticeable in ants is that moribund individuals leave their nests to die alone, as reported in *Temnothorax unifasciatus* (Latreille) [45, 46].

Undertaking behavior performed by subterranean termites can circumvent soil termiticide-based "barrier" treatment [47-50]. Most recently, an influx of studies have shown a complex series of undertaking behaviors in termites, including burial, avoidance, and cannibalism [7, 19-21]. Cannibalism of the dead in termites was considered to be a mechanism of recycling nitrogenous nutrients [47, 51], which is, in part, due to their nutritionally poor cellulosic diet [52]. *Coptotermes formosanus* Shiraki show cannibalism of cadavers when starved [53]. In another lower termite species *Reticulitermes speratus* (Kolbe) and a higher termite *Microcerotermes crassus* Snyder, living nestmates consume freshly dead and/or injured termites [7]. A precursor of necrophagy or cannibalism has been observed in subsocial woodroach species, *Cryptocercus punctulatus* Scudder and *Cryptocercus*

kyebangensis Grandcolas [54, 55]. In termites, cannibalism also functions as a hygienic strategy because by consuming the corpses it destroys the source of pathogens. The dampwood termite, *Zootermopsis angusticollis* (Hagen), eat both dead and diseased individuals, with higher chances of cannibalism toward the ones with higher spore concentrations of the entomopathogenic fungus, *Metarhizium anisopliae* (Metchnikoff) [56]. In *R. flavipes*, workers ingest harmful fungal masses of *Metarhizium anisopliae* while grooming nestmates and the conidia are inhibited through the alimentary tract [57]. It is also common that termites bury fungi-killed nestmates and old corpses to physically isolate them from the healthy nestmates [7, 16, 48, 49]. When challenged with the fungus *Metarhizium anisopliae*, *Coptotermes formosanus* displays undertaking behavior in a density dependent manner in which corpses would be cannibalized preferentially at a low level of mortality, while at higher level of mortality, burial was predominant [21]. In a fungus-growing species, *Pseudacanthotermes spiniger*, dealates buried the dead to prevent potential pathogen outbreak in the initial chamber [19], while in *R. virginicus*, the existence of insect corpses induces building behavior to separate the dead from the rest of the colony, which is also a form of burial [20]. In comparison to ants and bees, the propensity of termites for tunnel building plays an important role in their burial behavior [50]. In addition, the use of fecal material, chewed material or soil coated with saliva for burial provides antifungal components that act as further protection against fungal growth [19, 50]. In the case of fungi-killed corpses in *Coptotermes acinaciformis* (Froggatt) [58], and insecticide-killed (including fipronil and thiamethoxam) individuals in *Coptotermes formosanus* [49], termites have been observed to intentionally avoid dead individuals. Corpse removal seems less likely to be an end response in termites, as they do not have certain chambers or refuse piles that serve as waste storage sites, and they rarely leave their nests. Instead, corpse removal (Fig. 1A) is more likely to be a part of the dynamic process associated with other undertaking behaviors – corpses carried by workers would be eventually consumed or buried.

In addition to cannibalism and corpse burial, other behaviors including alarming, grooming, recruitment and aggression interact synergistically during undertaking processes [7, 16, 50]. When encountering a congeneric corpses, *R. flavipes* soldiers showed aggression and guarding behavior, while both worker and soldier castes exhibited strong recruitment activity [27]. Similarly, when fungal infection occurred, *R. flavipes* workers also aggregated and actively recruited fellow workers to cope with the

infected individuals [16]. Alarm behaviors in termite workers, characterized by oscillatory vibration and/or rapid walking to generate substrate-borne vibrations, are performed to alert or attract other colony members in the presence of competitors, predators, and entomopathogens [16, 59, 60]. In *Nasutitermes* termites, alarm pheromones have been identified in termite soldiers to function in recruitment of soldiers for colony defense [61, 62]. However, the sensory mechanisms of recruitment have yet to be determined.

Differential undertaking responses

Honey bees, ants, and termites often show species-specific undertaking responses toward corpses (Figure 1 and Table 1). Ants and termites also exhibit plastic responses to the nature of the corpses, including their postmortem time (age, indicator of decomposition status), infection status (whether harmful fungi are present), and origin (whether or not the corpse is a nestmate or of the same species). Honey bees removed 1h old corpses more quickly than freshly killed individuals [6], however, an undertaking response to corpses with longer postmortem time

was not investigated. Dead ants in *F. rufa* were consumed for food, but infectious ants were avoided [43]. In *T. lichtensteini*, workers discriminate old corpses from freshly killed individuals, with new corpses buried while old ones are transported outside [15]. Differential behavior patterns have been observed in subterranean termite species. Colonies of *R. virginicus* were found to isolate fungal infected individuals by burying the dead onsite, while the healthy corpses were cannibalized [47]. *Coptotermes formosanus* has been reported to attack, cannibalize and bury fungus-inoculated workers more frequently than uninoculated workers [63]. In *Coptotermes formosanus* and *R. speratus*, only new corpses and injured nestmates were cannibalized, whereas aged corpses were buried. In *R. flavipes*, conspecific corpses were taken back to the nest and possibly consumed, while workers opted to bury corpses of a congeneric species *R. virginicus* onsite with an additional colony defensive purpose [27]. Soldiers were also involved with guarding and attacking of congeneric corpses as the burial response was underway [27].

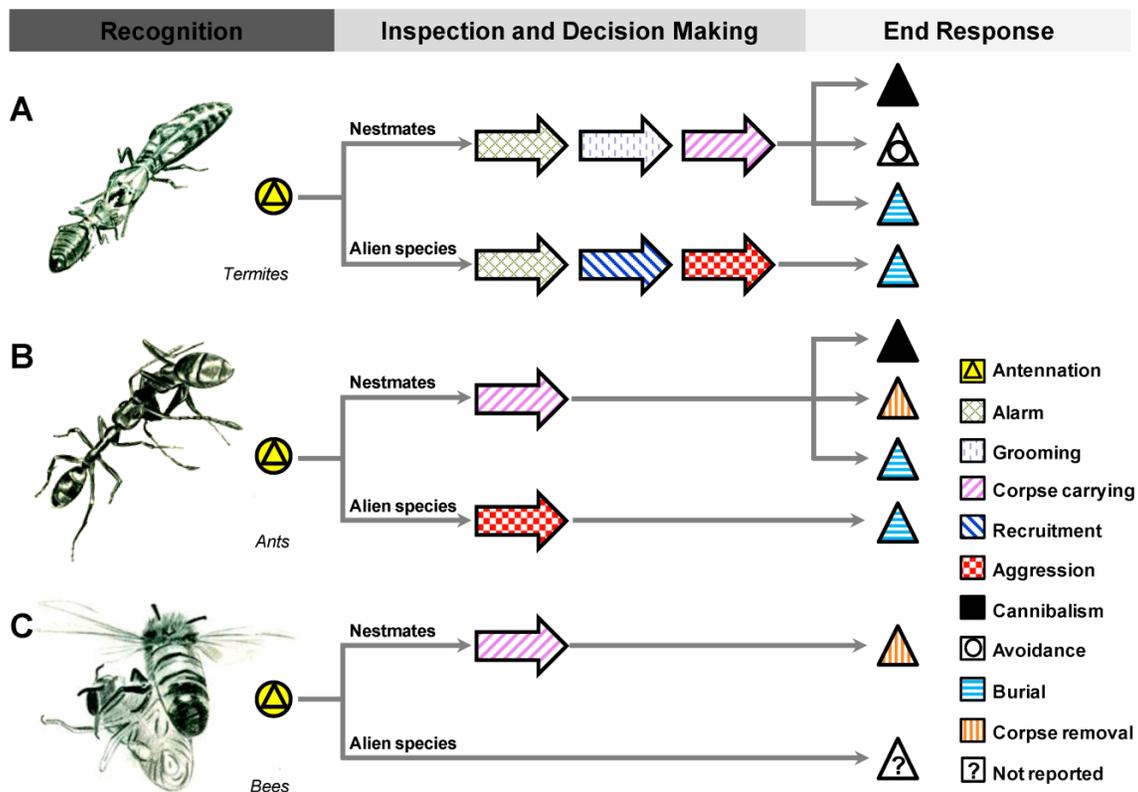


Figure 1. Undertaking process displayed by different social insects. **A** represents a termite worker dragging a dead nestmate; **B** shows an undertaker ant carrying a dead nestmate out of the nest; and **C** illustrates an undertaker bee removing a dead drone. *Reticulitermes flavipes*, *Linepithema humile*, and *Apis mellifera* are the representative species for termites, ants, and bees, respectively. Undertaking process involves three phases including recognition, inspection and decision making, and end behavioral responses. Illustrated by Zhou, X.

Table 1. Current knowledge of the undertaking process in Hymenoptera and Isoptera.

Undertaking Process		Hymenoptera		Isoptera
Phase	Behavior	Bees	Ants	Termites
Recognition	Antennation	<i>Apis mellifera</i>	Most species	Most species
Inspection and decision making	Alarm	NR*	NR	<i>Reticulitermes flavipes</i> [16, 50]
	Grooming	NR	<i>Pogonomyrmex badius</i> [5]	<i>Reticulitermes flavipes</i> [16]; <i>Coptotermes formosanus</i> [7]; <i>Reticulitermes speratus</i> [7]; <i>Microcerotermes crassus</i> [7]
End response	Corpse carrying	<i>Apis mellifera</i> [6]	<i>Pogonomyrmex badius</i> [5]; <i>Solenopsis saevissima</i> [5]; <i>Myrmecia vindex</i> [22]; <i>Solenopsis invicta</i> [26]; <i>Eciton</i> [39]; <i>Linepithema humile</i> [12]; <i>Atta texana</i> [41, 42]; <i>Acromyrmex versicolor</i> [34]; <i>Temnothorax lichtensteini</i> [15]	<i>Coptotermes formosanus</i> [49]; <i>Reticulitermes flavipes</i> [27]
	Recruitment	NR	<i>Solenopsis invicta</i> [26]	<i>Reticulitermes flavipes</i> [16]
	Aggression	NR	<i>Temnothorax lichtensteini</i> [15]	<i>Reticulitermes flavipes</i> [16];
	Cannibalism	NR	<i>Formica rufa</i> [43]; <i>Solenopsis invicta</i> [26]; <i>Pheidole</i> ; <i>Oecophylla</i> [17]; <i>Formica polyctena</i> [35, 44]	<i>Reticulitermes</i> sp. [47]; <i>Zootermopsis angusticollis</i> [56]; <i>Coptotermes formosanus</i> [7]; <i>Reticulitermes speratus</i> [7]; <i>Microcerotermes crassus</i> [7]
	Avoidance	NR	NR	<i>Coptotermes acinaciformis</i> [58]; <i>Coptotermes gestroi</i> [83]
Burial	NR	<i>Temnothorax lichtensteini</i> [15]	<i>Reticulitermes flavipes</i> [16, 27, 48]; <i>Reticulitermes virginicus</i> [20]; <i>Pseudacanthotermes spiniger</i> [19]; <i>Coptotermes formosanus</i> [7, 49]; <i>Reticulitermes speratus</i> [7]; <i>Microcerotermes crassus</i> [7]; <i>Globitermes sulphureus</i> [7]	
Corpse removal	<i>Apis mellifera</i> [6]	<i>Pogonomyrmex badius</i> [5]; <i>Solenopsis saevissima</i> [5]; <i>Myrmecia vindex</i> [22]; <i>Solenopsis invicta</i> [26]; <i>Eciton</i> [39]; <i>Linepithema humile</i> [12]; <i>Atta texana</i> [41, 42]; <i>Acromyrmex versicolor</i> [34]; <i>Temnothorax lichtensteini</i> [15]	NR	

* NR: Not Reported.

Undertaking responses are, in part, dependent upon the feeding habit and nest ecology in a given species, and also the risk associated with corpses [7]. Postmortem time of corpses is associated with the decomposition of the dead, indicating whether they are valuable for recycling in species practicing cannibalism [7]. Fungi infection is common in both ants and termites, which react accordingly to prevent epidemic outbreaks within their respective colonies [3]. The presence of non-nestmate corpses could be signals of competition, predation, or disease [27]. Therefore, through corpse management, social insects mitigate disease hazard [6, 7, 22]; and in termites, it brings additional incentives for recycling nutrients and contributing to colony defense [27]. Further research is needed to determine the chemical signature of corpses and mechanisms of decision-making during the complex undertaking processes.

Task allocation of undertaking behavior

Reproductive division of labor and subsequent task allocation are characteristics of the eusociality. Based on their morph and age, mechanisms underlying the division of labor in the non-reproductive worker caste can be summarized into physical polymorphism and age polyethism [64]. In addition, workers in some species show considerable behavioral plasticity in task allocations and partition their work force to meet the specific demands of a colony [65]. This flexibility is critical to the growth and survival of a colony, especially for disease management and colony defense. Undertaking behavior is performed by the worker castes [66], primarily due to their capability of corpse recognition. Not surprisingly, sensitivity to oleic acid is caste-specific in a leaf-cutter ant *Atta mexicana* (Smith), where workers are responsive but soldiers are not [67]. The study of

task specialization on undertaking behavior has been focused on whether there is worker polyethism and how it is regulated.

As a part of honey bees' repertoire, undertaking behavior was first reported to be specialized by a small group of workers that comprise only 1%-2% of the colony population [6]. Domination of the task by a few active individuals is frequently demonstrated in the literature with the longest recorded tenure of removing 114 corpses over a 13 day period by an extreme specialist [37]. In honey bee colonies, both age polyethism and genetic variation influence division of labor among workers. Undertaker bees are middle-aged workers, which are more likely to act on corpse removal during their entire pre-foraging career than other workers of the same age [68]. Genetic effects suggest lifetime differences in behavior preference in honey bee, and genetic factors constrain colony-level plasticity for undertaking behavior, given the fact that removal of undertakers failed to result in task-switching by other workers [69]. Such a result excludes the possibility of the "genotypic threshold model" proposed by Robinson and Page [70], which predicts that commonly a task will be performed by worker specialists with the lowest response threshold that is genetically influenced, while more workers with higher thresholds switch to this particular task with increased stimulation, i.e., a feedback loop of task regulation. Task specialization of undertaking behaviors occurs similarly in ant colonies, as reported in the desert leaf-cutter ant *Acromyrmex versicolor* in which genetic variation affects worker task performance [34, 71]. Both honey bee and desert leaf-cutter ant colonies are maintained by multiple mating events or multiple queens. This enriched genetic diversity increases the probability of having undertaking behavior in their behavioral repertoire at the colony level.

Learning and memory have not been suggested to be important components of corpse removal in honey bee, because undertakers demonstrated no obvious improvement with experience [68]. In contrast, in the common red ant *Myrmica rubra*, undertaker ants behaved as short-term specialists, and they disposed of dead bodies to specific locations (ceme-teries) based on spatial memory [40]. Emergent worker polyethism in Hymenoptera is affected by colony size, with increased group size leading to efficient allocation of individuals to different tasks (specialists) to meet colony demand [72-74]. Polyethism is likely the mechanism to govern undertaking specialists in some ants that live with heterogeneous surroundings. Complex cues could be present concurrently in a large ant colony, therefore focusing on one

task by specialists prevents inappropriate task-switching leading to high fitness cost. For example, a single decomposition compound, oleic acid, can elicit both foraging and undertaking responses [25].

In hemimetabolous termites, there have been no reports of task specialization of undertaking behavior. Intercaste flexibility is reported in a pleometrotic termite species *Pseudacanthotermes spiniger*, in which dealates performed corpse-burial behavior in the initial chamber before the first generation of workers develops [19]. In addition, termites employ various strategies such as removal, burial, cannibalism and corpse avoidance (Fig. 1), which makes it difficult to define "undertakers". The totipotent worker caste in termites is considered immature, whereas the worker caste in holometabolous ants, bees, and wasps is a developmental end (adult). Therefore, age polyethism in hemimetabolous termites includes both polyethism between different instars and age of the last instar [75]. Large workers of *Reticulitermes fukienensis* Light, undertake most tasks including corpse burial, but behavioral plasticity is present with all sized workers being able to perform the task [76]. In higher termites, however, there is evidence of age polyethism [77, 78], but whether undertaking behavior is amongst the age-related behaviors has not been determined.

Perspectives and future research

There is renewed interest in undertaking behavior, especially defining behavioral responses [7, 21, 27] and sensory cues [19, 20]. However, task allocation during the undertaking process is poorly understood. Since the worker caste in lower termites can be considered as "generalist" [66, 76], activation of reserve labor is a possible mechanism to compensate for the lack of specialists in lower termites. Activation of reserve labor has been documented in honey bees [79, 80] and ants [81, 82], and it was also implicated in a higher termite, *Nasutitermes exitiosus* (Hill) [75]. The role of reserve labor in the lower termites, however, has yet to be investigated.

Despite the differences in division of labor and task allocation, both eusocial hymenopterans and isopterans manage corpses effectively. In both holometabolous hymenopterans and hemimetabolous termites, the genetic underpinnings of undertaking responses remain an unsolved mystery and warrant further investigation. Given that undertaking behavior is one of the characteristics shared among eusocial groups, comparative studies in diverse eusocial lineages using integrative approaches involving behavioral observation, chemical ecology, genomic and functional genomic analyses will shed light on the proximate mechanisms of eusociality.

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Competing Interests

The authors have declared that no competing interests exist. All authors read and approved the final manuscript.

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