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Review

The funeral ways of social insects. Social strategies for corpse disposal

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ABSTRACT

The successful life of insect societies has evolved from the division of labor among more or less specialized individuals, who carry out all necessary tasks for the maintenance and growth of the colony. The extreme division of labor has produced workers specialized in the removal of dead members of the colony, an evident and highly stereotyped behavior called undertaking which consists of the ability to recognize and dispose of the dead members of the colony using specific chemical cues. Although living in enclosed nests has contributed to the ecological success of social insects due to environmental control, it also poses disadvantages. Nests of social insects, containing dense groups of genetically close individuals with frequent physical contact, present ideal conditions for the incidence and dispersion of infectious diseases. To maintain strict microbiological control inside the nest, these insects have evolved hygienic behavioral strategies to avoid and control the proliferation of pathogens. Undertaking behavior is one of the fundamental strategies to exert microbiological control inside the nest by means of suitable management and removal of dead members of the colony, to prevent the emergence of epidemics that may lead the insect society to extinction. Therefore, undertaking behavior has been fundamental to the evolution of social insects. This stereotyped behavior constitutes an excellent model for the understanding of both social evolution and the neurobiological basis of social behavior. In this paper, we review the present knowledge on undertaking behavior, and outline some perspectives of the study of such far-reaching behavior of social organization.

KEYWORDS: social insects, undertaking behavior, corpse management, necrophoric behavior, nest hygienics, division of labor, worker specializaion

1. INTRODUCTION

Social insects (Hymenoptera: bees, wasps and ants; Isoptera: termites) are the only animals, apart from humans, that have sophisticated behavioral strategies, known since ancient times, for the final disposal of dead conspecifics. The extreme division of labor in social insects has produced individuals who engage in very specialized tasks [1, 2], such as disposal of dead nestmates or those mortally sick due to easily-dispersed infections; these behaviors are known as undertaking, and the workers as undertakers [3-5]. Nestmates that have died inside the nests represent a high epidemiological risk for insect societies because of the opportunistic microbial proliferation they may cause, especially those that have died due to some infectious agent [6]. In fact, in bee and ant colonies, more or less specialized individuals engage in undertaking and

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quickly remove all the dead members of the colony inside the nests [1, 4, 7, 8] in order to prevent these potential sources of diseases from contacting other members of the society, mainly the queen and the brood.

Undertaking behavior is one of the most conspicuous behaviors of social insects, and was, therefore, the subject of great interest and fascination to ancient naturalists, many of whom made naive and anthropomorphized interpretations about ‘funerals’ and cemeteries of ants and bees [5]. Plinio even thought that the dead ants were introduced in a coffin made from some seed cases before being transported to the cemetery in a funeral procession; he stated: *“Ants, apart from the man, are the only animals who give sepulture to their dead”* [9]. André [10] mentions the story of Mrs. Hatton [also cited in 11], who wrote about funeral honors and processions offered to the dead and, even more, claimed to have observed the digging of one tomb for each honored dead ant [9, 11]. She claimed that those ants that refused to excavate a grave and to carry a dead ant to the cemetery would be judged and executed in the middle of the square of the ant city! Although André denies such a story, he admitted other curious stories about the cult of the dead, funeral processions, the respect shown by ants while transporting the dead, and the ordered ways in which cemeteries are organized, among other myths. Personally, Réaumur [9] was skeptical about ant funeral stories. Most descriptions of ancient naturalists about the transport of corpses have generally been anthropomorphic, anecdotal, and fanciful [9-11]. However, undertaking behavior has been studied scientifically in several species of insects since Wilson *et al*. [12] named corpse removal as *necrophoresis* (from the Greek etymology, *necros*: death, and *phoresis*: being carried), to distinguish it from other hygienic behaviors (such as other waste removal behaviors) because of its essential nature in social life and the evolution of eusociality.

Although undertaking behavior is a highly conspicuous behavior in social insects and an essential adaptation in the evolution of eusociality, its scientific study has been often disregarded. Presently, interest has been renewed in the study of undertaking behavior in social insects [13], due to the modern resurgence of the superorganism concept [14], with regard to the analogies between individual and social immunity [15] and the use of social insects as models for epidemiology and control of diseases [16, 17]. However, there has been little investigation on the ethological, neurobiological, sociobiological and immunological aspects of undertaking behavior. As a part of the social immunity of colonies, undertaking behavior involves the ways by which social insects dispose of the corpses through different strategies. In this paper, we provide current references and summarize the current status of our knowledge on undertaking behavior in social insects. We also review the strategies of corpse management, nest hygiene, microbiological control, releasing mechanisms, death recognition, and behavioral responses to death cues. In addition, we review the social organization of undertaking behavior from an evolutionary perspective. With this review, in addition to providing a summary of undertaking behavior in social insects, we are also interested in motivating future empirical and theoretical research on this important and forgotten topic of the life within the nests of social insects.

2. Nest homeostasis and the unseen epidemiological threat

2.1. Environmental control

The nest is a distinctive characteristic of social insects, and has been an important factor in the origin and evolution of their sociality [18]; even nomadic species have periods of habitation in temporal refuges or bivouacs [1]. Most of the life span of the members of the societies of insects, and sometimes also their death, occurs inside the nest, which is much more than a mere physical refuge for the members of the colony. Although it is, in fact, a physical shelter that provides some insulation and protection from the external environment, and is where the offspring is raised, the nest is actually part of the society, due to members’ dependence on it and the energy invested in it [19].

The nests of social insects may be built by digging in the soil or in wood, using living vegetal materials or constructed with a great diversity of other materials. Social insects are true ecosystem engineers [20-23], which modify the structure, as well as the chemical and biological composition of their nests and soils, to provide a stable environment that influences the fitness of their society [22, 24]. Nests of social insects provide several benefits such as protection against predators and enemies [25], facilitate communication, and improve the abilities to raise the offspring by means of food storage [1]. Moreover, enclosed nests confer to social insects the ability to adaptively control the environment [25] by means of active mechanisms based on cooperation, maintaining stable conditions and buffering environmental fluctuations [19, 26], and improving the development of the offspring [27]. Favorable temperature, humidity [1, 2, 14, 19, 28], and pH levels are maintained, and organic carbon is retained [29], while CO_2 concentrations are held in narrow ranges [30]. Nest architectural features prevent floods caused by rain [25, 29, 31] and have an important role in the defense mechanisms against parasites, parasitoids, and infectious diseases [18, 25].

2.2. The fortress at risk

In spite of the benefits, the life in society also involves costs, risks and disadvantages of living in overcrowded enclosed nests. As the group size increases, the competition for food and for the nesting site, as well as the exposure to diseases and parasites, also increases [6, 27]. Due to their stable environments and the presence of the brood and food reserves, insect societies are highly attractive for predators, competitors, and parasites [32]. Also, the nests of social insects create unique environmental homeostatic zones. This provides a habitat, not only for the members of the society, but also for a plethora of commensal, mutualist, and parasitic organisms, including bacteria, fungi, yeasts, ricketssia, viruses, protozoa, and a high diversity of invertebrates [1, 2, 33-38]. As a consequence of nutrient abundance due to the accumulation of different types of waste produced by the society, as well as temperature and humidity conditions, the microbial abundance and activity is usually high in the nests, creating “islands” in ecosystems where the diversity and abundance of litter transformers are higher than in the surroundings [1, 22, 23, 38-44].

Although construction of enclosed nests was essential in the geographic expansion of social insects through temperate environments [4], it also aggravated the disadvantages of living in groups and involved the necessity to increase hygienic behaviors [6, 45] to diminish the risk of diseases arising from microbial proliferation. It is well-known that, apart from predation, parasitism and diseases have considerable effects on survival and reproduction; therefore, they are powerful agents of natural selection [6, 46, 47]. Microorganisms, bacteria, fungi, and protozoa are everywhere; they abound in air, water, and soils [48-50], where all of them are distributed across different regions according to depth and soil composition [51]. This abundance and diversity in microbial populations represent a serious threat for all social insects, mainly for those which build nests in soil, because many of these organisms can be either opportunistic or entomopathogenic [16, 52-57]. It is well known that the non-airborne transmission of parasites and diseases depends on the frequency of contact between individuals and the population density [58, 59]. Therefore, social insects are highly exposed to epidemics. Living enclosed in stable humid environments even up to several years, in dense groups of genetically related individuals with frequent contact and exchange of fluids, and with high energy supplies stored in the form of brood and food reserves, the colonies of social insects offer ideal conditions for the invasion by and dispersion of parasites and infectious diseases [6, 34, 35, 60-62].

3. The nest sanitation

3.1. Social immunity: microbiological control

Since fitness of the whole colony depends on reproductive individuals, it is necessary to keep them, together with the offspring, safe from infections and parasites [32]. Although the homeostatic environment provided by social insect nests increases the risk of an epidemic, insect societies, especially large and long life colonies, have evolved sophisticated and effective individual and social mechanisms of microbiological control to prevent, control, and eliminate parasites and pathogens [43, 63, 64]. These mechanisms include individual, mechanical and immunological defenses [65]; chemical secretions [63, 64];

microbial symbionts [66, 67]; nest architecture and compartmentalization [59] and behavioral defenses [6, 68]. These strategies contribute to the strict microbiological control maintained in the interior of the nest and deter parasites that may enter, establish, and disperse in the colonies of social insects [6], thus preventing epidemiological sprouts [38]. The behavioral mechanisms of defense against parasites, known collectively as behavioral immunity [68], constitute part of what has been called social immunity [6, 61] and complements the individual immune system [65] of the colony members. Behavioral immunity in eusocial insects has been called antiseptic behavior [61], *i.e.*, behaviors that provide defense against pathogens to decrease transmission of, and increase resistance to, diseases. These include: grooming, hygienic behavior, undertaking, avoidance, glandular secretions and the use of resins in the nest. Thus, although living in groups increases the risk of exposure to a great diversity of pathogens [34, 35], it also increases the control of pathogenic infections. In fact, social insects show complex responses when they detect pathogens in the colony or in the nest [69]. Advantages of social living can only be achieved with the incorporation of sanitary mechanisms, even though these mechanisms are costly in terms of energy and time (for instance, waste disposal constitutes 10% of the work performed outside the nest of *Atta colombica* [70]). Benefits of nest sanitations must exceed such energetic costs.

3.2. The hygiene inside the nest

One of the main strategies of microbiological control, in which social insects invest much time and energy, is constituted by those behaviors related to the hygienics inside the nest, known collectively as nest sanitation [71]. Hygienics inside the nest comprises all behaviors that help to prevent invasion by micro- and macroparasites [72, 73]; these behaviors have been described in arthropods that live in dense groups [74, 75] and build enclosed nests: ants [1, 2], social mites [76-80], aphids [81, 82], and social spiders [83, 84]. Nest hygiene has been conserved from solitary and presocial ancestors of social insects [85], and can be found in the present subsocial species that remove feces from the nest and clean the brood to remove fungal spores and hyphae [74, 86]. These strategies constitute adaptations that are fundamental for the evolution of societies [71].

3.3. Prophylaxis inside the nest

Most social insect defenses against pathogens are prophylactic. Although insect societies that nest in soil, as ants and termites do, have the advantage of some plasticity in the construction of their nests, they also must work to avoid the invasion and proliferation of the abundant microorganisms, mainly the entomopathogens [52-54, 56]. Social insects disinfect nest materials and cover nest walls with antimicrobial substances that are either internally produced [32] or collected from the environment, such as propolis in honeybee, the stingless bee *Trigona sapiens*, and *T. hockingsi* colonies [32, 64, 87], and solidified tree resins in wood ants colonies [88]. This is important because ants and termites keep the brood directly on the substrate, exposed to soil microorganisms [51], and their eggs lack both cellular defense against invading antigens and protective chemicals against parasites [32]. When bees are incapable of removing foreign objects and dead nest intruders because of their size, they encapsulate them with propolis [89] to prevent their decay by constraining the proliferation of decomposer microorganisms that may compromise the entire colony [90]. Ants, on the other hand, cover any unpleasant or sticky substances with soil particles, to avoid being caught in them [1].

3.4. Grooming and allogrooming

Foragers of social insects require to go out of the nest in search for resources for the colony. As wasps and bees fly to and from foraging sites, they have less contact with potential parasites from the substrate. However, when they land on the foraging site, they can be exposed to a higher density of infectious elements [16]. On the other hand, ants and termites do not fly, except for the winged males and females in the reproductive season; instead, they forage at ground level, and hence are always exposed to higher concentrations of potential parasites [16]. Tens, hundreds or even thousands of foragers leave the nest every day, getting exposed to the environment and to different kinds of parasites, likely bringing some of them back to the nest, and thus placing the entire colony at risk. However, social insects may prevent hazardous contact by avoiding areas rich in parasites [6, 68], as termites do [44], or by changing the timing of their foraging activities, as leaf cutter ants do [91]. In spite of this, foragers are at high risk to be parasitized when they are away from the nest. Some infected foragers may be excluded when they return to the nest. Honeybees, for example, have specialized guards controlling the entrance to the nest and excluding all infected nestmates [6, 92, 93]. Besides this, members of social insect colonies practice grooming and allogrooming to eliminate, by mouth, detritus and other micro- or macroparasites from the cuticle [6, 42, 74]. In grooming, social Hymenoptera collect and store the waste and parasites in the infrabucal pocket, a cavity at the entrance of the pharynx [94, 95]. After some time, the insects eliminate them as waste pellets [1]. Frequency of grooming and allogrooming increases when the society has been exposed to pathogens [96] or with the size of the colony [6]. Grooming and allogrooming may be disadvantageous in some circumstances because it may increase parasite transmission [35].

3.5. Chemical defenses

The process of grooming and allogrooming is accompanied by the secretion and spread of antibiotic chemicals over the body surface [63]. These substances are produced by several exocrine glands such as the Dufour’s, mandibular, venom, and metapleural glands in social Hymenoptera [32, 63, 97, 98], and by sternal glands, head glands, as well as antimicrobial compounds in rectal fluids and feces of Isoptera [44, 63]. Social insects have an arsenal of antiseptic chemicals to defend their nests against predators and parasites: fungistatics, bacteriostatics, fungicides, bactericides, and agents against arthropods and other invertebrate parasites [32, 98]. For instance, social bees build honeycombs with materials mixed and impregnated with powerful antibiotics secreted by salivary glands [16] and collected resins [64], where the queen lays her eggs. In addition, royal jelly [99, 100] and honey [101, 102] also contain antiobiotics. External materials collected by bees, as well as secretions of the mandibular and Dufour’s glands, are used to coat the walls of the nest to provide a source of humidity, chemical cues, food and defense against microbial infections [32]. Social bees maintain their eggs in these combs covered with antibiotics. On the contrary, most termites and ants build their nests in soil and maintain the brood directly on the substrate, where microorganisms abound [22, 23, 38, 39, 41-44, 103]. To protect the brood and themselves against microorganisms, termites construct their nests with soil and feces, which have antimicrobial compounds and antifungal activity [44]. In addition, termites fumigate their nests with naphthalene, a powerful microbial inhibitor and anthelmintic [104]. Ants secrete, from the metapleural gland (a paired gland in the thorax present only in Formicidae), a broad spectrum of antimicrobial substances which are distributed all over the nest and on their bodies by grooming and allogrooming [2, 105]. The secretion from this gland increases during microbial infections [106]. In some groups of ants, like all weaver ants, some parasitic ants, and most *Camponotus* species, metapleural glands are secondarily atrophied or absent [105]. Those ants are not particularly susceptible to diseases, because they compensate with other glandular secretions that have antimicrobial properties, like mandibular and venom glands [97, 107]. These secretions can be deposited on eggs by the queen [108] or by the workers [109].

3.6. Defensive microbial symbionts

In addition to all the defense mechanisms mentioned above, social insects also use beneficial microbial symbionts to protect themselves against pathogenic microorganisms [67]. Symbiotic microorganisms provide protection through the production of antibiotics or chemical compounds that have direct harmful effects on antagonists, or by colonizing internal or external niches of the host that competitively exclude pathogens, or by interaction with the host immune system enhancing resistance to pathogens or parasites [43, 67, 110-112]. In fact, societies of bees, ants, and termites, require symbionts to keep a healthy colony [43]. The best-known symbiotic relationship between social insects and microorganisms is the tripartite symbiosis between fungus-growing ants, their fungus cultivar, and defensive actinomycetes. These ants cultivate a fungus from vegetal material that is used as food for the queen and the brood [14]. Despite the meticulous care of the ants and the secretions of the metapleural glands, the cultivated fungus may be invaded by *Escovopsis*, a parasitic fungus lethal for the cultivar. However, fungus-cultivating ants have, on the cuticle of their bodies, an actinomycete bacterium that produces antibiotics against *Escovopsis*, controlling its growth and maintaining an equilibrium between the pathogens and the cultivated fungus [14, 66, 113, 114].

3.7. Waste management in social insects

All societies generate a large amount and a great variety of waste that includes the excreta of the members of the colony, food waste, and their own dead members, that may promote the proliferation of parasites and opportunistic pathogens [6, 71]. As all this waste is a potential source of diseases and also reduces the space in the nests, there are strong selective pressures for the evolution of waste management as a part of nest sanitation [71]. For non-social animals, the best way to avoid the risk of diseases caused by exposure to hazardous waste material is to relocate themselves. However, for social insects that live in established nests, the generation and accumulation of waste and corpses represent a potential hazard and risk for epidemics. Also, nutrients in waste [40, 115] can promote the proliferation of invertebrates, microorganisms [116], opportunistic pathogens, parasites [6, 36], and harmful gases [117-119].

Social insects are very fussy about cleaning themselves, their nestmates and their nest interiors, mainly the brood and the queen chambers [32], through continuous hygienic activities. Foreign objects, debris, and the waste generated by the society are constantly removed from the nest, particularly from the queen and brood chambers, and are taken to garbage collector sites, known as refuse dumps (also refuse piles, waste dumps, waste heaps, garbage heaps and kitchen middens). Dumps may be located either at the exterior near to the border of the nest, at some distance from it [70, 120-122], or in special chambers inside the nest [123]. Honeybees remove diverse debris, larval excreta, remains of pupal cocoons, cappings and rotten material from cavities before building combs [64, 124] and perform a cell cleaning in preparation for egg laying [125]. Moreover, social and subsocial insects defecate “responsibly” [71, 74, 75] away from the nest: honeybees defecate away from the nest when they fly, whereas other species including ants [2, 75, 126-128], stingless bees [129], aphids [81], social mites [79, 80] and other subsocial insects [74], defecate in particular areas such as the borders of the nest or in the refuse dumps. Species that build open nests hanging from trees, such as paper wasps, eliminate feces from larval meconia and corpses by simply dropping them [18]. Termites have solved the problem of feces accumulation by using them in different ways. Fungus-growing termites will either fertilize their fungus by defecating on it, or use their feces with antifungal activity as material to construct their nests [44]. Ants keep the central chambers of the nest (with the queen and the brood) clean and separated from the waste traffic, showing a strict physical separation between the clean areas and those destined for waste [6].

4. Undertaking behavior: facing and responding to corpses

Non-social animals respond in different ways to injured or dead conspecifics, mainly through the avoidance of corpses (necrophobia) evoked by products of bacterial corpse decomposition, to reduce the risk of contagious pathogens [130-134]. On the other hand, when social animals die, the decomposition processes render them a threat to group survival, precisely because the corpse constitutes a source of opportunistic decomposers and pathogens that may initiate an epidemic. Those workers needing to leave the nest, including foragers, are exposed to death far away from home; and when they die naturally, their corpses are quickly devoured by other insect scavengers, mainly ants, maggots and beetles [135]. On the contrary, when social insects die inside the nest, they may not be consumed by scavengers as quickly as at the exterior, and their bodies could remain inside the nest for some time as rich resources where microorganisms progressively develop, while soft tissues may be consumed by microfauna carrion-eaters [136].

4.1. The corpses menace

Corpses become high-quality resources, providing ecological niches rich in carbon and other nutrients for the development of microbial detritivores and decomposers. Bacteria and spores of fungus are present in soils, air, and water, and within and over animals (mainly necrotrophic ones) before they die [42, 137]. As a result, decomposition initiates soon after the occurance of death and is helped by autolysis processes [138]. Dead animals create islands of fertility in which soil microbial biomass and activity increase dramatically [138]. Although individual insects are small, the number of individuals that die and may accumulate in a big society may be large. Although foragers have higher mortality than other workers in the nest [139, 140], in a big society workers in the nest may be extremely numerous. A mature colony of *Atta colombica*, for example, may have 2–2.5 million workers at any time [14], of which, around 70,000 workers may constitute the forager population [141]. It has been estimated that in order to maintain a population of 2 million workers in such a giant colony, the queen must lay at least 6 million eggs each year [1, 142], and if the average developmental time of workers is about 60 days [2], almost the entire worker force would be replaced every 4 months, on average. This would result in thousands of workers dying outside and inside the nest every day, whom, if not removed, would accumulate and overflow the fortress. Decomposition of carcasses in soil raises the populations of microorganisms, including a variety of bacteria (*Bacillus*, *Pseudomonas*), fungi (*Fusarium*, *Aspergillus*, *Penicilium*, *Rhizopus*, *Mortierella*, etc.), actinomycetes (*Streptomyces*), protozoa and nematodes [143, 144].

Although organisms involved in decomposition are not usually considered as pathogenic, they may become a threat with a large inoculum and high exposure occurrence [130, 131, 145]. However, corpses not only raise the populations of opportunistic microorganisms, but they may also release propagules of pathogens and parasites from dead bodies inside the nest [16, 132], as some entomopathogens actually do [146], along with the waste and toxins that decomposers may produce [147, 122]. Infected corpses can transmit pathogens to other members of the colony even some time after the occurance of death, only if the infectious agent is viable, if individuals are exposed to that agent, and if these individuals are susceptible to infection [130]. However, when death occurs, the environment in which pathogens live is no longer adequate and it progressively becomes incapable of sustaining them alive; eventually, all pathogens will die [131]. Nevertheless, this does not happen immediately, and viable infectious pathogens may remain in corpses for some time after death; also, transmission of infectious agents from corpses to living individuals may occur [130]. The duration of the viability of the pathogens depends on the pathogen, the host, environmental conditions, and other factors, but if conditions preserve the body and delay decomposition, it may extend for a long time after death [131]. In addition, some insect pathogens require some time after death to produce spores and complete the cycle of infection [146, 148]. Thus, corpses represent an epidemic threat for the colony that requires quick elimination.

4.2. Corpse management in social insects

As can be seen, undertaking behavior, *i.e.*, the opportune detection, recognition, and disposal of the dead, has been an essential evolutionary adaptation of eusocial insects to avoid the unleashing of an epidemic from pathogens that may be released from corpses. Thus, mechanisms for corpse disposal constitute a widespread characteristic in all eusocial insects. Undertaking behavior in social insects provides an altruistic protection of nestmates against pathogens, which results in the increased fitness of the whole society. Nevertheless, undertaking behavior also requires collateral prophylactic behaviors toward workers that have frequent contact with corpses and refuse piles, resulting in exposure to pathogens and a shorter life expectancy [121].

There is a variety of sophisticated behaviors by which social insects respond when they find dead conspecifics inside their nests, and, depending on the species, these insects will recognize and treat the corpses according to: 1) the time elapsed since death (the age of the corpse), 2) the origin of the corpse (whether or not is a nestmate, non-nestmate, or conspecific), and 3) pathogenic potential (whether or not the corpse is infected). The behavioral ways by which social insects respond and dispose of the corpses include necrophobia (avoidance of dead or injured conspecifics), necrophilia (attraction to dead conspecifics), intraspecific necrophagy (cannibalism of dead conspecifics), necrophoresis (the removal of dead conspecifics), and burial behavior. A brief description of such behavioral stategies follows:

1. Necrophoresis [12]: This refers to the removal of corpses by means of transport towards the refuse piles inside or outside of the nest, or simply by dropping them outside, far away from the nest. Necrophoresis is the main strategy employed by social Hymenoptera, and, although scarcely, carrying of corpse also has been reported in termites as part of their main corpse disposal strategies, *i.e.*, cannibalism or burying [149].
2. Intraspecific necrophagy or cannibalism of dead or injured conspecifics [1]: Termites dispose of their nestmates' corpses mainly by necrophagy, although this has also been reported in ants. Bees never eat their dead adults.
3. Burial behavior: This means that the corpses are covered with soil particles or other materials [150, 151]. Burying behavior is a common corpse disposal way in termites, and it has also been reported in ant colonies.
4. Necrophobia: The avoidance of corpses, or the areas in which they have been for some time [1, 151-156]. This behavior has been reported and documented in ants and termites.

5. Social insects' behavioral responses to death and dead

Through undertaking behavior, social insects place social barriers against pathogen transmission [157], cleaning the permanent home site by excluding, removing, or isolating corpses, and reducing contact with those potential sources of biological contamination. All undertaking strategies comprise a complex and sophisticated sequence of behavioral patterns which involves a specific stimulus: a dead corpse inside the nest. In the appropriate context, this stimulus leads to detection by undertaker individuals, inspection, recognition of the body as a corpse, and the decision on what behavior will be performed (necrophoric behavior, necrophagy, burying behavior, etc.). Social insects appear to rely in different undertaking strategies. Two main patterns of corpse disposal can be recognized according to taxa:

1. Hymenoptera: Social Hymenoptera tend to remove any object from the nest, and this behavior has been extended to corpses. However, although undertaking in Hymenoptera is based on necrophoresis, other undertaking strategies have been described that complement corpse removal. The main undertaking strategies in Hymenoptera are:
   a) Necrophoresis: This is the main strategy of social Hymenoptera; almost all corpses are removed from the nest to the exterior, even those corpses that have been partially eaten.
   b) Intraspecific necrophagy: Together, cannibalism and intraspecific necrophagy constitute the second important strategy used by Hymenoptera, and is mainly directed to the brood. It appears that necrophagy could be a useful strategy when other resources are scarce. When necrophagy is present, members of the colony consume the contents of the corpses and discard the carcasses by necrophoresis.
   c) Avoidance: Hymenoptera tend to avoid corpses and the refuse piles by keeping the waste transport away from queen and brood chambers and from the trails and sites of foraging. In addition, ants tend to avoid sites where corpses have been present.
   d) Burial behavior: This has been reported for a few species and described in detail for one species. It may be an atypical strategy present in species with small colonies or in specific situations.
2. Isoptera: As termites do not transport corpses out of the nest, undertaking in Isoptera is based on cannibalism, and is complemented by burial behavior and avoidance when corpses cannot be eaten. Undertaking responses in termites appear to be more complex and plastic, and depend on the feeding habits and nest ecology of species, as well as on the characteristics of the corpses, tending to the recycling of resources and cannibalism of nestmates.

a) Intraspecific necrophagy: Devouring corpses appears to be the main strategy in termites, due to their habits of nutrient recycling. Necrophagy also depends on the characteristics of the corpse and rate of mortality.

b) Burial behavior: When corpses cannot be eaten due to some threat in them or due to high mortality in the colony, termites prefer to bury them.

c) Avoidance: Termites also tend to avoid corpses and locations where they have been buried.

In the next sections, we describe how social insects respond behaviorally when they encounter these potentially dangerous "members" of the colony.

5.1. Necrophoresis

As dead members of the colony constitute a considerable risk of infection when they die inside the nest, removing them is the simplest solution. Bees and ants actually remove all corpses from the brood and queen chambers as fast as they can, taking them to the exterior or to specialized chambers. Necrophoric behavior is the term used to distinguish corpse disposal from other sanitation tasks, because bees and ants treat corpses in a different way than other waste materials, by isolating and removing the dead even further to keep the whole society protected from potential pathogens. Such sanitation behaviors evolved from and are shared with subsocial insects, like bark beetles, dermapterans and orthopterans, that also remove feces and wastes, keeping the nest clean [74]. Even in the gall aphids *Pemphigus spyrothecae*, the soldier caste specializes in the cleaning of the gall, removing feces, shedding skins, and dead aphids from the gall by manipulating them to the entrance and pushing them out [81]. The sequential behaviors that ants and bees perform during necrophoric behavior are basically the same.

5.1.1. Bees (and wasps)

Because of its economic and evolutionary importance, the honeybee *Apis mellifera* is the most well-studied social insect [1], and most of the knowledge about undertaking behavior in bees has been obtained from the pioneer work of Visscher on this species [3-5]. Other studies about undertaking in bees have been focused on genetic determination of division of labor [7, 158-160] and the development of traps to quantify mortality [see 161-167]. Honeybee researchers have differentiated between the removal of dead adult bees, which is necrophoresis itself, and that of dead or diseased larvae or pupae, called hygienic behavior [168]. This involves specific behavioral patterns such as the uncapping of cell and the removal of dead or diseased brood from the nest [61]. Both necrophoresis and hygienic behavior differ importantly: undertaking behavior detects dead adult members of the colony, while hygienic behavior detects diseased brood. Although there is lack of research on the topic, hygienic behavior is not exclusive to honeybees, as it has also been reported for ants [169] and stingless bees [170]. We will not discuss hygienic behavior here, because it has been reviewed elsewhere [61, 64].

As commonly occurs in social insects, most of the adult honeybees die outside the nest while foraging, especially those individuals infected by pathogens (like *Nosema* or *Varroa* mites) that undergo alterations in their flight and orientation abilities [171], thus diminishing the risk of infection spreading [64]. In addition to the thousands of individuals foraging every day outside the nest, a large number of individuals in the interior may also die and hence must be eliminated [4]. Although adult bees may cannibalize healthy brood when conditions are unfavorable [172, 173], social bees and wasps do not cannibalize adults at all [1]. Instead, they eliminate diseased, moribund, and dead larvae and adults by necrophoresis.

Honeybees construct their beehive inside natural cavities attached to the substrate, which advantageously favors that the debris carried by foragers and generated in the nest simply fall down to the bottom of the cavity [174]. Although Visscher [4, 5] could quantify that, on average, a colony removes around 50 dead bees daily, he did not specify the size of the five colonies he used to obtain such a data to understand the magnitude of the corpse removal within the hive. However, undertakers of honeybees *Apis mellifera* are very efficient at removing dead bees from the hive; as a consequence of this, adult bee corpses rarely exist in the interiors of the nests.

Corpses attract many individuals inside the nest; many of these not only inspect the corpses but also lick them, grasp them with their mandibles, and pull them to short distances within the nest. However, they do not fully remove the corpses. Those bees that actually perform the complete removal of a corpse seem to be more purposeful and fast [4]. Undertaking behavior involves behavioral patterns of the common bee repertoire. When an undertaker finds a corpse inside the nest, she performs the following sequence of behavioral patterns [4, 5, 175]:

1. Detection of the corpse and orientation towards it.
2. Approximation to the corpse.
3. Inspection of the corpse by antennation (there may be some licking of the corpses).
4. Grasping the corpse by its appendages (legs, mandibles, or wings) in the mandibles. In fact, it has been shown that appendages of the corpses are very important in transporting them. Corpses without appendages are difficult to remove and may remain in the hive longer than those with appendages. The appendages most frequently used, in descending order of their use, are: legs, wings, antennae, head, and tongue.
5. Dragging the corpse through the nest towards the exit of the hive (this path usually is not in straight line). Bees do not lift corpses as ants do when they perform necrophoresis; bee undertakers drag corpses by pulling them backwards by the appendages through the nest until they reach the exit of the hive.
6. Flying from the hive carrying the corpse in the mandibles. Once the undertakers reach the exit of the hive with the corpses, they attempt to initiate the flight, a process that may take some time as the flight of undertakers carrying corpses may be affected by the extra weight. When undertakers begin their flight, they move away from the nest carrying the corpse in their mandibles. Because of the extra load, undertakers usually fall to the ground and the corpse may be abandoned there.
7. Dropping the corpse.
8. Flying back to the nest.

Honeybees do not have refuse dumps or specific sites designated for garbage disposal, neither inside nor outside the nest. Thus, corpses removed are carried outside the nest by undertakers that fly for a short distance before dropping them 10-100 meters from the hive [4]. Cues or factors involved in the dropping or abandonment of the corpses by undertaker bees have not been described yet. Removing corpses from the hives seems to be a constant activity without a daily pattern and even takes place throughout the night [4, 5]. Even though the time in which corpses are removed can be variable, it is faster than the time required to remove other similarly sized waste materials; therefore, necrophoresis constitutes a well-defined behavior distinguished from other nest hygienic activities [4].

Necrophoric behavior has also been observed in the stingless bee *Melipona favosa* [129, 176], in which undertakers carry corpses in their mandibles to the refuse dump located on the ground under the entrance tube of the nest. In these refuse dumps are workers of all age categories, moving and manipulating waste [129]. Similar refuse dumps have been reported for other stingless bees like *M. beecheii* [170, 177], *M. bicolor* [178], *Scaptotrigona pectoralis* [178], *Plebeia remota* [179], and *Lisotrigona carpenteri* [180].

Studies about undertaking behavior in wasps are scarce. However, it has been reported that social wasps dispose of their dead members by necrophoresis [1]. In contrast, it has been mentioned that *Vespula rufa* allow the accumulation of waste and corpses of colony members on the nest floor, forming a kind of refuse dump [181]. In addition, *Polistes biglumis* wasps have shown the ability to discriminate dead nestmates from dead non-nestmates, and thus respond aggressively towards dead non-nestmates [182], similarly as other wasp species do [183]. Across the wide diversity of wasp species, there must be a variety of adaptations for corpse disposal that remain ignored and that might be explored. Most of the studies on wasp responses to dead nestmates are focused on nestmate recognition and aggression [183], and there is no mention of corpse removal [184].

5.1.2. Ants

Ants constitute the group of social insects in which undertaking behavior has been most studied because of their conspicuous refuse dumps where corpses are disposed. These have been known as ‘ant cemeteries’ since the time of ancient naturalists. Although a study by Wilson *et al*. [12] was the first to use ant necrophoric behavior as a model of research in ethology, a study by Howard & Tschinkel [120] constitutes one of the most complete works on undertaking behavior in ants. Previously, Sudd [185] studied the response of *Monomorium pharaonis* workers to fresh dead nestmates; what he describes is an alarm and avoidance behavioral response, due to the release of the glandular content; and Hunt [186] described the response of *Formica fusca* in removing the dead nestmate when the corpse was placed close to the nest. Studies on undertaking in ants have been focused on ethology and description of behavior [12, 120, 187-192]; death recognition and related cues [12, 120, 188-190, 193-196]; task partitioning and division of labor [8, 120, 122, 188-190]; orientation [120, 197, 198]; studies on waste management, refuse dumps, ant cemeteries, and corpse distribution [70, 121, 122, 199-204]; pest control and disruption of necrophoric behavior [205]; altruistic self-removal [206, 207]; and necrophobia [208]. As sources of pathogens, ant corpses are removed routinely, but infected corpses are specially eliminated. Corpses of the ant *Solenopsis invicta* infected with *Beauveria bassiana* are immediately removed from the nest before sporulation, which reduces colony reinfection [209].

Ants are well-known for their ability to recognize dead nestmates and, as fast as possible, take them out of the nest to the refuse dumps or to other sites faraway from the colony [1, 14] that are rarely visited by nestmates [198], thus isolating those potential sources of pathogens. Even founding queens of *Camponotus atriceps* kept in laboratory nests, tend to defecate in the most remote areas of the chamber and to pull apart wastes, empty cocoons, and dead nanitic workers [López-Riquelme, personal observation]. Ants also take charge of their dead aphid symbionts [210]. Necrophoresis has been described in several species of ants (see Table 1 and references therein, and 211-232). The treatment that the dead queens may receive from workers is also interesting. When the queen dies, she is not removed from the nest, at least for some time, and even she can be eaten by workers [1]. Similar observations have been reported elsewhere. For example, Maeterlink [233] mentions observations made by Huber regarding accidentally crushed queens of *Lasius flavus* that were cared for, over several weeks, by the workers who constantly licked the corpse. Haskins [234] also mentioned another similar observation, pointing out that the queen receives a different treatment when she dies than that received by dead or injured workers that are indifferently expulsed or dumped. The corpse of the queen, while recognizable, can be kept and treated with the greatest devotion and attention by the colony. In *Atta mexicana* laboratory colonies, the same behavior was observed when the queen was accidentally killed. Workers, instead of carrying the corpse out to the refuse pile, conserved it inside the nest, attending it and moving it from one place to another inside the nest. Workers finally devoured the tissues, though separated fragments of the cuticle were kept inside the nest, and spent time licking them [López-Riquelme, personal observation].

When an ant dies, its movement gradually ceases. Progressively, the body tends to curve toward the ventral side with the legs shrunken under the body. In this stage, the ant may not immediately be noted by its nestmates; however, after some time, the ant becomes attractive for a few, or many nestmates that inspect the corpse and lick it, grasp it, or move it for some short distance, and soon release it [8, 190]. However, when undertakers find corpses, they behave in a more targeted way, usually performing the task until they abandon their load in the refuse dump. Although slight variations among species exist, the general sequence of behavioral patterns that undertakers perform when they encounter corpses [based on 2, 12, 120, 188, 190, 192] can be divided into the following stages (see Table 2 and Figure 1):

1. Detection of the corpse and orientation towards it. Ants can detect corpses and corpse odor from a short distance before contact [190].
2. Approximation to the corpse. Ants approximate to the corpse with extended antennae.

3. Inspection of the corpse by contact antennations and with forelegs. Ants may lick the corpse and also climb on it.
4. Grasping the corpse with the mandibles by its appendages: legs, antennae, petiole, etc. In this phase, the ants lift the corpse, pulling it backwards and slowly raising the head, with the corpse in their mandibles. The position of the corpse can be adjusted by manipulation with the mandibles and forelegs until it is easy to lift from the substrate, and when its position permits the undertaker to walk normally.
5. Carriage of the corpse through the nest towards the exit. In this phase, undertakers carry the corpse almost overhead, with their heads upward and antennae extended forward and downward, and making antennations on the substrate and in the air in front of them. This march can be the longest phase of corpse transport towards the refuse dump. Occasionally, undertakers are followed by other workers for short periods.
6. Walking from the nest exit to the refuse dump.
7. Abandonment of the corpse in the refuse dump or in substations inside the nest. When undertakers carry the corpse directly to the dump, they may simply drop the corpses or spend some time maneuvering them in the dump. When necrophoresis involves task partitioning, as in fungus-growing ants, some ants carry the corpse to the garbage cache [122], and other workers complete the transport to the refuse dump.
8. Marching back to the nest (end of necrophoresis).

It has been mentioned that during necrophoresis, undertakers show agonistic behavior towards corpses [120, 192], mainly to those of non-nestmates [188, 235, 192], or even towards corpse-related odorants [194]. However, some ants do not discriminate between dead nestmates and dead non-nestmates [236] as wasps do [183].

The behavior of finding the refuse dumps and the deposition of corpses (the termination of necrophoric behavior) are stereotyped, involving various physical and chemical cues [120] that may depend on the species [2]. First of all, necrophoresis is a nest hygienic activity distinguished from other waste disposal because corpses are dumped in locations that are different from those for other rejected objects that ants remove from the nest: corpses tend to be removed further from the nest entrance and also from sites where foragers tend to explore [120, 197]. Diez *et al*. [197] established that dropping corpses by undertakers is a function of the distance from the nest: undertakers tend to keep carrying the corpses close to the nest but as they walk away from the nest, they become more likely to drop the corpses.

In the ant species *S. invicta* and *Myrmica rubra*, once undertakers leave the nest carrying corpses, they tend to walk in straight and radial trajectories from the nest entrance [120, 197]. When the nests of the fire ant *S. invicta* are located on a level surface, undertakers walk away from the nest entrance in random directions showing no preference in orientation, and without forming discrete corpse heaps; instead of it, corpses are scattered around the nest entrance [120]. The same lack of orientation preference and the scattered distribution of corpses around the nest entrance have also been reported for the ant *Myrmica rubra* [197]. The heaps of corpses *per se*, other landmarks, or even the position of light, seem to have no influence in the orientation of undertakers. This scattered distribution of corpses far from the nest may provide an advantage in societies with low death rates, because it prevents the sanitary risk that dense piles of corpses present in terms of high concentrations of pathogen propagules [6]. In addition, a scattered distribution of corpses has been found to be advantageous, as it provides the ants with a ‘corpse boundary’ that deters competitor species of ants from approaching the territory surrounding the nest [199]. A similar behavior has been reported in *Formica cinerea* workers [203, 204], that surround their nest entrances with corpses of their own nestmates when the presence of the competitor ant *Formica rufa* is detected close to the nest, thus using them as defensive guards. On the other hand, *F. rufa* workers use their corpses and pupal cocoons as offensive guards, carrying them to the place of confrontation with *F. cinerea*.

In *S. invicta*, any slight slope is detected by workers carrying corpses that tend to walk downwards in a show of positive geotactism.

Table 1. Corpse management in social insects.

Species	**Undertaking strategy**						
	Necrophoresis	**Carrying dead**	**Intraspecific necrophagy**	**Burial**	**Avoidance**	**Self-remotion**	**Reference**
HYMENOPTERA							
Wasps							
Wasps in general	X						1
Mischocyttarus labiatus			X		X		264
Bees							
Apis mellifera	X					X	4, 242
Melipona bicolor	X						178
Melipona favosa	X						129, 176
Scaptotrigona pectoralis							170
Ants							
Ponerinae							
Diacamma vagans	X						191
Odontomachus affinis		X					212
Odontomachus sp	X						López-Riquelme (personal observation)
Nothomirmeciinae							
Nothomyremcia marops	X						211
Myrmeciinae							
Myrmica rubra	X						197, 198
Myrmica schencki	X						203
Myrmecia vindex	X			X			194
Pseudomyrmecinae							
Pseudomyrmex elongatus		X					213
Ecitoninae							
Ecitoninae in general	X						214
Eciton burchellii	X						126, 214, 215
Eciton hamatum	X						214

Table 1 continued..

Myrmicinae							
Aphaenogaster cockerelli		X					217
Attines in general	X			X			123
Acromyrmex versicolor	X						8
Atta cephalotes	X						121
Atta colombica	X						70
Atta mexicana	X						189, 190
Atta texana	X						218
Cephalotes atratus		X					216
Crematogaster ashmendi		X					213
Erebomyrma nevermanni		X					219
Eurhopalothrix helsicata		X					220
Leptothorax curvispinosus		X					221
Messor sancta	X						201
Monomorium pharaonis					X		185
Oligomyrmex overbecki		X	X				222
Pheidole in general			X				2
Pheidole dentata		X	X				223, 224
Pogonomyrmex badius	X					X	1, 12
Pogonomyrmex barbatus	X						120
Solenopsis in general			X				1
Solenopsis invicta	X			X	X		69, 120
Solenopsis saevissima	X		X			X	1, 12
Strumigenys lopotyle	X						1
Temnothorax albipennis					X		289
Temnothorax lichtensteini	X			X			192
Temnothorax unifasciatus						X	206
Zacryptocerus varians	X						226

Table 1 continued..

Aneuretinae							
Aneuretus simoni	X						225
Dolichoderinae							
Linepithema humile	X						196
Formicinae							
Camponotus aethiops						X	207
Camponotus atriceps	X						López-Riquelme (personal observation)
Camponotus (Myrmobrachys) senex	X						227
Camponotus compressus	X						191
Camponotus floridanus		X					228
Cataglyphis bicolor		X					231
Cataglyphis cursor		X	X				248
Cataglyphis floricola		X	X				229
Formica fusca	X						186
Formica polyctena	X		X				230
Formica sp	X						López-Riquelme (personal observation)
Gigantiops destructor			X				2
Lasius niger	X		X				188
Oecophylla			X				2
Polyrachis lacteipennis	X						232
ISOPTERA							
Lower termites							
Coptotermes formosanus		X	X	X	X		251, 256, 259, 290, 291
Coptotermes lacteus			X				1
Kalotermes flavicollis			X				1
Neotermes jouteli			X				252
Reticulitermes lucifugus			X				1
Reticulitermes flavipes		X	X	X			149

Table 1 continued..

Reticulitermes speratus		X	X	X			251
Reticulitermes virginicus				X	X		278
Zootermopsis angusticollis			X		X		1, 260, 263
Higher termites							
Amitermes hastatus			X				252
Cubitermes ugandensis			X				252
Globitermes sulphureus			X	X	X		251
Microcerotermes crassus		X	X	X			251
Pseudoacanthotermes spiniger				X	X		277
OTHER SPECIES							
Cockroaches							
Cryptocerus punctulatus			X				255
Periplaneta americana					X		152, 153
Aphids							
Pemphigus spyrothecae	X						81
Beetles							
Xyleborus dispar			X				266
Social caterpillars							
Hyphantria cunea					X		156
Malacosoma americanum					X		156
Collembolla							
Protaphorura armata					X		154
Isopoda							
Armadillium vulgare					X		156
Oniscus asellus					X		156
Porcellio scaber					X		156
Porcellionides pruinosus					X		156

As the slope increases, the tendency of ants to walk downslope also increases until the slope becomes constant at 15º [120]. This walk increases the probability that workers will release the corpses downward, favoring an accumulative distribution and forming downhill refuse dumps. Walking downwards may be favorable for workers because they consume less energy carrying the corpses and prevent the flushing of corpses back into the nest by rain. However, the slope is not the stimulus involved in the dropping of the corpse, nor the heap of corpses on the ground. Howard & Tschinkel [120] showed that an important cue for the termination of necrophoric behavior is the fecal material, which is detected by ants through contact chemoreception. The proportion of ants going downwards increases with the increase in slope, which favors the defecation downhill. This results in the feces concentrating downhill on the substrate, which in turn increases the tendency of ants to drop the corpses there, forming the ant cemetery.

5.1.2.1. Refuse dumps: the 'ant cemeteries'

Although ants are well-known for their conspicuous refuse dumps, not all species in all circumstances exhibit them. In the nature, corpses removed from the nest to the exterior would not remain there for a long time due to scavenger soil fauna that devour them. The common red ant *Myrmica rubra* has been shown, when they are forced, to dispose of corpses in specific areas, forming ant cemeteries [200]. Due to their clustering behavior, the addition of corpses to a cluster leads to the increase of the size of the cluster, which, in turn, increases the probability of addition of more corpses, resulting in a self-organization of corpse piles, or cemeteries. *M. rubra* undertakers arrive to such cemeteries based on spatial short-term memory choosing the same pathway used in previous trips, without any chemical-based orientation towards refuse piles [197, 198].

Other ant species like Aphaenogaster iberica, Camponotus cruentatus, Camponotus vagus, Cataglyphis velox, Pheidole pallidula, Formica sanguinea, Formica lugubris and Lasius emarginatus, have been reported to have discrete refuse dumps and waste middens [237]. It is interesting to mention that Taylor [211] described refuse dumps in the primitive Nothomyrmecia macrops that include food wastes, discarded cocoons and both brood and adult corpses accumulated away from the nest, indicating that necrophoric behavior is as ancient as ant eusocieties. Ant societies with large populations, and with high quantities of waste and corpses produced, have conspicuous refuse dumps like those of harvester ants [2, 199, 238], army ants [126, 214, 215], and fungus-growing ants [70, 121, 122].

Army ants form refuse dumps [126, 214, 215], either diffuse or discrete, at a short distance from the bivouac or sometimes directly under the bivouac, as in *Eciton burchellii*. When the colony occupies a cavity or a log, the refuse is dropped off the end of the log's opening [215]. These dumps consist of the remains of prey and the carcasses of dead workers. Waste and nestmate corpses are carried to the refuse dump by the participation of many workers forming dense transport-rows. Such rows extend outwards from the bivouac to the deposits where the ants also defecate [214]. Refuse produced by a colony of *Eciton burchellii* may be considerable, and may reach a colume of 100 mL added each day, forming an enormous pile in the statary phase [215]. On the other hand, the refuse accumulations of the nomadic bivouacs are smaller and rapidly eaten by scavengers. Huge refuse dumps of *Eciton burchellii* have a particular fecal odor, different from the odor of the bivouac, that may attract many of the thousands of inhabitants (mites, springtails, staphylinid beetles, phorid flies, and a variety of insect larvae) to the refuse dumps of army ants [214, 215].

In all fungus-growing ants, the disposal of all the waste produced by the society is fundamental, first because large societies produce a huge amount of waste. For example, an *Atta* colony with 2 million of workers may contain in the interior waste chambers almost 500 kg of refuse material [121]. Waste is particularly hazardous because it is concentrated in separate discrete dumps, inside or outside the nest, and exposed to a plethora of opportunistic and pathogenic inhabitants that live and grow in there. Secondly, fungus-growing ants must not only protect the queen, the brood, and the adults, but also the fungus they cultivate from invasion by the lethal fungus *Escovopsis*, which is abundant in the waste material of the refuse dump [122]. Fungus-growing ants must remove from the fungus chambers, exhausted vegetal substrates where the fungus was cultivated, feces, and numerous dead members of the colony to the refuse dumps. Waste management in fungus-growing ants is organized in a sophisticated manner, which involves the organization of the way in which ants dispose of the refuse materials, the division of labor, and the location of the refuse dumps [70]. One of the most interesting features of the nests of most of the fungus-growing *Atta* species is that they may have refuse dumps inside or outside the nest [123]. Workers carry waste outside the nest and tend to drop it from elevated positions, likely avoiding contact with refuse dumps [70]. Although corpses of dead members of the colony are also found in the refuse dumps, Hart & Ratnieks [122] reported that they never observed necrophoresis within the nests of *Atta cephalotes*, and pointed out that old and sick workers, at the end of their lives, become dump workers removing waste material. However, necrophoresis has been reported by the same authors for *Atta colombica*, after they observed workers transporting not only dead workers, but also dead reproductives to the refuse piles outside the nest [122].

5.2. Self-removal: I'm not dead yet, but I will be

Workers of social insects are well-known for their altruism, not only because they sacrifice most or all of their own direct reproduction to enhance that of the queen, but also because they defend the nest against enemies and predators at the expense of their own lives [1, 2]. An extreme of such altruistic self-sacrifice is the remarkable behavior of some ants that tend to remove themselves when they are near to death. Wilson [1] mentioned that injured and moribund workers of *Pogonomyrmex badius* and *Solenopsis saevissima* remain outside the nest or abandon it. It has also been reported that *Formica rufa* workers infected with the fungus *Alternaria tennis* leave the nest hours before their death in apparently good health. Then, they climb to the tips of low grass blades in the vicinity of the ant hill. Once there, the ants adhere to the substratum through an exudate that emanates from their articulations and die. The next day, fungus mycelia grow throughout the corpse of the ant, and on the third day, the fungus sporulates [239]. Such behavior is better explained by parasite control strategies of host behavior, as that reported for the fungus *Ophiocordyceps unilateralis*, which parasitizes the ant *Camponotus leonardi*. *C. leonardi*, under parasite control, relocates itself to a site with optimal conditions for fungal growth [146, 240]. This phenomenon is also observed when ants are infected by the larvae of trematodes [241]. However, it has been shown that workers of the ant *Temnothorax unifasciatus*, when near to death due to different causes, or when infected by the fungus *Metarhizium anisopliae*, actually leave the nest on their own, hours or days before they die, and then die away from the colony in complete isolation [206]. This social withdrawal may constitute a mechanism to prevent infection of nestmates. Workers of the ant *Camponotus aethiops* [207] infected with *Metarhizium brunneum* reduce their social interrelation with adult nestmates, no longer interact with the brood, and spend more time outside the nest in isolation. A similar self-removal behavior has been reported for the honeybee [242]. Self-removal is a very interesting behavior because it may be a widespread mechanism for preventing epidemics in the colony and because, although it is predicted by kin selection altruism, the ability of workers to respond to their own health condition and to actively leave the nest, spending their last hours away, is remarkable. This altruistic suicidal behavior is an adaptation at the level of the colony, which behaves as a superorganism and it has been compared to programmed cell death in multicellular organisms [242].

5.3. Intraspecific necrophagy: cannibalizing the dead

Although it has been accepted that intraspecific necrophagy (or cannibalism) may favor disease transmission and may constitute a major factor of mortality in several species, cannibalism is widespread in the animal kingdom and has been recorded in different taxa [243]. In addition, necrophagy has been shown to be an important strategy of dealing with infected individuals in societies because pathogen propagules may be deactivated in the gut of cannibal individuals [44, 244, 245]. This reduces the probability that an epidemic arises since the massive transmission of pathogens by eating infected corpses would require that many cannibal individuals feed off the same body. In addition, diseases transmitted by cannibalism have been shown to be infrequent in animals, although trophic transmission of pathogens may be actually common [243] and may increase mortality [246].

5.3.1. Ants

Intraspecific necrophagy is quite different from brood cannibalism, to which different functions in social insects have been assigned [32]. Besides, necrophagy is common among ants when there are supernumerary workers in the colony and resources must be recycled [1, 19]. In fact, ants eat all injured eggs, larvae, and pupae [1]. However, it is interesting to note that when laboratory colonies of *Atta mexicana* reduce their fungus mass due to experimental, deprivation of vegetal substrate for their fungus, workers carry numerous pupae, apparently in good health, to the refuse piles [López-Riquelme, personal observation].

Although intraspecific cannibalism is very rare among ants, it has been described in some species [1, 2]. It has been mentioned that when queens in laboratory nests are accidentally crushed, her own workers devour her soft tissues. Wilson [1] mentions that ants will eat any other adults if they are also crushed open, exposing their fatty tissue. In fact, *Atta mexicana* workers frequently perform the same behavior in laboratory nests: when the queen suffers a wound by crushing, the workers begin to devour her exposed fresh tissues and organs. Instead of carrying the corpse of the queen to the refuse dump, workers keep it until it is completely devoured and only the carcass remains, which is also maintained within the nest and is continuously attended to and licked by small workers that stay inside the queen carcass [López-Riquelme, personal observation]. Although partial or total consumption of the dead adults in ants is not common, it has been reported that workers of *Solenopsis saevissima* may consume the majority of their dead nestmates, at least in laboratory nests [1]. Besides, Howard and Tschinkel [120] also observed cannibalism in the refuse pile of *S. invicta* nests. They also observed that ants frequently cannibalize the gasters of dead sexual partners and that workers occasionally took corpses from the refuse dumps to the nest. Hölldobler and Wilson [2] mention that cannibalism of the dead is observed frequently in *Pheidole, Solenopsis* and *Oecophylla*. Cannibalism of dead nestmates has also been described in *Gigantiops destructor*, where corpses are smashed and converted into a mushy paste that is eaten by workers and larvae [247]. Some other ant species have been observed eating dead nestmates: *Pheidole dentata* [223], *Cataglyphis cursor* [248], *Oligomyrmex overbecki* [222], and *Cataglyphis floricola* [229].

The wood ant *Formica polyctena* is a cannibal species that preys on neighboring colonies of the same species engaging in massive wars for the control and expansion of its territory. In these wars ants capture their intraspecific non-nestmate competitors, which are then transported, alive or dead, to their nests where they are eaten by adults and by the brood when other preys are scarce [230, 249]. However, this behavior is not intraspecific necrophagy, but intraspecific predation, which has been also observed in other ant species, for example, in *Myrmecocystus mimicus* [250]. Mabelis [230] noted that dead brood and adult nestmates are also consumed, mainly when food supplies are scarce in the territory. When a nestmate dies, ants carry the corpse to storage chambers, but never to the brood chambers. Soon, some workers approximate to the body and begin to examine the corpse by antennations, subsequently tugging the appendages until the legs are stretched obliquely upward. Workers also pull the head of the corpse until it deataches. In addition, workers nibble the abdominal segments close to the anus until the abdomen is opened in the last segment of the body. Once the corpse is opened, ants begin to lick and consume its contents sometimes pulling the organs and tissues out of the abdomen. After that, workers feed the larvae by regurgitation [230]. These food resources increase the survival of the workers themselves and also the production of new workers, mainly during winter. After consuming both non-nestmate workers captured in wars and corpses from dead nestmates, workers of *Formica polyctena* perform necrophoric behavior carrying the empty carcasses to the refuse dumps located a few meters away from the nest [230]. The sequence of behaviors can be summarized as follows [188, 230; see Table 2]:

1. Detection of the corpse.
2. Approximation.
3. Inspection by antennations and licking.
4. Grasping the corpse by its appendages with the mandibles.

Table 2. Comparison between undertaking behavioral patterns.

Phase of the process	**Necrophoresis**		**Necrophagy**		**Burial behavior**	
	Bees	**Ants**	**Ants**	**Termites**	**Ants**	**Termites**
Recognition and evaluation	Detection	Detection	Detection	Detection	Detection	Detection
	Approximation	Approximation	Approximation	Approximation	Approximation	Approximation
	Inspection	Inspection	Inspection	Inspection	Inspection	Inspection
Undertaking response	Grasping	Grasping	Grasping	Grooming	Group inspection	Grooming and allogrooming
	Dragging/ carrying	Carrying	Carrying to nest	Dragging to nest	Carrying soil material	Covering corpses with saliva and feces
	Flying	Walking/ Marching	Dismemberment of corpses	Feeding on corpse	Depositing soil materials on corpse	Drag corpses and group them
	Dropping	Abandonment/ dropping	Feeding on corpse		Packing	Carrying soil material
	Flying back to nest	Walking/ Marching back to nest	Feeding brood		Reordering	Covering soil material with saliva and feces
			Necrophoric behavior		Finalization: corpse is buried	Depositing Soil materials on corpse
					Change of behavior to necrophoresis (may or may not be present)	Finalization: corpse is buried

5. Carriage of the corpse to the food store chambers (never to brood and queen chambers).
6. Approximation of workers inside the nest to the corpses.
7. Dismemberment of corpses. After briefly inspecting, ants start to pull, tugging the head and the appendages until they deatach. Ants also nibble the abdomen until it is opened.
8. Feeding on corpses. Once the corpses are opened, ants begin to lick and feed on tissues and body fluids.
9. Feeding the brood. After workers feed on corpses, they feed the larvae in the brood chambers by trophallaxis. Larvae do not consume corpses directly.
10. Necrophoric behavior. After consuming all the corpse contents, ants perform necrophoresis, carrying empty carcasses to the refuse dumps outside the nest.

It is interesting that Mabelis [230] observed that ants in laboratory nests accept experimentally aged corpses to be cannibalized. In the field, ants accept aged corpses, but only if they are aged not more than a week, rejecting all moldy corpses and spraying them with formic acid, and then cutting them into pieces which are immediately taken to the refuse dump. In *Lasius niger*, Ataya & Lenoir [188] also observed that, after necrophoresis, corpses of nestmates are dismembered and the gaster content is devoured by workers. Marikovsky [239] reported that healthy *Formica rufa* ants tend to eat

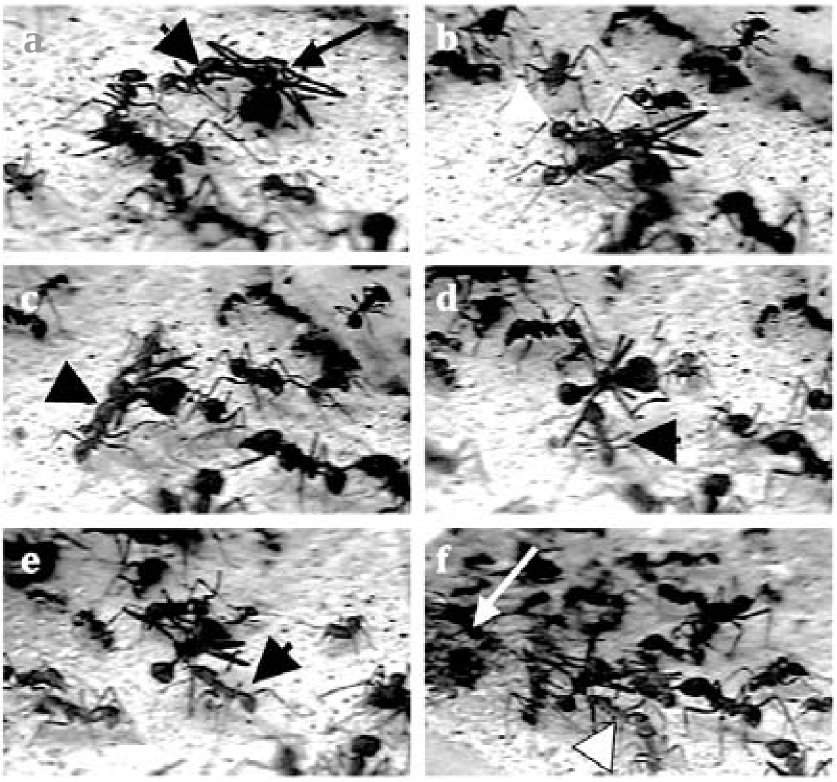

Figure 1. Photographs from a video sequence of necrophoresis stages in laboratory colonies of the fungus-growing ant *A. mexicana*. a) One corpse has been introduced into the nest, and one undertaker has encountered it. Short black arrow points to the undertaker and the large arrow points to the corpse. b) After some examination and inspection, the undertaker (pointed with a white arrowhead) manouvers the corpse by the legs. Some ants attracted to the corpse can be observed. c) The undertaker (pointed with a black arrowhead) is lifting the corpse. d) The undertaker (pointed with a short black arrow) has finally lifted the corpse by one leg. e) Once the corpse has been lifted, the undertaker (black arrow) carries it to the refuse dump. f) The undertaker (pointed with a white arrowhead) is carrying the corpse to an internal refuse dump (a cache) pointed with a large white arrow. It can be observed some ants, attracted to the corpse, surrounding the undertaker and its load (modified from 190).

infected corpses and discard the carcasses after they are devoured.

5.3.2. Termites

Although it has been assumed that termites dispose of their corpses mainly by eating them, this is a simplistic view of the rich and complex undertaking behavioral responses of termites. On the contrary, termites are able to evaluate a large amount of information obtained from the corpses and the social context to display a complex variety of undertaking responses according to the species, ecological adaptations of nesting, feeding habits, and intake of nitrogen in the diet [251]. All this information is processed and evaluated to decide the final destination of the corpses, and as termites do not perform necrophoresis, nor have refuse piles to dump the dead members of the colony, they dispose of the corpses by burial, necrophagy, or avoidance; all strategies that may be present in the same species.

Injured, moribund, dead individuals and exuvia from molts are routinely eaten, usually by larger larvae, nymphs, pseudergates or workers [252]. Intraspecific necrophagy and cannibalism have been observed in different species of termites (see Table 1): *Reticulitermes lucifugus* eat apparently healthy nestmates [1], *Kalotermes flavicollis* [1] and *Neotermes jouteli* [252] eat supernumerary reproductives, *Amitermes hastatus* lick to death the primary queens whose fertility is declining

[252], *Coptotermes lacteus* can kill and eat their alates [1], *Zootermopsis angusticollis* becomes an intense cannibal when are deprived of proteins [1], and *Cubitermes ugandensis* also display cannibalism [252].

It is well-known that, as a group, termites (Isoptera) have a diet based on cellulose that is likely low in proteins and nitrogen [1, 253]. A limited diet in quality and quantity promote intraspecific predation or cannibalism [254]. Thus, due to their nitrogen-limited diets, termites are prone to cannibalism and necrophagia as a way of recycling nitrogen. Some cockroaches, such as *Cryptocerus punctulatus*, recycle nitrogen by means of cannibalism and necrophagy [255]. In fact, starving workers of the termite *Coptotermes formosanus*, a species with a diet low in nitrogen, eat both live and dead nestmates, increasing cannibalism by almost 40% [256]. However, when *Coptotermes formosanus* eat their dead, this cannibalism is limited to fresh and experimentally oven-killed corpses (one day aged or more, and decomposed corpses are never consumed), and to alive mutilated workers that are dragged to the nest where they are groomed constantly until they are eaten [1, 251], since the blood from the wounds induces cannibalism [257]. The termite *Reticulitermes speratus*, another species with limited nitrogen in its diet, also drag to the nest and eat injured individuals as well as fresh and 1 day-old corpses, but they reject corpses more than 3 days old [251]. On the contrary, termites of the *Globitermes sulphureus* and *Microcerotermes crassus*, which have a higher nitrogen diet, rarely eat their dead. Only *M. crassus* eats injured nestmates on some occasions [251]. It has been supposed that the termite *R. flavipes* eats 1-24 hours old corpses because it has been observed that workers carry them to the interiors of the nest [149].

Hygienic necrophagy is performed in some termite species, such as *R. flavipes*. When members of the colony die from infection with *Metarhizium anisopliae*, corpses are eaten by healthy workers as a strategy to eliminate them from the society [151, 258, 259]. When workers of the termite *Zootermopsis angusticollis* detect the presence of spores of the fungus *M. anisopliae*, they alert nestmates showing an alarm behavior consisting in a striking vibratory display which communicates about the presence of pathogens; in response, non-exposed nestmates move away from the source of infection [260]. In addition, termites also respond by increasing allogrooming [261], which removes spores from the cuticle of individuals by eating them [262]. It has also been reported that the dampwood termite *Zootermopsis angusticullis* cannibalizes the youngest instars (they are susceptible to infection) as well as the moribund termites infected with the entomopathogen *M. anisopliae*, and, more over, they are able to detect those individuals with higher loads of spores and, then, eat them [263]. Furthermore, the termite *C. formosanus* shows adaptive responses to epidemics. When mortality induced by *M. anisopliae* is low, the main undertaking response is necrophagy, but when the mortality is high, termites opt for burying infected corpses, suggesting a limited capacity in the amount of corpses that workers can canibalize [259]. Sometimes, in massive infestations, social insects display desperate actions against parasites, even when in the end they are unsuccessful. When nests of the social wasp *Mischocyttarus labiatus* become infested by the phorid *Megaselia*, they begin to discard larvae from the cells and, in an attempt to recycle some resources, they chew these larvae and eggs and feed older larvae [264].

Cannibalism and necrophagy in termites may play an important role in recycling nitrogen and eliminating dead and injured individuals, but they also are important in controlling disease transmission. By eating infected moribund individuals or corpses, the potential sources of epidemics are removed from the population [263], and fungal spores are inactivated when they pass through the digestive tract. This inactivation is extremely important, since, due to the hostile environment in the digestive tract, it prevents the invasion of the host with pathogens through the gut [44, 244, 245, 265]. In addition, this inactivation prevents an epidemic in the colony because the ingestion of thousands of conidia could expose all members of the colony to infection by the fungus through allogrooming and trophallaxia [151]. By removing infected corpses from the society by means of cannibalism or burial, the ability of pathogens to replicate in other members of the colony is interrupted before pathogens reach their maturity and produce conidia: *M. anisopliae* fungus first needs to kill the termite before it can produce conidia 3 days after death [259]. In this manner, cannibalism in termites accomplishes the function of necrophoric behavior in bees and ants. Termites perform the following sequence of behavioral patterns in necrophagy [based on 1, 149, 251, 257; see Table 2]:

1. Detection.
2. Approximation.
3. Inspection by antennations, the frequency and duration of which depends on the type of the corpse. Fresh corpses and experimentally oven-killed termites tend to be more closely inspected by antennations than old corpses, which receive a cursory examination and are immediately buried.
4. Grooming and antennations. Fresh corpses and mutilated termites are groomed and licked extensively.
5. Dragging corpses. Corpses are removed to the interiors of the nest.
6. Feeding on corpses. Corpses are first licked, mainly in broken parts of the body or in wounds and then eaten. Corpses may be eaten by larger larvae, nymphs, and workers.

5.4. Burial behavior

Social insects are extremely dedicated to maintaining their nests clean by removing any foreign object and carrying it out of the nest to throw it to the garbage dumps. When they cannot remove objects, they tend to cover them with particles of soil or other material [1]. Although ants and bees do not bury their dead, ants cover the water or other liquids that they may find in the nest with soil particles, to avoid getting stuck themselves; and honeybees cover any dead intruders with propolis, preventing decomposition [64, 89, 90]. Among subsocial insects, maternal females of the beetle *Xyleborus dispar* eat or entomb their dead or weak progeny [266]. Although there are some reports on animals burying their dead, only a few of them have empirical and experimental support [267]; one of the well-known examples is the defensive burial behavior in rodents [268, 269], which involves displacing the bedding or substrate material with vigorous treading-like movements of their forelegs and shoveling movements of their heads towards a variety of noxious stimuli [270] such as unpalatable food, novel objects, chemical stimuli and dead conspecifics [271].

Burying corpses would limit the presence of opportunistic organisms by reducing decomposition, mainly if the soil is coarse-textured (sandy) with low moisture, because it promotes desiccation, which in turn, inhibits decomposition. If the burial is in a wet fine-textured (clayey) soil, decomposition is also reduced due to its limited diffusivity, which reduces the exchange of O_2 and CO_2, leaving the niche to anaerobic decomposers that are less efficient decomposers than aerobes [138]. In any case, burying corpses may be advantageous because it isolates the potential source of pathogens and keeps pathogens, if any exist, locally contained [6].

5.4.1. Ants

Ants tend to cover all unwanted objects with soil particles and other materials [2], but, in spite of this, ants do not bury their dead nestmates. However, fungus-growing ants use specialized chambers to dispose of waste and the large number of corpses that die normally inside the nest [123]. The sealing of the chambers with the refuse inside may protect the colony from such hazardous material. Either way, burying corpses may be more advantageous for large ant societies, as those of *Atta*, if they do so for a large group of dead, as fungus-growing ants appear to do in their waste chambers [123]. On the other hand, the burial of dead ants one by one seems neither viable nor practical, and the energy cost appears to be higher than for necrophoric behavior [192]. However, it has been reported that *Myrmecia vindex* ants respond to odorants present in corpses, by initiating necrophoric-, digging- and burial behavior [194], although such behaviors were not performed by ants on real corpses but in filter papers soaked in chemical substances commonly found in corpses. It has been reported that workers of *S. invicta* pack soil particles around dead individuals infected with *B. bassiana*, isolating the potential source of infection [Ph. D. thesis of Storey cited in 69]. Nevertheless, complex undertaking responses, including necrophoric and burial of dead nestmates, has been found and studied in *Temnothorax lichtensteini* [192]. In this species, ants may respond by removing the dead (necrophoresis), by burying them, or in a conflicting situation, by a mixed behavior including both necrophoric and burial behaviors. The strategy depends on the nature of the corpse. When ants find fresh corpses of other species, they tend to bury them, building a structure inside the nest; but when ants find old-corpses of nestmates, they tend to remove them by necrophoresis. Other corpses, like fresh nestmates and non-nestmates (but of the same species) seem to cause conflict in ants because, while some ants try to bury them, others try to remove them although a slight tendency to bury them has been observed. Although the ant that finds the corpse may make the decision to bury it, buryial behavior is actually a group task, because many ants can participate in the transport of burial materials and finally bury the corpse by stigmergy [272]: up to 25 workers may deposit around 200 pieces of materials to bury a corpse inside the nest. The sequence of burial behavior is as follows (see Table 2):

1. Detection of the corpse.
2. Approximation to the corpse.
3. Inspection by antennations.
4. Group inspection. Other ants are attracted to the corpse and they approximate and initiate inspection by antennations.
5. Carrying and depositing of building materials. Group activity.
6. Plugging using small pieces of material. Group activity.
7. Packing down materials. Group activity.
8. Reordering materials. Group activity.
9. Finalization (burying is complete). Licking and aggression may be present during the burying by one or many of the ants participating in the task.
10. Change of behavior (may or may not occur). One or a few ants may change the behavior of the group by trying to uncover the corpse and transport it. The change of behavior may be present at any phase.

In this behavioral sequence, the steps can be accompanied by additional behaviors as: antennations, weak agonistic behavior towards the corpse, and licking the corpse. Burial behavior of *T. lichtensteini* appears to be similar to that reported for termites. As undertaking behavior in this species may include both necrophoric and burial behavior, it is clear that sometimes a conflict in the corpse disposal decision may exist, which has been interpreted as behavioral plasticity [192].

5.4.2. Termites

Termites tend to isolate corpses by covering them with soil particles or by constructing walls around them [273] covered with antibiotic secretions to prevent the sporulation of pathogens [44]. Burial behavior, along with intraspecific necrophagy, is one of the main undertaking behaviors in termites and it is directed mainly to high risk corpses [149, 251] or when infection may become massive. Roy-Nöel [273] reported burial behavior in the termite *Coptotermes intermedius*: corpses were first grouped by the termites, and then covered with soil particles and other materials found in the nest. The termite *C. formosanus*, as was mentioned before, tend to cannibalize their dead when mortality is low, but when mortality exceeds a threshold, termites prefer to bury them. Corpses tend to be covered by workers with fecal material, saliva, and secretions of other glands that inhibit the growth of fungi due to the antimicrobial and fungistatic properties of such secretions [274-276].

Colony foundation is a critical stage of the development of a society, and reducing the risk of infections is crucial for incipient colonies. When colonies of the termite *Pseudoacanthotermes spiniger* are founded by multiple reproductives (pleometrosis), the reproductives are forced to perform all tasks, including corpse burial if necessary. Once reproductive dealates are near to 1 day-old corpses of termites, these are detected by the chemoreception of a blend of decomposition products; in response, the dealates perform allogrooming, and also licking the corpses to cover them with saliva. After this, the dealates move the corpses as far away as they can and one of them begins to deposit soil particles covered with saliva on the corpses. Then, the other dealates assist in covering the corpses until they are finally isolated [277]. When colonies are founded by pleometrosis, it is probable that some of the reproductives die during the process of foundation. In this manner, it is crucial to the surviving reproductives to prevent the risk of infections from corpses by disposing of the corpses by burial isolation. This is important also in those species in which the colony is founded by more than one reproductive, but where only one survives [2]. The subterranean termite *Reticulitermes virginicus*, that eats their dead, also tends to construct walls or caps to isolate corpses from the rest of the colony, and bury any corpse found: ant, beetle, and nestmate corpses [278]. Termites are also able to identify the origin and status of corpses and will either eat the corpses or bury them. The termites *C. formosanus* and *R. speratus* tend to bury aged corpses without dedicating much time to inspection; on the contrary, the termites *M. crassus* and *G. sulphureus* tend to bury injured nestmates [251]. For its part, the termite *R. flavipes* [149] is able to discriminate between conspecific corpses and corpses of other species. The former ones tend to be eaten, while corpses from other species are buried in the nest after alarming the colony. Corpses from other species trigger a differential response in the termites *R. flavipes*: soldiers respond with alarming behavior, and workers with both alarm and burial behavior. It has been supposed that there are different capacities among castes, since workers distinguish conspecific and congeneric individuals, while soldiers only respond with aggression towards congeneric corpses, suggesting that they are able to recognize nestmates but not the dead condition [149]. The sequence of burial behavior in termites can be summarized as follows (see Table 2):

1. Detection of the corpse.
2. Approximation.
3. Inspection (brief).
4. Grooming and allogrooming.
5. Recruitment of nestmates.
6. Corpses may be licked and covered with feces and saliva by workers. Group activity.
7. Removing the corpses and grouping them (in *Pseudoacanthotermes spiniger* dealates) or leaving them in the place they were found. For *C. formosanus*, *R. speratus* and *M. crassus*, a crawling behavior under the corpses was described. Soldiers of *R. flavipes* showed aggression towards corpses of other species.
8. Carrying building materials by workers. Group activity.
9. Covering soil particles with feces or saliva. Group activity.
10. Depositing soil materials on corpses. Group activity.
11. Finalization (burying is complete). Group activity.

5.5. Necrophobia: avoidance of the dead

Pathogen avoidance behavior has evolved in animals to prevent contagion of diseases using detectable cues from potential sources of contamination, which produce revulsion responses [72, 73, 279] as a kind of an instinctive microbiology [280] that provides a selective advantage. Necrophobic behavior has been observed in different animals that respond by avoiding the corpses of conspecifics or even the sites where corpses are or have been present. This has been reported in the mouse *Mus musculus* [133] and in fishes [281]. These repellent behaviors in animals have been of interest due to the potential use for controlling pests [282] and avoiding by-catch in the fishing industry [283]. For example, necrophobic responses to corpses of lampreys have been used as a strategy to control their invasive populations [284, 285]. In the same way, a shark repellent made of extracts from putrefied sharks has been developed based on the strong necrophobic responses of sharks to dead conspecifics [134].

Among insects, *Periplaneta americana* cockroaches [152, 153] as well as collembolans [154, 155] are repelled by their dead. These insects avoid shelters containing dead conspecifics or chemicals released by dead conspecifics, or in which conspecifics have been killed by crushing. Tent caterpillars and fall webworms also show necrophobic responses, as also isopod crustaceans, which tend to avoid body fluids, injured individuals, corpses, and dead extracts from conspecifics [156]. Dead or injured conspecifics indicate the presence of pathogens or predators, and responsiveness to them is highly adaptive. Although the avoidance of the corpses may be a simple way to eliminate the contact with such a potential source of pathogens, it is not a viable strategy in social insects living in permanent nests.

5.5.1. Ants

Avoiding infected and dead members of the colony may be an important behavior that limits or reduces the spread of infections [69]. For example, *F. rufa* ants tend to avoid nestmates infected with fungus and covered with conidia [239], and *S. invicta* avoids baits with *B. bassiana* conidia [69]. Many ants change their nest site when the nest is no longer habitable or when ants follow a colony movement or emigration cycle [2]. Colonies of the ant *Pogonomyrmex barbatus*, for example, tend to relocate their nests each year after summer rains [286]. Although the pattern of relocation is suggested to occur in response to competition, it has been mentioned that the movements of those colonies are an attempt to escape from infestations or infections in their nests [286, 287]. There are reports of nest relocation in other species of ants. The fire ant *S. invicta* relocates the nest when colonies are infested with nematodes [288] or with *B. bassiana* [69]. Sometimes infestations cannot be controlled, even by discarding the infected individuals or eating them. When the nests of the social wasp *Mischocyttarus labiatus* are infested by the phorid *Megaselia*, and after unsuccessful attempts to perform hygienic behavior, the queen cuts the nest comb from its petiole and lets it fall. Then, she starts to build a new nest. This strategy is extreme because renesting constitutes the main cause of nest failure in these wasps, but it has the advantage of completely nullifying the reproduction of the phorids [264].

When colonies of *Temnothorax albipennis* are forced to emigrate, a group of workers seeks for potential new nest sites employing specific criteria for the selection of the new location [289]: floor area, cavity height, darkness, width and abundance of nest entrances, and proximity to an established conspecific colony. If the newly found location was occupied previously by other conspecific colony and can be re-used, there is a biohazard risk due to some kind of persistent pathogens present in the site. Workers of *T. albipennis* are able to detect the presence of dead nest and non-nestmate conspecifics and reject even ideal new nest sites and building materials to avoid the risk of contagion [208]. Thus, ants not only are able to emigrate from their nests when these are infested with pests and diseases, but also to evaluate the biological safety of new potential nest sites.

5.5.2. Termites

Avoidance behavior in termites depends on the nature of the corpse and on the termite species [251]. In general, termites show avoidance towards contagion and poisoning risks. They avoid contaminated areas of their nests or infected corpses, or the sites where corpses have been buried [259]. The subterranean termite *C. formosanus* avoids contact with termites killed with and without insecticides and also avoids or seals off the contaminated zones [290, 291]. Several studies have demonstrated that termites respond with avoidance behavior to the presence of entomopathogenous fungus such as *M. anisopliae* [151] mediated through the so-called pathogen alarm behavior [260]. Termites of the species *G. sulphureus* showed necrophobia, limiting their contact with corpses [251].

6. Undertaking specialists: doing the dirty job

6.1. Division of labor: compartmentalizing risky tasks

Social insects are exceptional among insects due to their ecological success and dominance [292]. This success is based on the cooperative organization of division of labor among colony members, and is coordinated and regulated by a sophisticated communication system. The integrated behaviors result in a unified system known as a superorganism [14]. Division of labor is characterized by the specialization of groups of individuals, called castes, on subsets of tasks which favor the ergonomic efficiency due to the task allocation [2, 293]. Castes are defined as groups of individuals that specialize, in some degree and at least for some time, in specific tasks. Castes in social insects are associated with age, morphology, and other specific individual traits, such as anatomical or physiological differences [2]. The primary division of labor is between reproductive and non-reproductive individuals. Secondarily, labor is divided into subsets of more or less specialized non-reproductive workers that perform all necessary tasks for the maintenance, growth and development of the colony, like foraging, caring for the offspring, defense against enemies and predators, and nest sanitation [2]. The main specialization of non-reproductive individuals is among workers that perform tasks inside the nest and those that perform tasks outside the nest, although within these categories specialization and even task partitioning is present [122]. Social insects show a wide diversity in development, behavior, social organization, and ecology that contributes to the diverse division of labor strategies [294]. However, three general patterns of division of labor have been identified in social insects [2, 293, 295]:

1. Temporal polyethism, or age-correlated patterns of task performance, in which workers change task performance with age, beginning with tasks within the nest, such as brood care, and progressively changing to outside tasks like foraging and defense.
2. Morphological polyethism, in which tasks are allocated among castes that morphologically and functionally differ (with more extreme the morphology, the behavior becomes more specialized and narrow is the behavioral repertoire).
3. Genetic polyethism, which is based on genetic predispositions towards task performance preferences. This predisposition is based on genetical differences among castes, resulting in an even finer and sophisticated division of labor [294, 295].

In fact, many species of social insects have high levels of genetic variation among colony members due to the high recombination rates, the multiple mating of reproductives and the presence, in many social insects, of multiple queens [294]. It is common that the queens of social insects mate with several males (polyandry), which not only reduces the reproductive conflict within the colony, but also provides enough genetic variability in the colony to cope with parasites and to produce the necessary inter-individual differences for the complex and sophisticated division of labor that some societies may have [294, 296].

Task allocation, caste specialization, and task partitioning have evolved in insect societies because they contribute to the colony fitness, and favor ergonomic efficiency, because permanent or temporal specialists work more efficiently than less specialized workers [26]. In addition, division of labor has also been favored in insect societies because it compartmentalizes the colonies, which separates processes physically, reducing the interactions between individuals as well as pathogen transmission [16, 297]. In the first place, younger workers often work inside the nest tending the brood and queen, whereas older workers tend to forage outside and are exposed to predation and infections [1]. Division of labor in these two broad groups of workers performing different and separated tasks affects pathogen transmission, and it is plausible to assume that a finer division of labor would have stronger effects. By separating the care of the brood, the input of resources, and the output of waste among different groups of workers, societies diminish the probability of pathogen spreading by isolating them and maintaining control. Consider waste management in the large colonies of fungus-growing *Atta colombica*, which involves an external refuse dump where dense rows of workers arrive with refuse materials. In this species, waste management is separated spatially from foraging by different routes and by keeping the foraging trail far away from the refuse dump, and also temporally, because foraging shows circadian rhythmicity whereas waste removal is a constant and arrhythmic activity [70, 122]. A division of labor also exists between ants working in waste management and ants working in the rest of the nest, without the possibility of an interchange from waste removers to foragers or other tasks [122]. In fact, ants not involved in waste management, mainly foragers, avoid any contact with refuse materials, which include corpses [298]. In addition, waste disposal shows division of labor within itself, between transporting workers carrying waste to the dumps and heap workers that treat the waste by distributing and removing it. Dump ants (contaminated by garbage) are aged workers with a low life expectancy that never leave the dump; when they try it, they tend to be aggressively expelled by nestmates reinforcing division of labor [122, 299]. Dump workers have an increased mortality because waste is not just hazardous to the fungus, but also to ants, and not only because of microbial infections, but also due to the toxic compounds produced by microbes [121]. The function of the dump workers seems to be treating the waste to diminish its hazardous properties, bury the refuse, oxygenate it to promote aerobic decomposition and to allow toxic gases to escape, thus creating a suitable environment for commensal microorganisms that presumably facilitate refuse decomposition [121]. Although fungus-growing ants prefer drier chambers to house their refuse dumps [300], the high concentration of organic matter in the refuse chambers favors the proliferation of decomposers, increasing the production of waste byproducts such as CO_2 [118], which, along with that resulting from the respiration of the large population of ants and that of the fungus cultivated, may increase the concentration of this gas to high and dangerous levels. However, CO_2 concentration inside the nest is controlled by the architecture of the nest that promotes a wind-induced ventilation, supplying nest with fresh air [301]. Waste management in fungus-growing ants is also partitioned [122, 302]. Task partitioning is the process in which two or more individuals contribute sequentially to a particular task or piece of work [303]. In this manner, workers inside take waste from fungus chambers and deposit it in a garbage cache (a kind of waste substation) at the entrance of the refuse dump or even inside the nest (see Figure 1), where a dump worker takes it to the refuse dump [122]. Apart from task partitioning improving the efficiency in the organization of the work of societies [302] by reducing energy costs [14], taken together with the division of labor and physical and temporal separation of waste management from other activities in the nest, it may also reduce the pathogen spreading from refuse dump to the fungus garden [122].

6.2. Undertaking specialists in social insects

First of all, in mature colonies of social insects, undertaking behavior, as all other tasks, is commonly performed by workers, not reproductives [1, 12]; this also occurs among social aphid colonies, in which soldiers are responsible for defense and for removing refuse materials and dead conspecifics [81]. However, in the colony-founding stage, reproductives are alone and cloistered in an excavated chamber with no workers tending them. In this stage, reproductives need to perform all activities required for their own survival and that of their progeny [1] including nest sanitation. It has been reported that in the colony-founding stage, reproductives of *Pseudoacanthotermes spiniger* termites are able to perform undertaking behavior when an individual in the incipient colony dies [277], as also occurs among queens of *Camponotus atriceps* ants [López-Riquelme, personal observation]. This suggests that reproductives can recognize the dead and respond by isolating the threat, at least in the foundation stage.

In some social Hymenoptera, the extreme division of labor has produced specialized individuals, the undertakers, that take charge of corpse disposal. This worker-specialization separating the risky task of removing corpses from other processes that are carried out in the colony which could become contaminated if both processes or workers are mixed [5, 8]. On the other hand, in termites there are no reports on undertaking specialists (see Table 3). Why do some societies need undertaking specialists while others do not?

6.2.1. Undertaking specialists in social Hymenoptera

If undertaking behavior is a specialized task, then there must be a small proportion of individuals in the colonies of social insects that perform it. In fact, Visscher [4] found that undertaker bees comprise a reduced group of about 1-2% of the workers in a colony. These individuals specialize in corpse removal, while most of the other individuals of the same age apparently never perform undertaking behavior [304]. This is important, because division of labor among honeybees is based on temporal polyethism with no physical castes [1], and undertakers are a specialized subset of middle-age bees that perform undertaking behavior for several days [5]. Undertaking specialists in honeybees are neither hyperactive bees searching for corpses, nor quiescent reserves that become active only when a corpse

Table 3. Summary of undertaking behavior in social insects*.

Undertaking behavior traits	**Main groups studied**		
	Bees	**Ants**	**Termites**
Undertaking responses	Necrophoresis Self-remotion of moribund bees	Necrophoresis Necrophagy Burial Avoidance Self-remotion of moribund individuals in: *Temnothorax unifasciatus*, *Camponotus aethiops*, *Pogonomyrmex badius*, *Solenopsis saevissima*	Necrophagy Burial Avoidance
Postmortem time to initiate a response	N.R.	~5 min in: *S. invicta*	Within the first min. in: *C. formosanus*, *R. speratus*, *M. crassus*, *G. sulphureus*
		~12 h in: *C. japonicus*	~15 min in R. flavipes
		Within 15 min. in: *T. lichtensteini*	12 h in *P. spiniger*
Postmortem time to reach maximum response	12 min	~50 min in *S. invicta*	~first min. after death in: *C. formosanus*, *R. speratus*, *M. crassus*, *G. sulphuresus*
		~1 h in: *L. humile*	>12 h in: *P. spiniger*
		48 h in: *C. japonicus*	
Different undertaking responses	N.R.	Necrophoresis: almost all corpses in almost all species. Necrophoresis of infected individuals: *S. invicta*	Not shown necrophoric behavior (when the carrying of dead is present, it is part of other undertaking strategy)
		Necrophagy of fresh corpses in *F. polyctena*, *L. niger*, *L. niger*, *S. invicta*, *S. saevissima*, *P. dentata*, *C. cursor*, *C. floricola*, *O. overbecki*. Dead queen is not removed but eated in *A. mexicana*. Necrophagy of infected corpses: *F. rufa*	Necrophagy of fresh corpses: *C. formosanus*, *R. flavipes*, *M. crassus*. Necrophagy at low mortality in the nest: *C. formosanus*, *R. lucifugus*. Necrophagy of nest- or non-nestmate corpses: *R. flavipes*. Necrophagy of infected corpses: *R. flavipes*, *Z. angusticollis*. Cannibalizing injury individuals: *C. formosanus*, *R. speratus*, *M. crassus*. Canibalizing supernumerary reproductives: *K. flavicolis*, *N. jouteli*
		Burial of infected corpses: *S. invicta*. Burial of other species corpses: *T. lichtensteini*	Burial of corpses: *P. spiniger*, *R. virginicus*. Burial of aged corpses: *C. formosanus*, *R. speratus*. Burial of mutilated individuals: *G. sulphureus*. Burial at high mortality in the nest: *C. formosanus*. Burial of other species corpses: *R. flavipes*.
		Avoidance of infected corpses and nestmates: *F. polyctena*. Avoidance of nesting sites containing corpses: *T. albipennis*	Avoidance of burial sites: almost all species. Avoiding sites contaminated with entomopathogens or insecticides: *C. formosanus*. Termites can detect the presence of pathogens and alarm nestmates by a vibrational display that evokes a moving-away response from nestmates
		Nest-relocation by massive infection: *P. barbatus*, *S. invicta*	

Table 3 continued..

Refuse piles	Absent in *Apis mellifera*.	Present in many species, mainly in larger societies of Attini, Ecitoninae and harvester ant middens, in which dumps are discrete and conspicuous sites outside or inside the nest	Absent, wastes tend to be recycled or reused
	Present in Meliponini and located at the entrance of the hive	Other species have diffuse and scattered refuse dumps	
Division of labor	Marked division of labor with small population of middle-age, genetic determined undertaker specialists; with behavioral, hormonal, and probably neurological, differences	In species with large and long life colonies, there is a marked division of labor with small population of undertaker specialists probably genetically determined and with behavioral differences, and probably physiological and neurological. In species with small colonies division of labor could be less marked.	No division of labor and no specialization in undertaking behavior reported. In *R. fukienensis* median and larger workers perform most of all tasks, including burial behavior, and soldiers of *R. virginicus* appear not to participate at all in burial behavior.
	Necrophoric behavior is performed by one individual each time		Burial behavior is a task performed by groups of individuals
		Burial behavior is a task performed by groups of individuals	
		Cannibalism and necrophagy could be performed by individuals or in group	
Death recognition mechanisms	Chemoreception (olfaction). No compounds reported yet	Chemoreception (Olfaction and probably taste and tact). Different compounds found in corpses seem to be involved. Two main groups: 1. After death accumulation of cues: Fatty acids: oleic (the most active), linoleic, linolenic, palmitic, palmitoleic, myristoleic, stearic acids and triglycerides. 2. Life signals that vanish after death occurs: iridomyrmecin and dolichodial.	Chemoreception (olfaction and probably taste) and mechanoreception (tact). Different compounds reported up to now: After death accumulation of cues: 1. Fatty acids: oleic, linoleic, palmitoleic, octadecanoic, hexadecanoic, tetradecanoic acids. 2. Indol and phenol (the most actives)

* This table is for comparative purposes, for references and detailed information see text.
N.R.: Not reported.

appears [45]. However, among undertakers as a group, some extreme individuals are more highly active than others; these individuals can be so specialized that they can cover a high proportion of the tasks without needing further experience to improve their undertaking performance [45].

Undertaking specialists in bees also show a high tendency to perform tasks related with necrophoresis, such as handling corpses and removing debris, and, at the same time, they show a reduction in the performance frequency of most other behaviors normally associated with bees of their age [159]. Undertakers are developmentally advanced, showing a tendency to forage earlier compared to other middle-aged workers [159]. Undertaking specialists have a demonstrated genotypic component [7] that, when expressed, confers them with stable and permanent short-term and long-term task preferences [159], and, most likely, with a genetically determined sensitivity to corpse-related stimuli [7]. It has been demonstrated that undertakers (as other specialists) are hormonally distinct from other middle-aged bees: undertakers have higher levels of juvenile hormone (JH), the master hormone that controls molting and development in insects [305], compared to other bees of the same age, and have similar levels of JH as foragers that are 10 days older. The higher levels of JH in undertakers result in profound neurological and physiological differences underlying behavioral specialization [306].

The genetic determination of undertaking specialists in honeybees diminishes the behavioral plasticity of individuals for task-switching. This lack of plasticity of individuals results in the lack of plasticity at the colony level, constraining the ability of the colony to respond to changes in social composition [158]. Thus, when all undertakers and similarly aged workers are removed from colonies, undertaking in the colony decreases due to its dependence on the genotypic specialized subpopulation of middle-aged undertakers, and because no other colony members with the appropriate genotype can replace them to continue with corpse removal [158]. However, when such a genotypic group remains in the colony, undertakers may be easily replaced [160].

In ants, although in *S. invicta* there is a moderate polymorphism, Howard and Tschinkel [120] did not find evidence of a specialized caste or size worker that preferentially performed undertaking behavior. However, Wilson [307] found that in *Atta sexdens*, a polymorphism is correlated with polyethism, and that waste-removal workers constitute a group of middle-sized workers classified as within-nest generalists. In the fungus-growing ant *Acromyrmex versicolor*, Julian & Cahan [8] found that although most of the workers encountered corpses at least once, only a small group performed undertaking behavior independently of the corpse encounter rate, which suggests the existence of some internal cause for this task preference. This predisposition may be genetic in *A. versicolor*, since other tasks in this species are performed by workers with a genetic influence in task preference and in the rate of progression through age polyethism [308]. This genetic predisposition probably produces differences in the sensitivity to chemical cues related to undertaking behavior, *i.e.*, corpse odorants. Thus, it is possible that death recognition may be, at least in some degree, caste-specific, and that highly morphologically specialized castes not involved with undertaking, such as soldiers, are not able to recognize the dead, since soldiers of the ant *Atta mexicana* seem to be insensitive to oleic acid, the cue for corpse recognition [189]. In the same way, soldiers of the termite *Reticulitermes flavips* are not able to recognize the dead, but they do respond to non-nestmate stimuli [149]. In the ant *A. mexicana* [190] a small group of workers specialized in performing most of corpse removal tasks was also observed: from 30 observations, only 12 workers performed complete necrophoresis (from the site of first encounter with the corpse to the refuse pile) at least once, four of them performed necrophoresis on two occasions, and one worker performed complete necrophoresis 15 times. Undertakers that remove corpses more than two times (including the worker that performed it on 15 occasions) were, on average, faster than those workers that performed undertaking only once (470 ± 380 s), although the extreme undertaking specialist (that removed corpses 15 times) was not the fastest of all (necrophoric duration in the two-time undertakers = 106 ± 28 s; necrophoric duration in the 15-time undertaker = 131 ± 60 s). Moreover, it was not found that undertakers were more sensitive to oleic acid present in corpses [189]. In the same way, in the red ant *Myrmica rubra*, only a small group, a 3.2% of ants of the colony, performed most of the corpse removals contributing to a high proportion (20%) of the overall undertaking duties in the colony [197]. The colony efficiency of corpse carrying in *Myrmica rubra* was due to the variability of ants involved in the task and to the short-term specialists that become active, carrying corpses on repeated occasions, as an emergent polyethism response [309]. These short-term undertaking specialists are very efficient workers with a spatial memory that enables them to always find the same pathway to the refuse pile [197].

It is interesting to note that, apparently, genetic diversity in some species may be unrelated to division of labor and caste specialization, since in the Argentine ant *Linepithema humile*, an experimental reduction in genetic diversity did not show changes in efficiency of corpse removal, which suggests that, at least in this species, the genetic component of division of labor and task specialization could be small [310]. This finding could represent the starting point of the study on genetical control of undertaking behavior in species other than honeybees. For a more detailed discussion about undertaking specialists, see section 8.2 “Neurobiological specialization of undertakers” of this document.

6.2.2. Undertaking specialists in Isoptera

Division of labor and polyethism in termites is more complex and diverse than in eusocial Hymenoptera, probably due to their development, ecological and feeding habits, diverse strategies for corpse disposal, etc. Therefore, it is possible that they do not have undertakers, in the sense of a specialized caste, as those known in social Hymenoptera [1]. It has been suggested that due to their hemimetabolous development, termites may exhibit a fully discretized caste system where immature colony members, similar in form to adults, are capable of performing many of the same behaviors, and contributing to the colony needs [26]. On the contrary, in ants, wasps, and bees, larvae and pupae are unable to carry out tasks except food processing and distribution [311]. The term temporal polymorphism has been proposed to describe a change in task functions of a worker during its lifetime [312]. However, temporal polyethism has not been found yet in lower termites [311, 313, 314]. In contrast, higher termites exhibit polyethism for different tasks: foraging and processing material collected [315], processing and carrying food [316], and age polyethism related to the change from tender to forager [317]; but there are no reports of specialists, except for soldiers [1, 318]. Based on worker sterility, polyethism, and ecology of nesting and feeding habits, termites may be grouped into two life types [319, 320]:

a) One-piece type termites that construct one-piece nests in a piece of wood that serves as shelter and food and spend their entire colony life in this single piece of wood. In species of this group, individual termites retain the ability to reproduce throughout its life; it appears that labor is not organized into temporal castes and the work force consists of the late instar larvae and nymphs. All lower termites are one-piece type termites.

b) Multiple-pieces type termites. These species live in well-defined nests separated from foraging sites; thus, workers must go out for foraging. In these species, there are true morphologically differentiated and sterile worker castes and a well-developed age-related division of labor.

Traniello & Rosengaus [319] suggested that this separation of the nest and food may have created the spatial predisposition for the centrifugal movement of workers proposed by the algorithm, ‘foraging for work’ [321]. However, it has been shown that in the termite *Reticulitermes fukienensis*, most of the tasks are performed by the medium-sized and the older and larger groups [314]. Although they are relatively inactive, small workers are also involved at a lesser frequency in some tasks, except carrying larvae. The most interesting finding was that large workers performed all tasks, including undertaking behavior, at higher frequencies compared to other workers of any size, and even tending the queen and the brood. This is contrary to the common pattern in social Hymenoptera, in which the young workers care for the queen and the brood. Of course, this finding is completely opposite to the ‘foraging for work’ model. In other species of termites, as *R. flavipes*, different caste responses to corpses have also been reported, in which workers are involved in corpse disposal, but not the soldiers [149]. However, up to our knowledge, there are no reports on specialization in undertaking behavior in termites [13].

6.3. Who needs undertaking specialists?

Corpse disposal in social insects has evolved to protect, in the first place, the reproductives and the brood, and in the second place, the adults from infections and parasites that may be released by corpses after death [6, 32]. It is agreed that the main strong selective pressure for the evolution of corpse disposal is the potential risk of pathogen transmission from dead bodies to other members of the colony [3, 6, 32]. For this reason, corpse disposal strategies in social insects evolved to prevent contagion and epidemics [3, 4]. All undertaking strategies are aimed to isolate corpses from members of the colony. However, there are two main patterns of corpse disposal in social insects, *i.e.*, the hymenopteran and the isopteran (see Table 3). One important difference between them is that social Hymenoptera, especially in large and long-lived colonies, commonly exhibit well-defined undertaker subcastes and specialists, perhaps most of them genetically determined [7, 8]; whereas, in Isoptera, there are no reports about undertaking specialists, even in the complex societies of fungus-growing termites.

Differences in patterns of development and ecology, especially feeding and nesting habits, have been important factors in the divergent strategies of corpse disposal between Isoptera and social Hymenoptera. It is possible that, for the same reasons, termites have not been under strong selective pressure to develop undertaking specialists similar to those found in social Hymenoptera. Termites do not need to separate or compartmentalize processes, risky tasks, discrete physical sites for corpse disposal, or waste dumps from the brood and reproductives, because termite strategies for waste and corpse management are based on recycling and reusing. They can consume feces to acquire microorganism symbionts [75], or use feces to build their nest or to fertilize the fungus in fungus-growing termites [44]. In termites, corpse disposals are carried out within the nest (termites do not have refuse piles where corpses are dumped) and are based on the nutrient recycling resources by cannibalizing the soft bodies of injured, diseased, and dead conspecifics [44], and it seems that termites do not require specialists to carry out cannibalism or necrophagy. In addition, when they cannot eat some corpses, termites tend to bury them within the nest. Performance of such a task often requires the involvement of more than one individual. So, the concept of undertaking specialists used in social Hymenoptera may not be accurately applied in the context of the life of termites.

On the contrary, in social Hymenoptera, corpse disposal is based on the removal of corpses from the interior of the nest to the exterior, or to special chambers inside the nest with a continuous traffic of wastes and corpses [3, 70, 122]. On the other hand, ants, bees and wasps limit their cannibalism to immature stages [1]. When these insects cannibalize adult nestmates, live or dead, they tend to be restricted to the soft internal tissues of infected members of the colony; when other preys are scarce, after consuming the contents of the corpses, either nestmates or non-nestmates, carcasses must be removed from the nest anyway [230]. If corpses are not eaten as soon as possible (as in the case of termites) and pathogens are not deactivated in the gut, pathogens may be released by corpses after some time, which puts the entire colony at risk. Thus, undertakers must be effective in removing corpses from the nest to avoid risks of transmission among members of the colony inside the nest. In addition, workers that remove corpses have frequent contact with corpses and refuse piles exposing themselves to pathogens with a high risk of contamination and increasing the probability to contaminate other members of the colony. In this manner, it is important to keep those workers away from the brood, the queen, and the food. For instance, bee and ant foragers tend to be the oldest workers that go out of the nest in search for food. These workers are exposed to high risks since the predators may eat them or they can be infected by entomopathogens [2, 16]. For this reason, nursing is preferentially performed, not for foragers, but for young workers that have been performing tasks inside the nest without the risk of being exposed to infectious diseases [1, 2]. This division of labor between outside-nest foragers and within-nest workers compartmentalizes the colony and puts social barriers to pathogen transmission. In fact, for example, there is a strong division of labor between workers that forage and workers that remove waste and corpses in the colonies of fungus-growing ants. Those workers that remove waste and those that work in the refuse dumps are old workers that never switch to become foragers or nurses, and when they try to leave the dumps, are aggressively rejected by within-nest workers [122, 299]. Thus, corpse removal must be an effective activity, and must also be segregated from others activities in the colony, since those workers who perform it also represent a high biological hazard for the colony. In this manner, division of labor in social insects may reduce pathogen transmission. But division of labor can also be under the selective force of parasitism, which causes the reinforcing of the compartmentalization of the colonies, mainly in species with large and long life colonies with high rates of death. The result is that the queen and brood are kept segregated and away from risky duties [297].

7. Messages from the dead: cues involved in death recognition

The recent interest in undertaking behavior has led to the realization of a series of studies on different aspects of this sophisticated behavior. Also, there is a specific interest in the mechanisms involved in the releasing stimuli and also in behavioral mechanisms of undertaking [12, 120, 152, 155, 156, 189, 190, 196, 277, 278] due to the lack of conclusive studies on the specific identity of the cues from the corpses that lead to the recognition of the dead.

Although social insects have a great diversity of sensory organs that are important in their relationship with their environment and in their social life, chemical modality (and mechanical to a lesser extent) is the basis of their social organization [1]. Social insects live in complex societies coordinated by sophisticated communication systems based on the release and detection of small molecules called pheromones. All levels of sociality have a chemical basis, on which, regulation, integration, and cohesiveness relay. There are two main groups of pheromones in social insects. The first comprises different kinds and blends of pheromones produced by exocrine glands that, when detected by other individuals, release behavioral species-specific responses dependent on concentration and context [2, 19]. The second group of pheromones is collectively called the colony odor, and consists of a collective blend of hydrocarbons carried on the epicuticle of individuals, which participates in the discrimination between nestmates and non-nestmates [2, 14, 322]. Therefore, it is plausible to expect that death recognition depends on chemical cues from the bodies of dead individuals. As undertaking behavior occurs inside the nests of social insects, vision could not be involved in death recognition. Auditory stimuli, as well as the thermal, have also been discarded as signals involved in the detection of corpses [4]. The characteristic lack of motion of corpses also is dismissed as a cue of death, since anesthetized workers of ants are not carried to the refuse pile. The rigor of the corpses is not involved in the recognition of the death either, since the response elicited by freezing-killed and heat-killed workers appears at the same time [120]. Thus, in the same way in which social insects recognize nestmates, they are also able to recognize their dead, by means of particular chemical cues of corpses [2]. It is interesting to note that the entire nestmate and non-nestmate discrimination process occurs in a fraction of a second when, for example, two ants from the same or different colonies meet each other [14], but the process by which social insects recognize their dead seems to be longer, involving inspection behaviors as antennations, licking, grasping, biting, climbing, crawling, carrying for short distances, etc. This suggests that discrimination of live and dead individuals may involve complex processing of the signals emanated from the corpses and also signals from the context that lead to the behavioral decision.

7.1. When for social insects is a corpse actually dead?

If undertaking behavior has evolved under selective pressures to maintain healthy colonies, mechanisms may have also evolved to rapidly detect cues for unequivocally recognizing the dead members of the colony and clearly distinguishing them from the living ones. This means that, once death occurs, living members of the colony must detect some of the postmortem changes that initiate in the corpses. Postmortem processes can produce changes within the few minutes after death that modify the chemical signature of dead animals, leading to their recognition as a corpse.

The decaying process in all animal corpses follows the basic principles and processes. Decomposition of corpses, and associated chemical changes begin almost immediately after death occurs. As soon as the cells of the body are no longer receiving oxygen, CO_2 in blood and tissues increases, pH decreases, and wastes accumulate, intoxicating the cells and killing them by poisoning. This initiates the degradation process triggered by autolysis and causes the rupture of cells and the releasing of fluids rich in organic and inorganic nutrients. With time, the process gradually becomes generalized over the whole body, leading to the liquefaction of the soft tissues, and releasing the intestinal biota, which expands through the corpse, accelerating the decomposition. Once enough cells have released their nutrient-rich content the putrefaction process by bacteria, fungi, and protozoa begins, which completes the catabolism of tissues into gases, liquids, and simple molecules [see 138, 323, 324, 325]. After all soft tissues have been destroyed by putrefaction by the action of microorganisms, only the insect exoskeletons remain, which will be subjected to slow weathering and decomposition by microorganisms, mainly fungus, bacteria, and actinomycetes that grow on the chitin [143, 144]. As social insects present a plethora of pathogens that may be released after death [34, 35, 41-43, 137], it is vital to detect, recognize and dispose of the corpses as soon as possible to limit the risk of epidemics in the colony. But, how do social insects recognize dead members of the colony? What is the nature of the cue responsible for the unequivocal death signature? Where does this cue come from? What appears or disappears in the corpses after death occurs that directs live members of the colony to detect and remove them from the interior of the nest?

The main detectable changes that dead bodies develop can be grouped in two categories: a) cues associated with the progressively ceasing of living processes, and b) cues associated with decomposition. Thus, it has been proposed that social insects recognize dead members of the colony by detecting either: a) the appearance of chemical cues produced by the decomposition process, or b) the loss of chemicals associated with life that inhibit undertaking behavior [4, 120].

7.2. Deadness or lack of liveness: cues or signals to recognize the dead

It has been mentioned that identification of the dead, although not considered as communication, has common features with communication, particularly its dependence on stereotyped responses triggered by narrow chemical cues [2, 14]. It is important to take into account the distinction between signals and cues. Signals are information-bearing actions or structures that have evolved for specific functions in communication, whereas cues are variables that also convey information, but have not been molded by natural selection to convey such information for the receivers. Both kinds of variables provide reliable information to the individuals that receive them, but signals evolve for a specific communication role, and cues inform incidentally [174]. Important cues in communication evolve from adaptive responses to a pre-existing stimulus (the cue), while signals evolve from the adaptive modification of both the stimulus (the signal) and the response when there are no cues that express the information that the signals convey [174, 326]. If the recognition of dead members of the society depends on incidental by-products of decomposition, the ‘deadness’ smell would be a cue, but if those odors are the result of simple or complex interactions of exocrine gland secretions, the smell of death would be a signal [326]. For instance, laboratory rats appear to recognize the death by the decomposition products cadaverine and putrescine, which direct surviving mates to bury the cadaver using the substrate present in the container [271]. In the same way, other animals such as sharks [134] and lampreys [284] show necrophobic responses to byproducts of decomposition.

7.3. Necromones: conserved cues for death recognition

In their pioneering study about necrophoresis in ants, Wilson *et al*. [12] assumed that the releasing stimulus of undertaking behavior is chemical in nature and appears after death as one of the postmortem changes. Following this line of thought, they attempted to isolate from the corpses the chemical substance or substances that, by themselves, may elicit the necrophoric behavior in the ants *Pogonomyrmex badius* and *Solenopsis saevissima*. They made acetone extracts of worker corpses, with which they daubed different objects, filter paper pieces, seeds, and living workers, and placed these close to the nest entrance. All objects, even live and moving nestmates, were treated as corpses and were carried to the refuse piles. When corpses were treated with solvents for more than 3 weeks to remove any chemical releaser, they were not transported to the refuse pile; however, they were licked and chewed, and even carried into the nest. After some minutes, those treated corpses were transported to the refuse pile, indicating that the cue appeared again after some time. After this, Wilson and his coworkers analyzed the corpse extracts and found the presence of fatty acids, which were effective in eliciting undertaking behavior. From these fatty acids, oleic acid is the only substance that elicits necrophoric behavior in the same manner as ants behave toward nestmate corpses. From these experiments, Wilson *et al*. [12] concluded that the substances acting as cues of death, triggering undertaking responses, are exclusively chemical and are common products of the decomposition of insect corpses, such as oleic acid. Blum [193] confirmed that, of the fraction of the extracts of corpses of *S. saevissima* ants rich in fatty acids, myristitelic, palmitoleic, oleic, and linoleic acids elicited undertaking responses. He assumed that fatty acids accumulate in corpses as a result of decomposition caused by bacterial hydrolysis of triglycerides. Interestingly, Bomar and Lockwood [327], studying the cannibal behavior of grasshoppers, found that some ants (the species was not mentioned) were attracted to baits prepared with linoleic and linolenic acids but not to those baits prepared with oleic acid. Bomar and Lockwood concluded that ants are attracted to oleic acid only inside the colony. In fact, Gordon [187] demonstrated that behavioral responses elicited by oleic acid are more complex than the univocal rigid response to only one releaser, since they depend on the context and can even be opposite, confirming Bomar and Lockwood's assumption [327] that is: when a colony is engaged in midden work or nest maintenance, oleic acid evokes undertaking behavior and ants transport oleic sources to the midden, but when the colony is foraging, sources of oleic acid are taken into the nest as food items.

It has been found that fatty acids, mainly oleic and linoleic acids, elicit necrophoric behavior in different ants, including the primitive *Myrmecia vindex* [194], *P. badius* [12, 187] and *S. saevissima* [12, 193]. In the fungus-growing ant *A. mexicana*, it was also demonstrated that oleic acid is an important compound found in extracts of corpses of up to 10 hours [189, 190] that elicits necrophoric behavior by means of antennal sensorial responses. In Isoptera, in the fungus-growing termite *P. spiniger* [103], it has been shown that the reproductives perform burial behavior in response to corpses and to the extract of corpses. The compounds identified in such extracts were a complex blend of indole, phenol, and fatty acids (among which are oleic, palmitoleic, linoleic, tetradecanoic, and hexadecanoic acids). To elicit burial behavior, all compounds must be present at the concentrations found in corpse exctracts; none of the compounds alone elicits burial behavior. In the subterranean termite *R. virginicus*, it was found that burial behavior requires a combination of chemical (oleic acid) and tactile information to be released. Chemical or tactile cues alone did not elicit undertaking behavior [278]. It seems that in those termites, undertaking behavior responses depend on the synergism of multimodal cues.

The recognition of death occurs in very diverse varieties of animal species. However, since members live in enclosed and permanent nests, it is in insect scocieties that such recognition provides greater benefits by preventing disease. Subsocial and gregarious insects also respond to conspecific corpses. Grasshoppers tend to be attracted to corpses of conspecifics and non-conspecifics to feed on them, although necrophobic responses are also present [327]. It has been shown that fatty acid decomposition products, mainly linoleic and linolenic acids, on grasshopper corpses are even more effective as death cues than grasshopper corpses alone [327, 328]. Cockroaches avoid shelters containing dead conspecifics or filter paper pieces treated with crude extracts of dead cockroaches [152]. The content of the dead cockroach extracts found in corpses of both sexes is active against adults and nymphs. The fraction of the extract that elicits high repellency (necrophobia) contained methyl esters of four fatty acids: palmitic, linoleic, oleic and stearic acid as well as other triglycerides. Those compounds are highly repellent to cockroaches, but oleic and linoleic acids are the most effective. Of these, linoleic acid is 10 times more repellent than oleic acid, although there is no synergistic effect with the combination of the two compounds. In addition, the extract of corpses of *Periplaneta americana* is also highly repellent to other cockroaches [153]. It has been reported that Collembola [154, 155] are also repelled by corpses and corpse extracts from conspecifics. The compounds found in those extracts were palmitic, oleic, and linoleic acids, but only linoleic acid had a strong repellent activity and oleic acid had no effect at all. Other insects, like

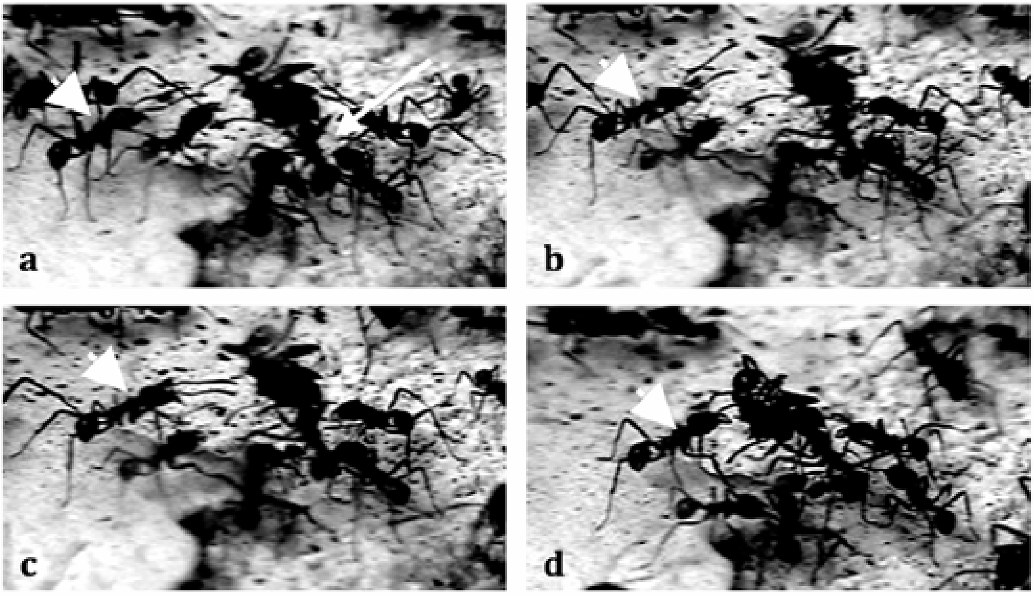

Figure 2. Images taken from a video recording of necrophoric behavior in the fungus-growing ant *A. mexicana*. In this sequence of images, it can be observed how an ant attracted to the corpse orientates her antennae towards the corpse before establishing physical contact with it. a) The large white arrow points to the undertaker that is lifting and carrying the corpse to the refuse dump. The short white arrow points to the ant that is orientating her antennae towards the corpse. Other ants surrounding the undertaker can be observed. b and c) It can be observed how the ant, pointed with the short white arrow, makes antennations without touching the corpse, which suggests that this ant is smelling some odor from the corpse. d) Finally, the ant makes contact with the corpse. Undertakers perform similar antennations before making physical contact with corpses. In each image can be observed ants surrounding the undertaker carrying the corpse (modified from 190).

aphids [329], beetles [330], social caterpillars, and even terrestrial Isopoda crustaceans [156] have been shown to be repelled by fatty acids present in the extracts of their bodies, either oleic or linoleic acid. In addition, the sternal gland secretions of the wasp *Polistes dominulus* and *P. sulcifer,* which are highly repellent to *Crematogaster scutellaris* ants, contain fatty acids such as linoleic, oleic, stearic, etc. [331].

Due to this ubiquitous presence of fatty acids in corpses of different species across diverse taxa, Rollo *et al*., [152] named such compounds necromones, whose major function is the adaptive recognition of dead con- or heterospecifics to avoid risks related with predation, parasites, and diseases. Fatty acid necromones have important properties as indicators of corpses, since long-chain fatty acids are the most stable among all the products of decomposition and have a very low volatility, which allows their disproportionate accumulation in insect corpses [12]. Due to the low volatility of these fatty acids, it was suggested that the dead might be identified through contact or near-contact chemoreception [120]. It has been observed in behavioral assays that ants first orientate their antennae towards corpses at a considerable distance even without touching them (Figure 2), and then they approach to the corpse and finally make contact with it [189, 190]. Moreover, electrophysiological studies indicated antennal detection of oleic acid molecules transported by air, although other volatile compounds that emanate from corpses might also participate in identification of the dead [189]. Notwithstanding the above, it should not be assumed that fatty acids are present only in the corpses of insects. On the contrary, they are important constituents of insect tissues and serve in many physiological functions, for example, as sources of energy, to form biological membranes, and as a precursor to pheromones, wax, and eicosanoids [332, 333]. Fatty acids may be found in different parts of the body of insects, for example, in some glands [334-336]. In addition, besides the cuticular hydrocarbons, insects present lipids and fatty acids in their cuticles [337], of which the most common are long-chain fatty acids of 14-20 carbons, such as palmitic and oleic acids [338].

In any case, if fatty acids elicit undertaking behavior in many social and subsocial insects, they require some time to appear in the corpses of the studied bees and ants to have an effect: about 12 minutes in honeybees [4], 5 minutes in the ant *S. saevissima* [120], within the first hour in the ant *L. niger* [188], 12 hours in the termite *P. spiniger* [277], and within 1 hour in the termite *R. flavipes* [149]. For their experiments, Howard & Tschinkel [120] killed ants by heating at 100 ºC, thus blocking bacterial and enzymatic activity needed for the production of oleic acid. In spite of this, it has been reported that *P. americana* cockroaches can enzymatically convert oleic acid to linoleic acid [152]. Thus, it has been suggested that fatty acid necromones released after cell death or rupture are indicators of injury or death to conspecifics across diverse phylogenies, from plants to animals [339, 156].

Nevertheless, the appearance of the cue or signal after the occurance of death must be consistent with behavioral data provided by different authors. However, studies are scarce regarding the postmortem temporal generation and accumulation of fatty acids in insects that supported behavioral data. In their study, Wilson *et al*. [12] did not mention exactly how the extracts were prepared. In studies on cockroaches, extracts were prepared from frozen cockroaches maintained at low temperature (-5 ºC) for 24 hours and fatty acids were found even when corpses were not allowed to age at ambient temperature [152]. Collembola extracts were made from completely crushed insects and the released body contents were left for 2 hours at room temperature, and then overnight in the solvent to complete the extraction [155]. Although Howard & Tschinkel [120] explain how their corpse extracts were prepared, they did not subject them to chemical analysis. Yao *et al*. [156] prepared extracts from recently killed animals (isopods and caterpillars) by freezing. Extracts from corpses of the ant *A. mexicana* were prepared from ants killed by freezing, and then incubated for 10 hours at room temperature and, finally, treated with organic solvents for 24 hours to complete the extraction [189]. Choe *et al*. [196] found triglycerides in extracts from live, 1 hour-dead and recently killed Argentine ants, which elicited necrophoric behavior and aggression in workers. In their study, Chouvenc *et al*. [277] showed that the appearance of fatty acids coincides with the beginning of undertaking behavioral responses towards corpses. They prepared extracts from the termite *P. spiniger* corpses, killing individuals by freezing and incubating them for 10 minutes, 24 hours, or 8 days; after this period, the corpses were extracted [277]. They found that compounds such as indole, phenol, oleic, linoleic acids and other fatty acids increase in concentration in the corpses over the time in which corpses were left to decompose. Their results coincide with the necromone appearance hypothesis, since in *P. spiniger,* the cue of death appears in corpses after 12 hours following the death of individuals. Also, the 8-days aged corpse extract, with the higher concentrations of the different compounds, were the most effective in eliciting burial behavior in reproductive termites.

Although it has been proposed that fatty acids begin to generate and accumulate after death, the actual mechanism by which these substances may be generated is not yet known. It has been suggested that the increase of fatty acids in corpses is due to the autolytic catabolism of the necrobiotic processes and/or due to the hydrolytic activity of the bacteria present in the insect corpses, which may rapidly hydrolyze triglycerides, producing high concentrations of fatty acids [193]. Many triglycerides of plants and animals contain one or a few types of long-chain fatty acids in their three residues, which may be released upon hydrolysis, leading to the increase of fatty acid concentration [340]. This hypothesis was tested by Akino & Yamaoka [195], who observed that, in the ant *Formica japonica*, the undertaking response (necrophoresis) to corpses increased according to postmortem time, suggesting that the cue required time to appear on the corpses. The response of workers to corpses began to appear after 12 hours of postmortem incubation and, after 48 hours, the undertaking response was considered to be maximum. The fatty acid fraction of surface and within-body extracts was found to be more effective in eliciting undertaking behavior compared to other fractions (hydrocarbons, triglycerides). The fatty acids found in triglycerides in the surface and in the hemolymph were linoleic, oleic, stearic, palmitoleic, and palmitic acids, and the main fatty acid stored in those triglycerides was oleic acid. It is interesting that the internal and surface fatty acids increased with postmortem time, reaching a maximum at 48 hours, whereas internal triglycerides declined, which suggests that internal triglycerides are the sources of the increase of fatty acids on and within the corpses. When Akino & Yamaoka irradiated corpses with microwaves immediately after death, the free fatty acids on the cuticle did not increase and the triglycerides in the hemolymph did not decrease, but the amount of triglycerides in the cuticle was higher than that present in not-irradiated corpses. This suggests that oleic acid increases in the cuticle within 48 hours after death by enzymatic hydrolysis of internal triglycerides, and that the enzyme is activated after the death occurs. It is interesting to note that *F. japonica* workers respond only to 48-hour old corpses [195] while other species tend to respond within the first postmortem hour [120, 196].

Although there is strong evidence supporting the hypothesis that fatty acids act like necromones in the recognition of death in very diverse taxa, some behavioral evidence suggests that some cues appear or disappear in a shorter time than that required by the fatty acids to accumulate in the corpses [120, 196]. Thus, it is important to study the interaction of different compounds involved in undertaking behavior and the recognition of dead.

7.4. "Lifeness signals" fade after death

Several decades after Wilson and his coworkers identified the releasers of necrophoric behavior in ants, data continue to accumulate with regard to the appearance of a death smell based on fatty acids, reinforcing the hypothesis of evolutionary conservation of fatty acid necromones as death cues across a great diversity of arthropods. However, it has been noted on repeated occasions that, although freshly killed workers are not removed to the refuse piles, corpses constitute a source of attention for many workers. It was suggested that the absence of an undertaking response was due to the lack of higher concentrations of free fatty acids in freshly killed workers [193]. This is an important observation because, if fatty acids were identified as the chemical releaser of necrophoric behavior in ants, they should start to be produced immediately after the death occurs, and gradually accumulate over the corpses until they reach a threshold that can be detected by undertakers. Although fresh corpses do not elicit undertaking behavior, they actually attract the attention of and inspection by several workers in the colony. Some authors have been looking for differential responses to corpses by introducing different types of corpses to termite nests: from the same species but with different postmortem times, from different colonies of the same species, or from other species. What is interesting is that termites show strong undertaking responses, i.e., necrophagy, burial behavior, or avoidance towards freshly killed individuals [149, 251, 278]. It would be interesting to determine what kind of cues or signals lead termites to recognize the dead immediately after death occurs. In the same way, the ant *Temnothorax lichtensteini* shows burial behavioral responses to freshly killed ants of different species [192]. Certain cues in the corpses of those species elicit such undertaking behaviors immediately after death occurs, and should be studied in detail.

In the same way, Howard & Tschinkel [120] also observed that fresh corpses of *S. invicta* are very attractive for workers that congregate around them, but are not removed in the same proportion as aged corpses. These authors also confirmed that completely extracted corpses do not elicit necrophoric behavior, but corpse extracts do, as Wilson *et al.* [12] found. However, Wilson and his coworkers found that the completely extracted corpses begin to elicit undertaking behavior after some time. In honeybees, Visscher [4] also found that extracted or paraffin-coated corpses were removed more slowly than non-extracted dead bees, and that the extract of dead honeybees elicits necrophoric behavior. In addition, aged corpses of the ant *S. invicta* are removed within the next

5 minutes of their introduction to the colony, whereas fresh corpses require more time to be removed [120]. However, after 30 minutes of being introduced to the colony half of the fresh corpses were transported to the refuse pile. Then, Howard & Tschinkel [120] prepared corpses by exposing ants either to 100 ºC or freezing temperatures and leaving both types of corpses to age for various periods of time at room temperature; after this time the corpses were presented to the colony. They found that the sign of death, in all the carcasses, appears gradually over a period of 60 minutes, but that the signals evoke responses within the first 5 minutes postmortem. Finally, after 60 minutes, all corpses were treated in the same way as 24 hour-old corpses. They concluded that internal postmortem changes in the corpses lead to an increase in the death signal, which plateaus at 60 minutes postmortem. As these experiments involved heat-killed workers, the authors also concluded that the cue may not have an enzymatic or bacterial origin. On the other hand, Ataya & Lenoir [188] found that in *L. niger* ants, the removal of corpses was completed within 50 hours after the corpses were introduced in the nest. They also found that the death cue appears gradually, but concluded that 3 hour-old corpses were the most effective in releasing necrophoric behavior. After this time, the response declines.

Visscher [4] found similar results when he prepared freeze-killing honeybee corpses of different ages and left them to incubate for different periods and then introduced the corpses to the hive. He found that the death cue in bees also appears rapidly postmortem, reaching a plateau after 12 minutes. These results suggested that the releaser may be present but masked by a competitor odor which fades rapidly after death, maybe changing a critical balance between both ‘liveness’ and ‘deadness’ smells, which provides the advantage of rapid detection and removal of corpses [4, 120]. Recently, the hypothesis proposed by Howard and Tschinkel [120] and Visscher [4], regarding a vital signal that fades after death, was studied and demonstrated in the Argentine ant *Linepithema humile* by Choe *et al.* [196]. These researchers found that live and freshly killed ants present in their cuticles large amounts of two compounds, iridomyrmecin and dolichodial, which are also present in the pygidial glands. When death occurs, both compounds fade rapidly from the cuticle, diminishing in concentration by 50% in 10 minutes and becoming undetectable after about 1 hour. Despite this, the titers of both compounds remain unchanged in pygidial glands. Choe *et al.* [196] also found that live and fresh corpses have pre-existent triglycerides (which constitute the principal lipid content in insects) that alone induce aggression and necrophoric behavior. They conlcuded that live ants are not transported to the refuse piles because they have chemical life signals, iridomyrmecin and dolichodial, that mask or inhibit pre-existing necrophoric releasers in live insects. However, how those compounds vanish whithin one hour after death is not known yet.

Thus, according to evidence, mechanisms and cues for death recognition and undertaking releasing may be based on death-related compounds such as necromones. Fatty acid necromones, associated with injury and death, would act as reliable cues of death and contagion across the phyla, which, therefore, suppose an ancient origin of the risk avoidance by these means [156]. Although necromones, as cues for the recognition of death, may be widely distributed across arthropods, it is plausible to expect that in social insects, they were opportunistically exploited by social evolution due to the advantages of detecting dead members of the society inside the nest and disposing of them to avoid the risks of epidemics associated with potential pathogens in corpses. It is plausible that during the evolution of some species, especially eusocial, other signal or cue mechanisms, such as life-fading signals, may be incorporated (in addition to the ancient necromones system) providing improved efficiency and speed in death detection. However, it is necessary to establish the postmortem occurrence among taxa of life-fading signals, to determine if signals associated with life are restricted to social insects or are widespread.

8. Perspectives: sketch for a neuroethology of undertaking behavior

The purpose of neuroethology is to attempt to understand how nervous systems generate and control the natural behavior of animals by determining causal relationships between nervous systems and animal behavior. According to Huber [341], neuroethologists use natural behavior to understand sensory, central nervous system, and effector events that underlie behavioral strategies shaped by natural selection to improve survival and reproductive fitness of animals during evolution. This is a fundamental point because the mechanisms neuroethologists study are adaptations tailored to particular ecological needs, rather than general-purpose processing devices, and represent one of the various ways to solve a particular problem [342]. Thus, the study of behavior involves research on behavioral ecology and its underlying neural mechanisms [343].

Social insects are useful models, in comparison with other higher social animals, since their social behavior may provide rich material for analyses that integrate neuroscience and evolutionary biology, as well as genetic analyses, constituting the molecular biology of social behavior. A variety of sophisticated behavioral patterns can be studied under natural conditions and can also be manipulated in the field and laboratory, and because their behavioral patterns tend to be stereotyped, they can be more easily assayed [343]. Social behavior has recently become part of the neuroscience agenda [343], and of the molecular genetics of social behavior known as sociogenomics [344], which has made outstanding progress in the understanding of the molecular basis of social life [294]. Thus, insect social behavior constitutes an excellent model for the understanding of social behavior as a wide natural phenomenon. We consider that undertaking behavior is an interesting example of social behavior, which is complex enough to constitute an excellent model for both neuroethological and genetic analysis approach. It can be perfectly studied in the field and in the laboratory, it can be assayed easily, and, since it is both sufficiently complex and simple, it can be addressed by many neurobiological and genetic analysis methods. It is the kind of behavior suitable for studying the neurobiological basis of social behavior that would be selected by neuroethologists because it may be, as Hölldobler and Wilson said [345]: "…analyzed as though it were a bit of anatomy…" and dissected from behavior to molecules and backwards in order to attempt a comprehensive understanding of it as deeply as possible.

8.1. Processing of death-related stimuli

Consider, for instance, the mechanisms involved in detecting and responding to corpses. When Wilson *et al.* [12] discovered that fatty acids, mainly oleic acid, accumulate in ant corpses as decomposition products, and when live workers daubed with oleic acid were carried by nestmates to the refuse pile, it seemed that undertaking behavior was a rigid all-or-nothing behavior. On the contrary, although the behavior of social insects is mainly stereotyped, it also involves individual plasticity regulated by social information. Thus, multimodal processing, learning, and memory must also be considered [346, 347]. Undertaking responses seem to involve more than the appearance or disappearance of one cue or signal, since data have shown that behavioral responses are very complex. In this manner, it is feasible to expect that these responses would require more than just the information regarding deadness or liveness. It seems that two fundamental types of information are required for undertaking behavior: information from the context that appropriately predisposes the workers to recognize the corpses, and the information from the corpse. Undertaking behavior, in this manner, would be a context-specific dependent behavior that requires a specific context and a specific group of stimuli to be released. In fact, death recognition, as well as other semiochemical information, may also be affected by complexity, synergy, and context [322, 348]. Information that workers must process to make a decision on the behavioral response to be performed can be categorized as follows (see Figure 3a):

1. Social and ecological context information. This information may act as a 'primer' and may be required to predispose individuals to respond when a corpse is encountered, and to perform undertaking behavior according to the situation. It comprises information regarding the location of the corpse and the workers, as well as the social activities of the colony. Context information can be subdivided into:

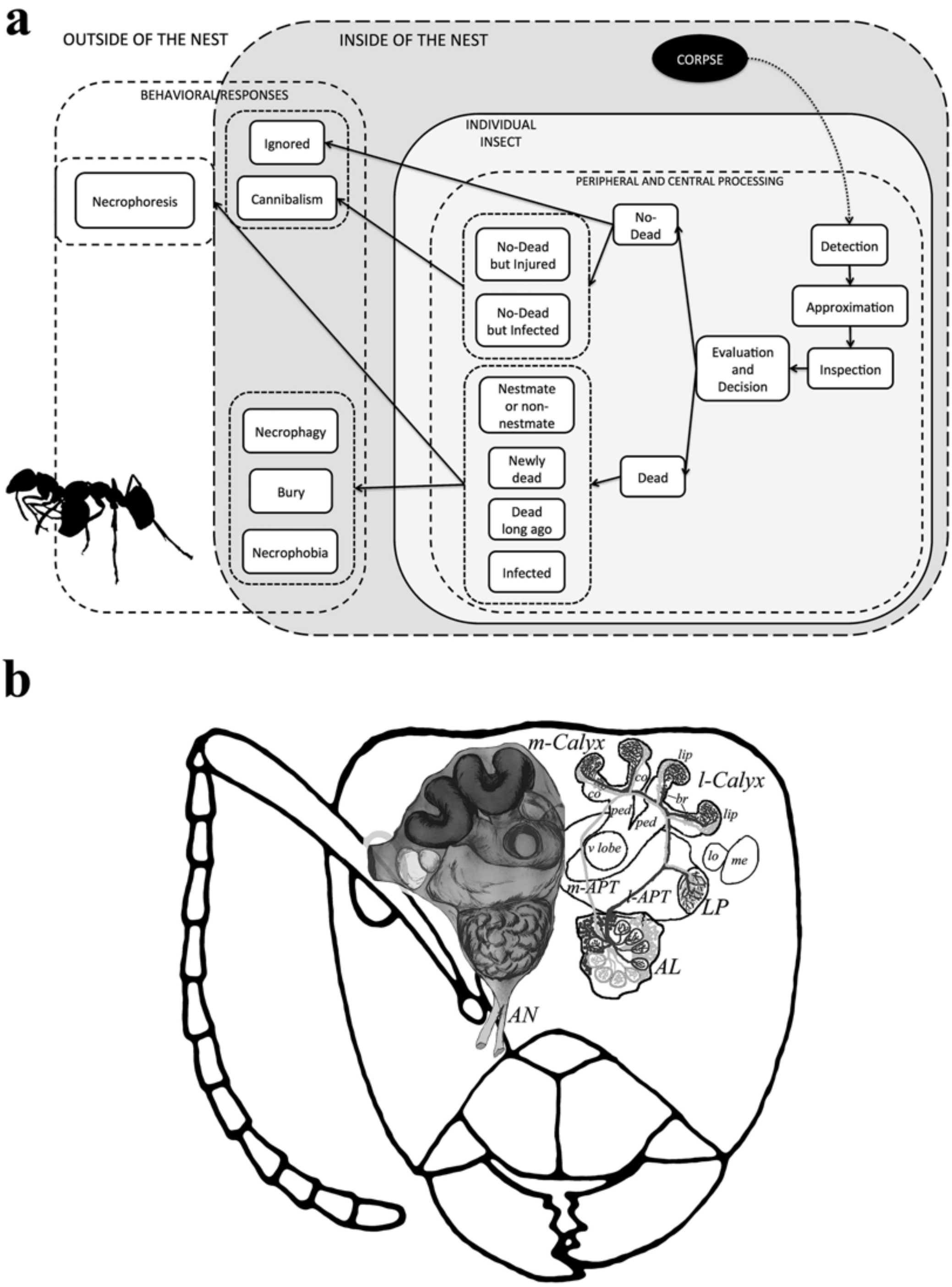

Figure 3

a) Within-nest information. First of all, as social strategies for corpse disposal have evolved to maintain the nests clean from potential pathogens and to prevent epidemiological risks, it is necessary to obtain the information about "*being inside the nest*", *i.e.*, about the interior of the nest. Till now, there has been no research on this issue and no substance has been identified. It is possible that the walls of the nest chambers and tunnels are covered by hydrocarbons and other substances secreted by the social insects [322, 349]. This information is highly important since, for example, it has been shown that context affects nestmate recognition [350, 351].

b) Social activity status of the colony. Workers may require important contextual information on the main social activities of the colony to perform undertaking in an appropriate manner [187, 208].

2. Corpse information. With the contextual information as a primer, corpses can elicit one of the different ways of corpse disposal, which depend on the taxa and the information provided by the corpse. This information seems to be more extensive and complex than what was considered before, when it was assumed that only one releasing stimulus was involved. In fact, many social insects are able to identify not only deadness or liveness, but also other fundamental information from the corpse. Thus, the information from corpses considered for proper decision-making in terms of the behavioral response would be:
    a) Death cues or lack-of-life signals (fatty acid necromones accumulation or diminished iridomyrmecin/dolichodial).
    b) Origin of the corpse, which involves discrimination between nestmate and non-nestmate [182, 183] and/or conspecific and non-conspecific discrimination [149, 192] of corpses.
    c) Age of the corpse or time elapsed since death [192, 251].
    d) Infection status [260, 263, 251].
    e) Levels of mortality inside the nest [259].

This implies a more complex information-processing than has been supposed until now. It has been said that recognition of dead members of the colony shares common features with communication [2, 14]; moreover it also has common features with nestmate recognition. Social insects have well-developed nestmate recognition systems based on chemical labels on the cuticular surface of individuals [1, 2, 352]. These chemosensorial labels allow them to recognize and reject non-members of the colony and help to maintain the cohesion and stability of the colonial organization, avoiding the infiltration of intruders [2]. In the encounter between two ants, each one sweeps with its antennae, in a stereotyped manner, the body of the other, smelling the hydrocarbon molecules on the cuticle. If both ants belong to the same colony, they may continue their way or they may engage

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Legend to Figure 3. Processing of corpse and contextual information by workers during undertaking behavior. a) Scheme showing the sequence of the peripheral and central processing that the information detected from corpses must follow, as well as the behavioral responses evoked according to this information. Undertaking behavior is context dependent. Thus, to be released, corpses must be found inside the nest, where they are detected by workers, who analyse information from the corpse by peripheral and central nervous mechanisms. After detection, approximation, and inspection, workers must evaluate the traits of the body and determine if it is dead; and then, they must make a decision. If the body is dead, it may, depending on other information that has been extracted by the worker, be eaten, buried, avoided or removed out of the nest. On the contrary, if the insect is not dead, it may be ignored or devoured depending on its health condition. b) Information on the corpse must be 'extracted' by sensory organs on antennae of workers of social insects and, after that, it must be processed and coded, first in the ALs, and then in higher brain centers, mainly the MBs. In the scheme it can be observed, the main regions of the brain of social Hymenoptera, ants in this case. AL is afferently organized in groups of glomeruli according to the innervation tracts from AN, whereas is organized efferently in two main regions that connect, by segregated pathways, with different regions in the calyces of the MBs. As can be seen in the scheme, the anterior region of the AL is connected to the inner layers of the lip and basal ring (*br*) of the calyces of MBs (in dark gray) through the lateral antennoprotocerebral tract (*l-APT*); while the posterior region of the AL is connected to the outer layer of the lip and the basal ring of the calyces of MBs (in light gray) through the medial antennocerebral tract (*m-APT*). This pattern of connections forms an odotopic map of the AL organization in the MBs. Abbreviations: *AL*: antennal lobe; *AN*: antennal nerve; *br*: basal ring; *m-Calyx*: calyx medial; *l-Calyx*: calyx lateral; *co*: collar; *lo*: lobula; *LP*: lateral protocerebrum; *me*: medulla; *ped*: peduncules; *v lobe*: ventral lobe. See text.

in common tasks like exchanging food, etc. But if one of the ants comes from another nest of the same species, the intruder can be accepted with limitations or killed [14]. The entire recognition process occurs in a fraction of a second when ants meet each other, and involves mechanisms and neural pathways that, despite belonging to the well-described olfactory circuit, are still unknown. Death recognition also involves the detection and the unequivocal recognition of the dead status, by means of a label (either the disappearance of life signals, the accumulation of decomposition products, or, in some extent, both of them) on the corpse but in a specific context. Social insects follow the same behavioral pathway of nestmate recognition: they are attracted to the corpse, they sweep their antennae on the corpse surface, they may or not lick and/or bite, and then, after smelling the label, they must make a decision on what to do with the corpse; if it has recently died, it may be ignored or devoured, if not, it may be buried, removed, or avoided. However, the process of death recognition seems to be more complex and prolonged than the nestmate and non-nestmate discrimination, although it also must involve the same general olfactory neural pathways and mechanisms.

In neuroethology, it is very important to know the anatomical description of the species-specific neural structures under investigation, by neuroethological approaches, to reveal the significance of such structures and their physiological properties for the generation and control of behavior [353]. Currently, the pathways for olfactory processing are well-known, although odor-coding is not completely understood [354]. However, we know with a certain degree of confidence the regions of the olfactory pathway that a scent must follow when an insect smells. Death-related stimuli must first interact with olfactory receptors on the antennae. Chemicals must interact with receptor proteins on the dendritic membranes of olfactory receptor neurons (ORN) located in the sensilla. Sensilla are the minute sensorial organs on the antennae that detect chemical or mechanical information, whose distribution and number on antennae may vary with species, sex, and caste in social insects [355, 356]. As accumulated fatty acids, and those chemicals remaining on the cuticle after the life-odors vanish, are ubiquitous chemicals in insects [357] and common in insect cuticle [338, 337], it is possible that death recognition does not require a specialized kind of sensillum as that described for nestmate recognition [358]. This sensillum is somewhat unusual, because it contains nearly 200 olfactory receptor neurons, compared to the 1-6 contained by the common sensilla [359]. However, on cockroaches, a fatty acid-sensitive sensillum constituted by four cells has been described [360]. Also, it has been suggested that the pyronkinin β-neuropeptide alters necrophoric behavior by disrupting corpse recognition [361], which, if confirmed, would imply the presence of receptors sensitive to death stimuli that participate in corpse recognition.

In any case, when social insects inspect the stimuli from the corpses (death cue, origin, time elapsed since death, infectious status, etc.) within a context (inside or outside the nest, social activity) the information must be detected by sensilla. If one species is able to discriminate between nestmate and non-nestmate corpses, then the specialized sensillum described by Ozaki *et al.* [358] may also be involved. Moreover, sensilla must detect changes in the pattern of the chemicals on the cuticle and compare them with the label of living ants. Either way, one sensillum, or a few sensilla, on the antenna must detect the pattern of chemicals on the corpse and may be also some tactile features of it. Then, the interaction between cuticle odorants and receptors would alter the electrical properties of ORNs, transducing the chemical stimulus into action potential trains that would run on their axons through the antennal nerve (AN) inside antenna to the antennal lobe (AL) of the deutocerebrum, the region of the nervous system in which olfactory information is first processed. Once in the AL, axons from ORNs sensitive to death odors must segregate from the AN and, as separated tract, must direct to one or few glomeruli, spheroidal structures of neuropil where axons from ORNs end to form synapses [362]. The size and number of glomeruli depend on the species and development, and are grouped into clusters, each of which receives one of the tracts from the AN [190, 363]. In glomeruli, ORN axons form synapses with different kinds of neurons; but one of them, the projection neurons (PN), connect the AL with higher brain centers, mainly the mushroom bodies (MBs) in the protocerebrum. Once in the AL, the information induces patterns of AL activation, as it happens with nestmate information [364], during the coding of corpse information. In fact, these pathways may also be activated when the workers discriminate nesmates from non-nestmates. Glomeruli clusters are organized into two efferent regions according to the type of PN that connects them with the MBs [190, 363]. MBs are higher-brain centers where multisensory information converges [363], and are composed of input regions called calyces and output regions called lobes. Calyces are divided into compartments or layers: the collar (receives visual input), basal ring (receives olfactory and visual input), and the lip (receives olfactory input). PN axons are segregated when they leave the AL, and follow different paths through the brain until they terminate in the different compartments of the MB calyx (different layers in the lip and basal ring). This segregation represents different properties of olfactory and visual stimuli that form a map of the sensory neuropils in the brain [190, 363, 365, 366]. In MBs, sensory information may be combined and integrated to form a kind of complex image from the environment and from the rest of the animal [363].

Undertaking behavior may be analyzed according to the stages of the information processing within the nervous system and the phases of the behavioral responses. In this manner, undertaking behavior may be divided into (see Figure 3b):

1. Sensory-perceptual phase. In this phase, the worker detects the corpse and is attracted to inspect it. In this phase, antennal chemoreception and mechanoreception are involved in the inspection of the corpse and can be subdivided into three stages.
    a) Detection of the corpse
    b) Approximation to the corpse. In this stage, corpses seem to be attractive for many workers, rather than repellents.
    c) Inspection of the corpse. Corpses are meticulously inspected by antennations, licking, climbing on them, or crawling under them.
2. Coding, integration, and decision-making in central structures. Corpse information (chemical and tactile) and context information (mainly chemical, but possibly other forms, such as thermal and hygroscopic) may be processed, integrated, and evaluated in the central structures of the nervous system. These structures constitute the olfactory pathway:
    a) Antennal lobes (AL) and antennal mechanosensory and motor center (AMMC) in the deutocerebrum. Deutocerebrum is the central nervous structure where antennal information (olfactory and tactile) arrives and is first processed and coded.
    b) Mushroom bodies and lateral protocerebrum (LP). Information coded in deutocerebrum is then sent to the protocerebrum, mainly to the MBs, where information is processed and integrated with multimodal information.
3. Behavioral response (involves central and motor structures). According to the information processed, workers may perform one of the following undertaking behaviors (as described previously):
    a) Ignoring
    b) Necrophoric behavior
    c) Burial behavior
    d) Necrophagy
    e) Avoidance

Some structures of the AL may be specialized in the processing of information of death-related stimuli. Then, the information may be directed, through one or all tracts connecting the ALs with the protocerebrum [190, 363, 367, 354], the MBs, and the LP. In this manner, information may be specialized, and the structures involved in the detection and processing of death information might be experimentally identifiable constituting a neural pathway for processing death odors, as occurs for other social information processing, such as the alarm pheromone in ants [368].

8.2. Neurobiological specialization of undertakers

As undertakers of some species are highly specialized workers, determined genetically in honeybees and perhaps in ants, it is plausible to expect functional and structural differences in the brains and physiology of these individuals compared to other castes, like those described among castes of ants in relation to the morphology of the brain and behavior [369]. If division of labor can produce extreme worker specialization, the underlying neurobiological mechanisms and structures may also be specialized and may show differences among different castes. The honeybee undertaking specialists are determined genetically [7], and compared with other worker bees of the same age, they are behaviorally and hormonally different [159]. Undertakers tend to perform necrophoresis and have higher levels of JH. As gene expression in honeybees is regulated by JH, which is known to have effects on metabolism in neural plasticity [370], undertakers must have brain-identifiable differences. Several studies have demonstrated that temporal polyethism-based division of labor in honeybees is regulated by JH and vitellogenin (Vg) [304, 371]. As workers age, levels of JH increase and Vg decrease [294, 372-375]. Young workers have low levels of JH and high levels of Vg, which are associated with within-nest behavior, but after 3 weeks, the activity of the corpora allata increases along with the levels of JH, and the levels of Vg decrease, and workers begin the forager life outside the nest. This increase in JH has other physiological effects such as the reduction of the hypopharyngeal glands (which produce food for the larvae), and also induces the production of alarm pheromones. As a consequence of their high levels of JH, undertakers have smaller hypopharyngeal glands compared to other middle-age bees, but larger hypopharyngeal glands than foragers [304].

Those changes in levels of JH also have remarkable effects in the structure and function of the nervous system since the brain has receptors for this hormone [295]. Workers that become foragers develop activity-dependent increments in glomerular volume in the AL; prolonged exposure to floral odors causes increments in the volumen of glomeruli that process such odors [376]. Higher levels of JH in undertakers may also induce changes in different structures of the brain that cause differences in behavior. It is quite possible that activity-dependent changes, such as exposure to corpse odors, favored by JH may also lead undertakers to develop changes in some specific glomeruli of the AL. In addition, higher regions of the brain, such as the MBs, also increase in volume as bees get old and become foragers [377]. These changes modify the behavior and sensory physiology, causing the bees to no longer perform within-nest tasks and begin to forage. These changes are reversible, and when it is necessary, due to lack of workers that performs tasks inside the nest, the levels of JH in foragers decreases, which leads to the return of the workers to the nest and to the activities of nest care.

It has been demonstrated that temporal polyethism is associated with circadian rhythms: young workers that care for the brood inside the nest at any time are arrhythmic, while older workers that forage outside the nest, show strong circadian rhythms used for sun-compass navigation. However, these changes in rhythmicity are not under the control of JH [378]. This is important because Visscher [4] showed that honeybee undertakers perform corpse removal continuously without any circadian pattern, as also *A. colombica* ants that remove waste [70, 122]. So, it is possible that undertakers have flat circadian rhythms.

Sensitivity to stimuli is also related to caste. Newborn workers with low response thresholds to sucrose, become water foragers, while those with high thresholds become pollen and nectar foragers. These thresholds are related to genotype and age [379-381]. However, a correlation between caste and antennal olfactory sensitivity to the alarm pheromone could not be demonstrated [382]. Masterman *et al.* [383] demonstrated that bees bred for hygienic behavior have lower thresholds to odours of diseased brood than non-hygienic bees. Although hygienic behavior has been considered apart from undertaking behavior, in both behaviors the dead members of the colony are detected. However, hygienic bees detect odorants of the brood infected by pathogens, while the undertakers detect odorants emanated from corpses. The odorants involved in hygienic behavior have been identified as phenethyl acetate, 2-phenylethanol, and benzyl alcohol [384]. Thus, undertakers may also exhibit sensorial specializations to detect stimuli associated with adult corpses. However, when antennal sensitivity of three castes of *A. mexicana*, including undertakers, was compared to task-related odors (forgers and floral odors, soldiers and alarm pheromones, and undertakers and oleic acid) it could not be found that undertakers have lower thresholds to oleic acid present in corpses [189]. In spite of this, it is quite possible that increased sensitivity in undertakers may be demonstrated by testing other odorants related with corpses. Another possibility is that sensitivity may reside in the processing of olfactory information carried by the AL.

Besides these changes, discrete regions of the calyx of the MBs also increase their volume in the transition from nurse to forager, which is also correlated with an increase in levels of JH [306, 377, 385-388]. These plastic changes are the result of developmental programs under hormonal control, but they also depend on experience and sensorial afferences, since the exposure to illumination results in the increased volume of some regions of the calyx of the MBs [386]. This is important, because when workers change from nurses in the darkness of the hive to foragers outside the nest, light exposure changes notably. Similar, increases in brain volume have been described in different species of ants [*Camponotus floridanus*, 353; *Cataglyphis bicolor*, 389; *Pheidole dentata*, 390]. It is possible that similar changes may be present in undertakers, especially if they have increased levels of JH and they mature faster than their sisters of the same age. Differences in architectural structure could be present in some specific regions in the MB calyx lip region, in zones of the collar and in a part of the basal ring in the calyx of the MBs where visual input from optic lobes is received [363]. This is quite possible if bee undertakers begin to remove corpses and are exposed to chemical stimuli from dead members of the hive, and also if they begin to fly out of the nest to drop corpses, which exposes them to different conditions of illumination.

Some neurotransmitters are also related with division of labor. In honeybees, it has been demonstrated that older workers have higher levels of three biogenic amines (serotonin, dopamine, and octopamine) in the MBs and in ALs than younger workers that perform tasks inside nests [391, 392]. In the ants *Pheidole dentata*, it was also found that serotonin and dopamine levels increase with age [390]. This suggests that biogenic amines may be important in the control of division of labor based on temporal polyethism. Biogenic amines appear to regulate the behavioral development influencing the expression of different types of behavior by modulating olfactory sensitivity and the response to different stimuli [391, 393]. Once more, it is quite possible that undertakers show increased levels of biogenic amines in ALs and MBs because of the high dependence of olfaction in undertaking behavior. This hypothesis is particularly plausible since octopamine facilitates the detection and response of hygienic honeybees to diseased brood [394].

Taken together, it is plausible to expect that undertakers exhibit the following characteristics that remain to be explored:

1. Genotypic predisposition to undertaking performance.
2. Peripheral sensory system specialization (antennal specializations). A higher proportion of some kind of sensilla may be sensitive to fatty acids, which may provide a lower threshold to corpse odors.
3. Sensory-perceptual specializations. Lower behavioral and physiological thresholds to corpse-related stimuli.
4. Antennal lobe specializations. Some differences in the architectural structure of ALs, perhaps one particular glomerulus that is larger than others, to which the additional afferences from the death-responding sensilla would arrive.
5. Circadian specializations. Undertakers may be arrhythmic or show a flat circadian rhythm, since undertaking behavior is continuous throughout the day.
6. Brain specializations. Undertakers may exhibit increments in the size of specific regions of the MBs, such as in certain layers of the lip region of the calyx. These regions must be related with the increased size of the hypothetic larger glomerulus or glomeruli in the AL, whose PN axons must arrive to the lip region in the calyx.
7. Neurotransmitter specializations. Undertakers could have increased levels of biogenic amines mainly in the ALs and in the MBs.

8. Neural pathways for the processing of death stimuli. Undertakers may have specific afferent neuronal pathways from the antennae to MBs that process the information related to corpse stimuli.

CONCLUSION

Social insects have evolved sophisticated behavioral systems of corpse management to isolate corpses, which represent potential sources of pathogens, to avoid the risk of epidemics within the nest. Undertaking behavior, as one of the behavioral mechanisms of social immunity, has been essential in microbiological control that social insects carry out since it prevents the accumulation of decomposing corpses within the nest. Through this, insect societies prevent the proliferation of pathogens and the risk of infection among the members of the society, mainly the queen and the brood, on whom the fitness of the society depends. As the handling of corpses and garbage from the societies represents a dangerous task, both the workers and the cues involved in undertaking behavior must have specialized and stereotyped during evolution due to the strong selective pressures against the negligent hygienic maintenance of the nest. Non-social animals avoid dead conspecifics for self-protection; this is to prevent the pathological risk that decomposing corpses represent. However, undertaking in social insects, despite its complexity and sophistication, represents an altruistic protection for relatives that has significance only for the survival and fitness of the colony.

The variety of sophisticated undertaking systems among eusocial insects is the result of the remarkable diversity of development, ecology, and social organization. The differences between both social taxa of insects also have produced two basic systems of corpse disposal in social insects. Social Hymenoptera, which are holometabolous insects, may exhibit sophisticated systems of division of labor with specialized castes, some of them genetically determined, tend to remove all corpses from the nest as soon as possible and drop them as far as possible. In contrast, Isoptera, as hemimetabolous insects with a high tendency towards cannibalism to recycle nutrients, with a complex division of labor system, rely on a combination of intraspecific necrophagy, burial behavior and avoidance, which depends on the context and on the characteristics of the corpse, but is mostly based on the recycling of resources. Nevertheless, there are subtleties and variations in undertaking patterns among species, and in each case, social insects evaluate the situation to respond properly.

Although corpse disposal in social insects basically depends on necrophoresis, intraspecific necrophagy, burial behavior, and avoidance, sometimes two or more mechanisms are present at the same time in the same species, and the proper choice of one of them depends on the complex information that must be processed in those minute social brains. The information involved in the process of evaluation of a corpse is complex and must take into account the context and the information obtained while the corpse is inspected by chemosensory and tactile organs. The cues released by corpses provide information to make decisions that have evolved to safeguard the fitness of the colony. In spite of the evidence that supports both perspectives regarding the mechanisms of corpse detection and recognition, a lack of consensus about cues and sensory mechanisms involved in undertaking behavior still remains; therefore, although once it was believed to be fully solved, the full panorama of undertaking behavior and its releasing mechanisms is not yet understood completely. It will be important to carry out careful comparative experiments across species with regard to postmortem changes in the corpses to determine the identity and function of cues and signals involved in the releasing of undertaking behavior. Although undertaking behavior is known to some extent in the honeybee [3-5, 7, 159, 160], the general mechanisms of division of labor, in relation to undertaking behavior, as well as their genetic and neurobiological control are yet unknown, and it may be important to perform studies on undertaking behavior in different species. Due to its ease of manipulation in the laboratory and in the field, we consider undertaking behavior to be an interesting example of social behavior sufficiently complex for an integrated analysis of behavior that includes ecological, behavioral, physiological, and neuroethological approaches. It is the kind of behavior that may be a useful model for studying the neurobiological basis of behavior, and that may contribute to our understanding of social behavior.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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