A review on self-destructive defense behaviors in social insects.

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Abstract:

Colony defense is a necessary but dangerous task for social insects, and nest defensive behaviors often lead to a premature death of the actor. As an extreme form of colony defense, self-sacrificial behaviors have evolved by kin selection in various social insects. Most self-sacrificial defensive mechanisms occur in response to an acute threat to the colony, but some behaviors are preemptive actions that avert harm to the colony. Self-sacrifice has also been observed as a form of preemptive defense against parasites and pathogens where individuals will abandon their normal colony function and die in self-exile to reduce the risk of infecting nestmates. Here, we provide an overview of the self-destructive defense mechanisms that eusocial insects have evolved and discuss avenues for future research into this form of altruism.

Keywords: altruism | autothysis | defensive behavior | host suicide | sting autonomy | social insects | biology

Article:

Introduction

Altruism, an action that will decrease the actor’s direct fitness to benefit a recipient, is the foundation of cooperation and cohesion in eusocial groups (Ratnieks and Wenseleers, 2008; O’Gorman et al., 2005; Oster and Wilson, 1978; Hamilton, 1964). Individuals in eusocial groups will often sacrifice their reproductive ability, food resources, and even their life, for the benefit of their nestmates. Self-destructive defensive behavior has evolved independently in a number of social insect species in response to different natural enemies (Table 1). Self-sacrifice has been recorded mainly in the context of nest defense, attesting to the importance of nest defensibility in social evolution (Thorne, 1997). As with other forms of altruism, these defensive behaviors persist in social insects because they function to increase the fitness of the colony’s reproductive individuals, which will pass on the genes for self-sacrificial behavior to subsequent generations (Deligne and De Coninck, 2006).

Table 1

A list of social insects with their known self-destructive defensive behaviors

Species name or group	**Description of behavior**	**Citation**
Apis	Sting autotomy	(Hermann, *1971*; Hermann, *1984b*)
Pogonomyrmex (harvester ants)	Sting autotomy	(Hermann, *1971*; Hermann, *1984b*)
Species in certain tropical wasps: Epiponini, Polistini, Ropalidiini, *Polybia rejecta*, *Brachygastra lecheguana*, and*Protopolybia pumila*	Sting autotomy	(Hermann, *1971*; Hermann, *1984b*; Sledge et al., *1999*)
Camponotus (Colobopsis) cylindricus complex (COCY)	Autothysis	(Maschwitz and Maschwitz, *1974*; Davidson et al., *2009*)
Serritermitidae	Autothysis	(Sobotnik et al.,*2010a*; Costa-Leonardo and Kitayama, *1991*)
Apilitermes longiceps	Autothysis	(Deligne and De Coninck, *2006*)
Globitermes sulphureus	Autothysis	(Bordereau et al.,*1997*)
Ruptitermes	Autothysis	(Costa-Leonardo,*2004*)
Dentispicotermes	Autothysis	(Sobotnik et al.,*2010a*; Bordereau et al., *1997*)
Quadrartus yoshinomiyai	Adhesive self-sacrifice	(Uematsu et al., *2007*,*2010*)
Nipponaphis monzeni	Gall repair self-sacrifice	(Kutsukake et al.,*2009*; Kurosu et al.,*2003*)

Species name or group	**Description of behavior**	**Citation**
Forelius pusillus	Nest burying self-sacrifice	(Tofilski et al., *2008*)
Temnothorax unifasciatus	Altruistic self-removal	(Heinze and Walter,*2010*)
Apis mellifera	Altruistic self-removal	(Rueppell et al., *2010*)
Trigona	"Death grip" biting behavior	(Buchwald and Breed,*2005*)

In general, insect defenses are diverse, ranging from physical adaptations, such as coloration, protective cuticle structures, and toxins to behaviors, such as clicking, stinging, biting, spraying venom, grooming, wing shimmering, posturing, and structure building (Hermann, 1984a). In social insects, general defensive functions are provided by the nest architecture and morphological adaptations, while behavioral defenses are often specific to particular types of enemies. Social insects face four principal classes of natural enemies: (1) arthropod predators, (2) vertebrate predators, (3) insect parasitoids, and (4) parasites and pathogens (Hermann, 1984a). Defensive behavior can be performed by individuals or a group, which correlates with the body size difference and numerical ratio between attackers and defenders (Batchelor and Briffa, 2011).

It is common for individuals to die in defense of their colony (Wilson, 1975), but here we focus on morphological and behavioral specializations that will inevitably lead to the self-sacrifice of the defender. In some sense, the distinction between normal self-defense and suicidal defense in social insects is a human abstraction, as these workers have already sacrificed 100% of their direct fitness by forgoing reproduction. However, their behaviors and tasks are optimized through indirect fitness, and unnecessary loss of workers would harm the colony. There are numerous other actions that we do not discuss here, which are costly and also shorten the lifespan of the worker that performs them, e.g., foraging (Rueppell et al., 2007), and corpse and waste removal (Hart and Ratnieks, 2002). Suicidal defense behaviors can be divided into three main classes: instantaneous defense, preemptive defense, and altruistic self-removal (host suicide). Instantaneous defense leads to the death of the defender by actively engaging an enemy. These facultative responses include sting autotomy and autothysis. Sting autotomy is the self amputation of the stinger and poison sac (Hermann, 1971). Autothysis (also referred to as abdominal dehiscence) is the secreting of a harmful substance onto a predator through rupturing of the body. The second type of suicidal defense covered here, preemptive suicidal defensive behavior, can take place even before a predator is encountered through concealment or repair of the nest (Bourke, 2008; Kurosu et al., 2003). In these cases, mortality results from a specialized, non-aggressive task that has evolved to ensure colony survival. A third class of suicidal defense, termed host suicide or altruistic self-removal, occurs when sick individuals leave the nest to die in isolation, which lowers the risk of infecting nestmates (Heinze and Walter, 2010; Rueppell et al., 2010). As in the two previous cases, colony fitness is presumably increased by individual self-sacrifice. In the following, we will provide an overview of the known examples of defensive behaviors in eusocial insects that lead to the self-sacrifice of the defenders, discuss the mechanisms and adaptive advantage of these behaviors, and suggest new avenues for future research.

Instantaneous defense: sting autotomy

In many social Hymenoptera, stings have evolved from the female ovipositor as a defensive weapon. In addition to the physical damage, they usually deliver harmful chemicals that are synthesized in the associated poison glands. Sting autotomy occurs when the stinger and associated glands remain in a target after being severed from the distal end of the defender's abdomen (Hermann, 1984b). This occurs only in eusocial Hymenoptera and has evolved independently in three aculeate groups: bees of the genus Apis, ants of the genus Pogonomyrmex, and several species in the tropical wasp tribes Epiponini, Polistini, and Ropalidiini (Hermann, 1971; Hermann, 1984b; Sledge et al., 1999). These groups are all characterized by a well-developed barbed sting lancet, which ensures autotomy and abdominal muscles that can easily tear from internal structures. The mechanical details of autotomous stinging are similar across the stinging Hymenopterans. Upon penetration of the sting lancet into the victim, the barbs lock into the tissue, then muscles at the end of the abdomen contract, releasing venom into the wound. A weakening in the connection between the abdominal segments facilitates the separation of the stinging apparatus from the rest of the abdomen upon pulling away of the stinging insect (Hermann, 1971). Adaptations in muscle structure and support of the stinging apparatus also contribute to autotomy. Species that exhibit sting autotomy have muscles that will easily tear from the internal structures, while species without autotomy have well-developed abdominal muscles that prevent this separation (Manzoli-Palma et al., 1997). Sting autotomy has also been observed in clinical conditions in the yellow jackets Vespula maculifrons and Vespula flavopilosa (Greene et al., 1989; Mulfinger et al., 1992). However, this finding was not replicated in field studies. The occurrence of sting autotomy in species without specialized muscles and a barbed sting can be explained by an unusual sting delivery method or interrupting the retraction of the lancet by the insect (Mulfinger et al., 1992).

Sting autotomy has likely evolved as a defense against vertebrate predators. This defense is less effective against other arthropods because they often can be killed by a small amount of venom and can be numerically equal to the defenders (Hermann, 1971). Sting autotomy is much more efficient against few, larger attackers because the severed sting apparatus aids in group defense by releasing alarm pheromone (in honeybees, primarily isopentyl acetate), which will function to attract other workers to the area for increased defense (Millor et al., 1999). Against a vertebrate predator, venom from the separated poison sac can still be delivered for up to 1 min after the insect is removed, and may be equivalent to many stings (Cunard and Breed, 1998; Hermann, 1971). Autotomy with a barbed stinger is ideal against a mammal because the elasticity of skin makes the stinger difficult to remove. Species that employ autotomy may also have more potent venoms as measured by their LD50 (Schmidt et al., 1980), possibly as an adaptation against larger enemies. The effectiveness of stings depends on the volume of venom injected into the victim. However, allergic reactions to small quantities of venom can also result in fatalities (Williams and Williams, 1965; Schumacher and Egen, 1995). Sting autotomy is not immediately fatal to the defender. In honeybees, 50% of workers that sting die within 18 h, but some can live over 114 h after stinging (Hydak, 1951). Bees that have lost their sting organ partially retain their residual value as defenders by continuing to participate in colony defense through biting, harassing, and pursuing the colony attacker (Cunard and Breed, 1998). A large colony workforce may also explain the persistence of sting autotomy, as the cost of a few workers is minimal when compared with the benefit of driving away a predator (Hermann, 1971).

Instantaneous defense: autothysis

Suicidal defense can also take place through autothysis, which is an endogenous rupturing that releases a caustic secretion externally, killing the attacker(s) and the defender. This type of defense has been observed in workers of the carpenter ant Camponotus saundersi and later in the Camponotus (Colobopsis) cylindricus complex (COCY) (Maschwitz and Maschwitz, 1974; Davidson et al., 2009, 2011), but is particularly prominent in the soldier and worker castes of several termite species. To date, it has been reported in Glossotermes oculatus, Apilitermes longiceps, Globitermes sulphureus, the genera Dentispicotermes, and Ruptitermes (Sands, 1982; Bordereau et al., 1997; Sobotnik et al., 2010a; Deligne and De Coninck, 2006; Costa-Leonardo, 2004; Costa-Leonardo and Kitayama, 1991). While the morphological release structures and the chemical nature of these substances are variable, the application of this defensive behavior is very similar across disparate groups (Sobotnik et al., 2010a). In all cases, the released substance is sticky and binds to predators, congealing when exposed to air and causing distress, immobility, or death to the target. Autothysis has probably evolved primarily against arthropod predators rather than larger vertebrate predators such as lizards and birds. The sticky substance released during autothysis is very effective at adhering to the legs and mandibles of other arthropods, but is relatively ineffective against vertebrates (Maschwitz and Maschwitz, 1974; Jones et al., 2004). The explosive discharge also allows a single defender to disable multiple small attackers, resulting in a numerical advantage in combat. Additionally, the sequestering of substances for autothysis makes all individuals in a colony equipped with these chemicals inedible to predators and may deter certain predators altogether (Sands, 1982).

Among 17 investigated species in the carpenter ants COCY complex, 16 species have unique hypertrophied mandibular glands, which extend from the head to the gaster (Cook, 2008). In the nine COCY species with self-sacrifice, minor workers can violently contract their abdomen until their body wall splits open, splattering mandibular gland compounds in the immediate area, which can then adhere to the body, mandibles, and limbs of arthropod predators (Davidson et al., 2009, 2011; Jones et al., 2004; Cook, 2008). The workers may also bite and wrap themselves around an opponent with their gaster placed onto the face before the worker expels the adhesive substance from its mouth and gaster (Davidson et al., 2011). The released substance is corrosive and an irritant in addition to being sticky, and it is presumably composed of aliphatics such as octadecanol and sugars (Jones et al., 2004). Workers will use this type of defense in territorial combat and one-on-one confrontations far away from the nest (Davidson et al., 2007). This strategy does not necessarily result in a numerical advantage, but may be adaptive because minor workers require less resources to develop than larger workers from competitor species (Cook, 2008). Through attrition in one-on-one battles, the smaller workers are able to deplete colonies of larger ant species through this type of self-sacrifice, ultimately driving away competition and gaining more territory for the colony (Cook, 2008). Important pre-adaptations for this type of defense include the secondary-compound-rich diet and the well-developed mandibular gland compounds used for antiseptic defense against microbes in the COCY species (Davidson et al., 2009; Cook, 2008).

In the termite Globitermes sulphureus, the autothytic secretion is released through a rupture in the frontal gland and accumulates as a droplet at the inner face of the head capsule, but “very excited” workers contract violently and release the substance through the ventral side of thorax (Bordereau et al., 1997; Sobotnik et al., 2010a). This process is comparable to the one described previously in carpenter ants, but in most species of termites the substance is secreted from the frontal gland rather than the mandibular gland (Sobotnik et al., 2010a). Ants that try to attack the termite are caught in the “sticky” substance, which congeals when exposed to air. Soldier termites are still able to defend against predatory ants for a few minutes after internal rupture, assailing the ants with their mandibles (Bordereau et al., 1997), much like honeybee workers that continue to defend the colony after sting autotomy. This behavior appears to be an effective means of defending a termite colony by blocking tunnels during raids (Bordereau et al., 1997).

In Glossotermes oculatus, body rupture occurs from a frontal gland, and its main function appears also to be the blockage of galleries in the colony (Sobotnik et al., 2010a). When soldiers are disturbed outside the nest, they attempt to escape or hide rather than use autothysis, providing further evidence that autothysis in these termites is specialized for tunnel defense. Apilitermes longiceps also uses autothysis, which is achieved in this species through a violent contraction of the mandibles. When in close combat with an enemy, a soldier will suddenly cross the mandibles, causing the frontal integument to crack. The thin dorsal wall of the frontal gland is simultaneously torn open, and a defensive secretion is poured out toward the enemy (Deligne and De Coninck, 2006). Originally, secretion may have occurred through a small pore at the front of the head, but the pore has likely regressed and is non-functional because dehiscence proved to be more efficient (Deligne and De Coninck, 2006). Suicidal defensive behavior through autothysis has evolved independently in Serritermitidae, Apilitermes, Glossotermes, Dentispicotermes, and Ruptitermes (Sobotnik et al., 2010a, b). The hypothesis of multiple evolutionary origins of autothysis is supported by the variety of structures and mechanism involved despite the functional similarity. Thus, these different groups of termites have converged on an effective defense mechanism against arthropod predation. It would be interesting to relate termite autothysis to predation pressure on the respective species and to the typical colony composition and polyphenism. For example, in Ruptitermes, the soldier class is absent and autothysis is only present in workers (Costa-Leonardo, 2004; Sands, 1982; Sobotnik et al., 2010b). The phylogenic association between autothysis and lack of soldiers remains to be explored systematically.

Aphids have also been observed to release a substance through self-sacrifice that can immobilize a predator. When their colony is in danger, wingless adults of Quadrartus yoshinomiyai release a waxy substance from their cornicle, a paired abdominal tube, onto the predator. The stickiness of the excretion will adhere the aphid to the target, effectively immobilizing the predator (Uematsu et al., 2007, 2010). The aphids that secrete the substance onto the predator are not able to remove themselves, leading to their self-sacrifice. The self-sacrificial individuals are specialized, post-reproductive females (Uematsu et al., 2010). After reproduction has ceased for these individuals, their abdomens will manufacture and store the waxy secretion used in defense and these menopausal females will congregate on the outer edges of the gall (Foster, 2010). Therefore, the age-related menopause may not be due to senescence but part of an age-based division of labor, with the individuals of the lowest residual value fulfilling the most dangerous task.

Instantaneous defense: biting

Bee species that lack a stinging form of defense may resort to other forms of instantaneous self-destructive defensive behavior (Buchwald and Breed, 2005). For example, stingless bees in the genus Trigona will lock onto an insect attacker in a “death grip” with their jaws to immobilize it. In some species, these defenders commit self-sacrifice rather than disengage from an intruder (Buchwald and Breed, 2005). Trigona corvina defenders are also very persistent when locking onto human hair (M. Breed, pers. comm.). However this “death grip” has only been described in the literature in passing. Other stingless bees (Tetragonisca angustula) that perform this locking jaw behavior will eventually release an intruder after 30 min (van Zweden et al., 2011).

Preemptive self-sacrifice

Most social aphids inhabit plant galls as a safe feeding place (Kurzfeld-Zexer et al., 2010) and exhibit nest construction and repair. It is important that any damage to the gall is quickly repaired to prevent attacks from parasitoids and predators (Pike, 2007; Kurosu et al., 2003). Soldiers in the gall aphid Nipponaphis monzeni sacrifice their lives to repair the gall even in the absence of predators. When these aphids discover an opening in the gall they secrete a fluid from their cornicles that functions as a plaster and seals the hole and forms a scab, which increases the recovery time of the plant tissue (Kutsukake et al., 2009). This behavior may result in self-sacrifice of the aphid nymphs. Some may shrivel to one-third their body size after repairing damage and sometimes their bodies will be included into the plaster scab (Kurosu et al., 2003). This repair behavior may have originated from instantaneous defense because the same mechanism is involved, and a similar secretion is dabbed onto predatory lepidopteran larvae (Edwards, 1966; Kurosu et al., 2003; Uematsu et al., 2010). Another aphid species, Pemphigus spyrothecae, also repairs its gall nest when it is damaged, but not through suicidal plastering (Pike and Foster, 2004). In P. spyrothecae, it takes ten or more days for a colony to seal up the gall, mainly relying on directing an overgrowth of undamaged gall tissue into the wound. While more costly, the self-destructive defensive behavior taken by N. monzeni is sustainable due to its larger colony size, usually containing thousands of individuals (Kutsukake et al., 2009), but no comprehensive cost-benefit analyses have been done in any case of autotomy, autothysis, or nest sealing behavior.

Workers of the tropical ant species Forelius pusillus defend their nest through preemptive self-sacrifice. In this species, the nest entrance is routinely closed every night to avoid detection by nocturnal ant species that prey on F. pusillus nests (Tofilski et al., 2008). This behavior is very common (Buschinger and Maschwitz, 1984; Hölldobler and Wilson, 1990) and other ant species seal their nest at night as protection against predators. However, in F. pusillus colonies, a few workers remain and presumably die outside the nest to conceal the entrance. The behavioral repertoire of these workers is distinct and their non-random numbers also suggest an adaptive role of this phenomenon (Tofilski et al., 2008). The number of workers performing this behavior ranges from one to eight, with zero almost never occurring. These workers outside the nest were not late-returning foragers, but were identified as workers sealing the nest when entrance closure began. The self-exiled ants were not trying to tunnel back into the colony either, but rather were kicking sand particles over the entrance for up to 50 min after closure, making the entrance indistinguishable to an observer. The ants that remain outside the entrance will likely encounter other ant species or will be blown away from the entrance by wind. They are unlikely to survive the night and are not found in the vicinity of the nest entrance the following morning when the colony is reopened from workers inside (Tofilski et al., 2008). Forelius pusillus lives in relatively large colonies (>105 workers) and can easily sustain a daily loss of one to eight workers to ensure that the entrance is properly hidden by covering it from the outside (Bourke, 2008; Tofilski et al., 2008). Similar adaptations in other ground-nesting ants that experience significant predation pressure are likely, but it remains to be seen how common this behavior is. Many questions remain unanswered on F. pusillus nest closure, such as whether workers are genetically predisposed to perform this behavior or the nest concealing specialists are older workers that are approaching the end of their life (Bourke, 2008).

Host suicide

Self-sacrifice is a particularly effective defense strategy when a sacrifice of a small number of colony members can effectively protect the entire colony. This is the case in the incipient stages of a contagious epizootic disease, because all members of a colony are vulnerable to the attack, but the removal of the few diseased individuals could contain the pathogen (Fraser et al., 2004). A sick or parasitized worker that leaves the colony will reduce the probability that nestmates become infected, and inclusive fitness could select for this behavior over a wide range of parameters (Rueppell et al., 2010; Smith-Trail, 1980). Thus, the host suicide hypothesis predicts that when a host living in a social setting becomes reproductively sterile from a parasite or pathogen, it should abandon the group to die in isolation, provided that its group includes kin (Smith-Trail, 1980). However, hosts can be behaviorally manipulated by parasites or pathogens when infected, so that host behavior after infection should be carefully studied to avoid any misinterpretation (Libersat et al., 2009; Poulin et al., 1994; Hohorst and Graefe, 1961). The host suicide hypothesis has received little attention, and many of the cases used to originally support it have alternative explanations (Poulin et al., 1994). Interestingly, those examples did not involve eusocial insects, but rather insect aggregations, such as butterfly larvae and pea aphids (Shapiro, 1976; McAllister and Roitberg, 1987). Eusocial insects may provide the best test systems for the host suicide hypothesis due to the relative strength of kin selection.

Worker ants of Temnothorax unifasciatus that die of fungal infection, unknown causes, or exposure to CO2 leave their nests hours or even days before death, never to return (Heinze and Walter, 2010). In this study, workers were first infected with spores from the fungus Metarhizium anisopliae, causing a 74% mortality rate within 10 days. Of those who died, 70.5% were observed to leave the nest to die in isolation. A control treatment of CO2 to induce artificial sickness resulted in the same behavioral response, rejecting parasite manipulation as a possible cause of the voluntary self-exile (Heinze and Walter, 2010). Additionally, these workers were not observed as being forced away or carried out by other ants, and they did not receive any special treatment such as excessive grooming or trophallaxis even when infected with a fungus (Heinze and Walter, 2010).

The disappearance of individuals is thought to be a factor in the phenomenon of colony collapse disorder in honeybees (van Engelsdorp et al., 2009; Khoury et al., 2011). It has been observed that infections with the microsporidium Nosema ceranae and the parasitic mite Varroa destructor affect the ability of honeybees to navigate and return to the hive (Higes et al., 2008; Kralj and Fuchs, 2006, 2010). This decreased orientation ability has been interpreted as an adaptive behavior that removes parasites and pathogens from a colony (Kralj and Fuchs, 2010), but other possibilities such as host manipulation by the parasites or simple loss of function of diseased workers are conceivable. Complementary evidence for self-removal of health-compromised honeybee workers comes from experiments on artificially treated workers (Rueppell et al., 2010). Workers were exposed to CO2 narcosis or fed the cytostatic drug hydroxyurea (HU), which increased mortality in either case. However, even treated individuals that showed no sign of morbidity abandoned their foraging role to remove themselves from the colony. Their behavioral response to treatment included prompt attempts to leave their hive, decreased food uptake, and the cessation of distributing food to colony members. No general functional deficiency or antagonistic behaviors toward these individuals were observed and both treatments resulted in the same behavioral changes (Rueppell et al., 2010). These findings are consistent with the results in Temnothorax unifasciatus (Heinze and Walter, 2010) and the interpretation of adaptive host suicide. Parasitized bumble bees also leave the nest, but in this case there is no direct infection of nestmates and may have evolved simply to slow the growth of the parasitoid (Poulin, 1992; Muller and Schmid-Hempel, 1993).

In contrast to directed self-sacrificial colony defense against an acute attack, host suicide or altruistic self-removal presents a distinct behavioral program, which bears some parallels to cellular apoptosis that rids multicellular organisms of sick or superfluous cells (Ellis et al., 1991). It can only be understood as a colony-level adaption, providing a textbook example of the power of kin selection and the concept of the superorganism (Rueppell et al., 2010; Heinze and Walter, 2010). Host suicide is an effective general strategy against disease outbreak in large eusocial groups because of its cost–benefit ratio (Kralj and Fuchs, 2006; Smith-Trail, 1980). In most circumstances, the potential benefit of removing an infectious individual to prevent future infections of nestmates far outweighs the costs of altruistic self-removal (Rueppell et al., 2010). It has been predicted that host suicide would not evolve if the workers were an intermediate host to a parasite, as parasites usually manipulate behavioral changes in these cases (Schmid-Hempel, 1998). More behavioral studies of diseased social insects are necessary, including cost–benefit analyses and mechanistic studies to evaluate its general importance and relation to honeybee colony collapse disorder.

Division of self-sacrificial labor

Overall, the proximate mechanisms that govern self-sacrificial defense tactics in social insects have not been worked out, except for some genetics components of defense behaviors that have been identified in honeybees (Hunt, 2007; Breed et al., 2004; Arechavaleta-Velasco et al., 2003; Hunt et al., 1998). In particular, we do not understand the decision-making process and environmental modulations that trigger a self-destructive defensive response. However, the principles that govern the general division of labor among social insect workers (Beshers and Fewell, 2001) may explain why certain workers are more likely to perform self-sacrifice. Individuals that perform “risky” or self-sacrificial behavior tend to have the lowest residual value in the colony (Woyciechowski and Kozlowski, 1998; Tofilski, 2009). Division of labor in workers is likely driven by the different risks associated with the tasks being performed and workers can adjust their labor tasks according to life expectancy (Woyciechowski and Moron, 2009; Moron et al., 2008). Residual value theory (Kolmes and Fergusson-Kolmes, 1989) predicts that individuals with a shorter future life expectancy and a lower ability to perform future work will engage in more dangerous tasks. For example, older honeybee workers (>10 days from eclosure) and workers with low amounts of gathered nectar sting more readily in individual sting assays (Kolmes and Fergusson-Kolmes, 1989). Post-reproductive workers of the aphid Quadrartus yoshinomiyai also are the colony's suicidal defenders (Uematsu et al., 2010).

As described above, self-destructive behavior also relates to physical caste in addition to the age-based division of labor. Minor workers in the COCY complex are the only workers with a distinct morphological self-destructive mechanism (Cook, 2008). In most termites, the soldiers are the primary defenders, specialized for fighting and, in some species, self-destructive tactics. The mechanistic basis of caste divergence in termites has been increasingly understood (Moura et al., 2011), but little is known about the development of the self-destructive autothysis apparatus. Several social aphid species produce nymphs that are differentiated from normal nymphs and are unable to further develop and function as a sterile soldier caste (Kutsukake et al., 2009), similar to ant and termite soldiers. However, in Nipponaphis monzeni, first-instar nymphs seem to invariably develop large globular cells and serve as the only gall defenders, performing self-sacrifice when repairing galls. In the laboratory, adults of this species do not discharge a defensive secretion in response to tapping the body with a fine instrument, but almost all first-instar aphid nymphs do (Kurosu et al., 2003).

The evolution of either an age-based or caste-based division of labor can have fundamentally different consequences for individual life history and colony demography, although both mechanisms are presumably adaptive. Theoretical analyses show that age polyethism can increase the life expectancy of workers in general (Tofilski, 2002, 2006, 2009; Jeanne, 1986). Self-sacrificial colony defenders tend to be old in most species and thus can be understood within the general framework of temporal polyethism. When the division of labor is controlled though a caste system, life span in general may be shortened (Tofilski, 2006). However, the actual life expectancy of the specialized defensive caste will depend on the frequency of attacks. Defenders that do not participate in other colony functions may experience a lower mortality and represent a relatively long-lived defense force. However, empirical data are missing to evaluate these scenarios. It is also not clear how ordinary defense and self-sacrifice relate to each other in specific cases. The relationship may not be trivial, as suggested by the case of Quadrartus yoshinomiyai where first-instar defenders exist, but older post-reproductive females are the individuals performing self-destructive behavior (Uematsu et al., 2010). In addition, research is needed to understand strategies that mix age-based and caste-based defense within a species.

Discussion

The protective structure of the nest is central for social evolution in insects, but proves vulnerable to predation, parasites, and diseases (Hughes et al., 2008). An organized and collective defense from predators is needed to make social groups successful. Vigilance against predation is much easier when in a group (Quenette, 1990), and efficient specialized defenders and unique defenses have evolved a number of times in eusocial insects. Some defensive adaptations are intentionally self-destructive and persist because the benefits of an efficient form of defense outweigh the cost of a worker, particularly in colonies with a large workforce. The diversity of these mechanisms reflects the different types of natural enemies that attack social insects, different preadaptations in the principal social insect lineages, and perhaps chance. Every fight has the potential to leave a combatant mortally wounded, but adaptations that inevitably lead to death deserve special consideration, because they are an extreme form of defense and the switch from self-preservation to self-destruction is of general scientific interest. While self-defense occurs in many solitary species and in many contexts, self-sacrifice can only persist through kin selection (Foster et al., 2006). The ultimate mechanism and persistence of self-destructive behaviors in social insects can generally be understood through the division of labor into reproductives and sterile worker classes. The proximal mechanisms that shape the decision making between alternative behavioral outputs—choosing whether to perform a self-destructive behavior at this point in time or continuing to perform non-lethal colony defense or worker duties—are currently not well-understood. Although some genetic factors have been investigated (Hunt, 2007; Breed et al., 2004; Arechavaleta-Velasco et al., 2003; Hunt et al., 1998), the neuro-physiological process, the effect of other individual variables, and the environmental triggers are not known. Physiological and neurobiological studies, as performed to study Drosophila courtship (von Philipsborn et al., 2011; Benton, 2011; Kohatsu et al., 2011), are needed.

Another field to draw conceptual lessons from may be immunology (Cremer and Sixt, 2009). In return, understanding self-destructive defensive behaviors in social insects can inform other fields of research. Parallels between individual disease defense and social immunity in insect societies exist (Cremer and Sixt, 2009), but social insect colonies are experimentally much more accessible. Social insect colonies provide dense networks, similar to human societies (Fewell, 2003) and may prove as fertile experimental testing grounds for epidemiological models to investigate the implications of social isolation of infective nodes (Naug and Camazine, 2002). Furthermore, understanding whether a switch in decision making exists that will cause a defender to perform a behavior that is self-destructive over behaviors that are for self-preservation could be informative in a comparative perspective across different taxa. Only a few species with self-destructive morphological specializations are currently known, but it may be more common. The production of a “cannibalism” signal by sterile diploid male honeybees to signal their infertile status is another example of self-destructive behavior that warrants future research: even though some characteristics that might differentiate diploid and haploid males have been identified (Herrmann et al., 2005), no evidence supports the hypothesis that social insects engage in self-destruction of infertile offspring through a cannibalism signal (Santomauro et al., 2004).

Social insect workers do not always sacrifice their lives. Some will choose self-preservation and flee from a battle (Human and Gordon, 1999). However, there are certain triggers that will switch a defender from behaviors increasing self-preservation to behaviors increasing self-sacrifice. While direct reproduction in many social insect workers is impossible or improbable, they should not commit unnecessary acts of self-sacrifice (Batchelor and Briffa, 2011). When a majority of the colony dies in defensive behaviors (Schumacher and Egen, 1995; Nogueira-Neto, 1964), defenders make the colony more vulnerable to future attacks and face a decrease in indirect fitness. Understanding that balance between self-preservation and self-sacrifice in social insect defenders at the colony level is very important and may shed light onto the evolution of specialized defenses that intentionally lead to self-sacrifice of the actor.

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