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Guests of Social Insects



Thomas Parmentier
Terrestrial Ecology Unit (TEREC), Department of
Biology, Ghent University, Ghent, Belgium
Laboratory of Socioecology and Socioevolution,
KU Leuven, Leuven, Belgium
Research Unit of Environmental and
Evolutionary Biology, Namur Institute of
Complex Systems, and Institute of Life, Earth,
and the Environment, University of Namur,
Namur, Belgium

Synonyms

[Inquilines](#); [Myrmecophiles](#); [Nest parasites](#);
[Symbionts](#); [Termitophiles](#)

Social insect nests provide a rich microhabitat, often lavishly endowed with long-lasting resources, such as brood, retrieved or cultivated food, and nutrient-rich refuse. Moreover, nest temperature and humidity are often strictly regulated. The precious nest spaces are commonly closely defended by a multitude of workers equipped with strong mandibles, venom, and/or a battery of other chemical weapons. The nest is therefore to be regarded as a resource-rich but impenetrable fortress.

A remarkably diverse group of arthropods other than the resident social insects thrives in just such a situation, exploiting the nest's

resources and homeostatic conditions. At the same time, successful adaptation to the inner environment shields them from many predators that cannot penetrate this hostile space. Social insect associates are generally known as their guests or inquilines (Lat. *inquilinus*: tenant, lodger). Most such guests live permanently in the host's nest, while some also spend a part of their life cycle outside of it. Guests are typically arthropods associated with one of the four groups of eusocial insects. They are referred to as [myrmecophiles](#) or ant guests, [termitophiles](#), [melittophiles](#) or bee guests, and [sphecophiles](#) or wasp guests. The term "myrmecophile" can also be used in a broad sense to characterize any organism that depends on ants, including some bacteria, fungi, plants, aphids, and even birds. It is used here in the narrow sense of arthropods that associated closely with ant nests. Social insect nests may also be parasitized by other social insects, commonly known as [social parasites](#). Although some strategies (mainly chemical deception) are similar, the guests of social insects and social parasites greatly differ in terms of their biology, host interaction, host distribution, behavior, and diversity. In contrast to the mutualistic [trophobionts](#), like some aphids and other homopterans, guests do not provide clear benefits to their host but range from commensals to severe parasites.

The founding father of the study of this remarkable group was Erich Wasmann (1859–1931) of Austria, who collected and described hundreds of social insect guests, as

well as writing extensively about their relationships to their hosts [11]. Other important pioneering scholars were Charles Janet, William M. Wheeler, and Horace Donisthorpe. They were followed by a number of influential researchers in the second half of the twentieth century, most notably David H. Kistner [4, 5], Bert Hölldobler [1], and Carl Rettenmeyer [9].

The greatest diversity of guests is found in nests of ants and termites. The number of myrmecophile species is estimated at between 10 and 100 thousand, but no catalogs have been compiled in recent times. In comparison, social bees and social wasps support a relatively low number of guests. This difference is evidently not due solely to the sizes of the potential host groups, as several factors promote diversity and coexistence of symbionts found in ants and termites, but not in bees and wasps. The largest diversity of guests lives in very large ant or termite colonies peaking at millions of workers, much larger than those of any social bees or wasp. In addition, the density of ant and termite nests per unit area is often much higher, and these nests are stable and of long duration. Furthermore, ant and termite nests typically contain much more organic material and debris which attract scavengers. Finally, ant and termites probably defend their nest less efficiently. In spite of the low number of bee guests, they gain much attention because of their destructive effect on commercial [apiculture](#). The most notorious bee guests are *Varroa* mites, but the small hive beetle (*Aethina tumida*) and wax moths are also considered as serious [parasites of honey bees](#).

Evolution

The transition from free-living organism to inquiline in social insect nests has evolved in many terrestrial arthropod lineages [2, 4, 5]. Guests come from multiple insect orders, as well as in spiders, mites, isopods, pseudoscorpions, and millipedes. Nevertheless, inquilinism is heavily skewed to particular groups of arthropods that appear preadapted to a shift toward this peculiar habit. Small scavenging or predatory arthropods with some sorts of defensive features (chemical,

physical or behavioral) seem to be preadapted in this way. Mites and beetles form the largest groups of guests. The majority of beetle guests are rove beetles (Staphylinidae), particularly of the subfamilies Aleocharinae and Pselaphinae. Other species-rich groups are flies (especially the Phoridae), parasitic wasps, silverfish, and the beetle families Carabidae, Scarabaeidae, Tenebrionidae, and Histeridae [5, 7].

The fossil record hints that the intricate relationship between guests and social insects has developed early in the radiation of social insects and has been sustained over geological time. The oldest unequivocal termitophile is an aleocharine beetle from 99-million-year-old amber. Recently, a clown beetle preserved in amber of the same period was described as the earliest myrmecophile fossil.

Wasmann already recognized that social insect guests greatly differed in their strategies to bypass host vigilance. He placed guests in different categories according to degree of specialization [11]. *Synechtrants* (persecuted guests) are unspecialized inquilines that are recognized as intruders and provoke an aggressive response. They can survive by means of hiding, swift movements, repellent secretions, or mechanical defensive structures. *Synoeketes* (indifferently tolerated guests) are also relatively unspecialized but are ignored because of their slow movement, small size, lack of protruding appendages, or an apparently indistinct odor. *Symphiles* (true guests) are highly specialized inquilines that have evolved different types of chemical, morphological, and behavioral adaptations that deceive the host. Because of this trickery, they are not attacked but are accepted as members of the colony. They are rewarded with food, grooming, protection, and transport. These arthropods have succeeded in “breaking the code” of their hosts. The last group of guests in Wasmann’s classification is *ectoparasites* which live on the body of their host.

Kistner devised an alternative classification with only two categories, *non-integrated* and *integrated* species [4] that is now preferred. The group of non-integrated species roughly encompasses Wasmann’s *synoeketes* and

synechtrans, as well as most ectoparasites, whereas the category of integrated species is almost equivalent to Wasmann's symphiles.

While these and other classifications have their merits, they leave out the fact that the degree of specialization in guests is continuous, so that the proposed categories are situated at the extremes of the generalist-specialist spectrum. Many guests thus do not fit into the distinct categories of these classifications. For example, the rove beetle *Dinarda maerkelii* is recognized by its *Formica* ant host and provokes a strong aggression response. On the other hand, it frequently begs for food and engages in ► [trophallaxis](#), a highly specialized behavior typically seen in symphiles.

Strategies

In the course of adapting to life in social insect nests, guests have evolved specialization in different traits. Surprisingly, different arthropod lineages often evolved independently the same strategies to facilitate integration into the colony. As a general rule, an associate that shows an intimate relationship with its hosts will capitalize on advanced integration strategies, whereas unspecialized species that avoid their host will use, or at best, fine-tune strategies that were already present in their free-living relatives. Host specificity appears to be strongly related to the level of guest specialization. Specialized species target only one or a very few closely related hosts. In some cases, such as in *Microdon mutabilis*, guest populations show even adaption to an individual host population and cannot survive in other populations of the host. Generalists, in contrast, are guests that may thrive in nests of distantly related hosts. *Panmyrmecophiles* (e.g., the isopod *Platyarthrus hoffmannseggii*) are even found with most ant species in their distribution range.

Chemical Communication

Communication in social insects is largely chemically mediated. These signals play a vital role in coordinating the colony's activities, such as

response to danger, allocation of food sources, and distribution of fertility and dominance signals. Chemical cues are also pivotal in ► [nestmate recognition](#), which is based on a colony-specific blend of low-volatile cues present on the cuticle. In ants, wasps, and termites, the colony odor is a bouquet of linear ► [cuticular hydrocarbons](#), whereas other compounds such as fatty acids and esters are important in bees as well. Workers treat individuals with the same odor as members of the colony and reject or attack individuals with a deviating chemical profile [10]. A large group of arthropods has succeeded in exploiting this sophisticated communication system [6]. The same chemical deception strategies can be found in social insect guests and in ► [social parasites](#). The mimicking of the host's chemical profile may result in complete acceptance into the colony [2].

It appears that highly specialized guests with a narrow host range can synthesize the components prior to the contact with their host (chemical mimicry), but this strategy is rather rare. Other guests, such as the infamous *Varroa* mites, acquire the colony odor passively by transfer of components from the host (chemical camouflage). This strategy is more flexible, as it allows the exploitation of hosts with different profiles. Associates gain the host's odor primarily by physical contact with the workers (e.g., active rubbing in the myrmecophilous silverfish *Malayatelura ponerophila*) and nest material. When isolated they lose the host-specific hydrocarbons, indicating that these are provided by the host. Alternatively, they can obtain the host's profile by eating its larvae and subsequently recycling the hydrocarbons. This strategy was first described in the spider *Cosmophasis bitaeniata* associated with ► [Oecophylla weaver ants](#) but has, for example, also been suggested in the wasp-associated beetle *Metoecus paradoxus*.

Phengaris (former *Maculinea*) butterflies (Lycaenidae) are by far the best-studied myrmecophiles, because of their flagship role in butterfly conservation but also due to their fascinating parasitic biology and use of chemical trickery. *Phengaris* females lay eggs on specific host plants (e.g., *P. alcon* on *Gentiana*, *P. arion* on *Thymus*). A *Phengaris* caterpillar feeds on the host plant

during the first instars and then drops to the ground. It starts to produce cuticular secretions resembling the odor of the host's larva. The caterpillars are taken by foraging workers to their nest, where they either devour the ant brood (predatory strategy, e.g., *P. arion*) or are fed mouth to mouth by the workers (cuckoo strategy, e.g., *P. alcon*). Once the adult emerges, it is recognized as an intruder and must escape from the nest. Pre-adopted caterpillars of *P. rebeli* mimic a large fraction of the hydrocarbon profile of the host's larvae (chemical mimicry), but they perfect their integration by the acquisition of additional recognition hydrocarbons in the nest (chemical camouflage). Selection will favor host ants that discriminate the chemical profile between nestmates and parasites. Infected *Myrmica* populations slightly alter their profile over generations to allow discrimination of the parasite. However, this results in an evolutionary arms race in which the chemical profile of the parasite must keep pace with the host's changing profile.

Guests could also persist within a colony by suppressing the number of recognition cues on the cuticle. This strategy, commonly known as *chemical insignificance*, allows the guest to remain undetected. Again, this deception strategy can be used to target multiple hosts and is widespread in nonhost-specific guests. Some are able to apply chemical insignificance and mimicry in sequence, which was clearly demonstrated in ► [social parasites](#). They carry few or no recognitions cues when they invade the nest of their host, but in time they acquire the host's odor, which facilitates their integration. As nestmate recognition is probably based on only a subset of the cuticular profile, lacking or carrying low amounts of some key components (chemical transparency) could already mask their presence in the colony. To date, this strategy has not been conclusively demonstrated in any guest.

While most studied social insect guests take advantage of one of these advanced chemical deception strategies, unspecialized associates tend to be undisguised and carry an idiosyncratic cuticular profile. They are detected by their host as intruders, but they escape from host attack by fleeing, agile movements, crouching to the

ground, hiding, feigning death or emitting repellent substances. Note that the detection of these guests may be hampered once they succeed to enter the nest. The inner walls of the nests passively accumulate high concentrations of compounds from the colony, which seem to be non-colony-specific. This nest odor coating may cause a saturation of the ants' antennal receptors, resulting in a failure of intruder detection.

Guests could also target their host by secreting volatile substances from epidermal glands. Many free-living rove beetles possess a tergal gland through which they secrete defensive and toxic chemicals. It seems that non-integrated or poorly specialized rove beetles do not chemically mask their presence but rather deter their aggressive host using general tergal gland secretions. Some myrmecophilous rove beetles exhibit a more advanced strategy and deceive their hosts with glandular secretions. *Pella* beetles associated with *Lasius fuliginosus* release the ► [alarm pheromone](#) of the host using their tergal gland, which results in the ants panicking and fleeing. The use of deceptive volatiles has been brought to its highest point by the symphiles, or highly specialized symbionts. Our knowledge of this mainly comes from detailed observations and experiments with the rove beetles *Lomechusa* and *Lomechusoides*. In these, the adult and larval stages of the beetles use multiple glands to appease the host and induce it to carry them to the colony's brood chambers. Symphiles typically possess a battery of glands whose substances are conducted to adjacent tuft-like structures (trichomes) (Fig. 1). The hosts regularly lick the exudates from these trichomes. Although the mechanistic role of glandular products has not been demonstrated in other symphiles than *Lomechusa*, it is expected that they also help to appease the host and are needed for an intimate association. Social parasites also use volatiles to facilitate their integration.

Morphology

Social insect guests are typically of the size of the host or smaller. Small size facilitates crypsis and makes the symbiont harder to catch. During evolution, some body parts were reduced or even



Guests of Social Insects, Fig. 1 The specialized myrmecophile *Lomechusa emarginata* (Staphylinidae: Lomechusini) has an alternating life cycle. The adults reside in the nest of *Myrmica* ants during winter. Adoption and integration in these nests are promoted by different glands and yellow trichomes. The larvae of this beetle live

in the nest of a *Formica* host during spring and summer. Similar to the adults, they are groomed, transported, and fed by trophallaxis. (Photos by Pavel Krásenský – <http://www.macrophotography.cz> (adult) and Thomas Parmentier (larvae))

lost in many inquilines. As social insect nests are dark inside, vision became less important for inquilines, and many inquiline silverfish (e.g., *Atelura*), Collembola (e.g., *Cyphoderus*), Isopoda (e.g., *Platyarthrus*), and crickets (*Myrmecophilus*) are blind or possess reduced eyes and show reduced pigmentation, similar to what we observe in cave-dwelling or cave-burying organisms. The stable nest environment promoted the loss of wings in guests such as in the ant cricket *Myrmecophilus* (Fig. 2), the myrmecophilous cockroach *Attaphila*, the bee louse *Braula cauca* (Diptera) (Fig. 3), and several myrmecophilous and termitophilous phorid flies. Some termitophilous sciariid flies emerge with wings, which are later shed to promote mobility

(Fig. 4). Interestingly, some specialized guests such as the pselaphine rove beetle supertribe Clavigeritae (Fig. 5) show recessed mouth parts which favor the exchange of food with their ant host. Many guests, both unspecialized and specialized, have compacted and relatively short legs and antennae (Fig. 5), presumably to avoid damage or loss in antagonistic interactions with host workers. The coxae of the termitophilous rove beetle tribe Trichopseniini are protective plate-like structures, under which the metalegs can be retracted. In some specialized guests, most remarkably in the myrmecophilous Paussinae beetles (Carabidae), the antennae have evolved to complex truncate, flattened, tubular or disc-like structures possessing a cavity with



Guests of Social Insects, Fig. 2 The ant cricket *Myrmecophilus albicinctus* (Orthoptera: Myrmecophilidae) receives a food droplet from its host *Anoplolepis gracilipes*. This cricket has no wings and small eyes, typical reductions seen in many social insect guests. It possesses modified mouth parts to facilitate food transfer through trophallaxis. (Photo by Taku Shimada – <http://www.antroom.jp/>)



Guests of Social Insects, Fig. 4 The black fungus gnat (Diptera: Sciaridae) *Nyxiopalpus rosarii* living with its termite host *Nasutitermes* sp. The wing stumps (highlighted with arrows) indicate that this fly sheds its wings after eclosion as an adaptation to an inquiline life. (Photo by Taisuke Kanao)



Guests of Social Insects, Fig. 3 The bee louse *Braula coeca* (Diptera: Braulidae) is a wingless fly with special comb-shaped tarsi helping to cling to the hairs of its host *Apis mellifera*. (Photo by Yuanmeng Miles Zhang)

secretory cells. These structures probably secrete appeasing substances that promote integration in the colony. Highly specialized myrmecophilous beetles, such as the pselaphine rove beetle *Claviger*, enjoy a royal treatment and are often picked up and transported in the nest. They often possess notches, which ants use to grasp them (Fig. 5). These furrows or cavities are often accompanied with glandular structures. Trichomes, which are tufts of mostly yellow- or golden-colored setae on the thorax or abdomen,



Guests of Social Insects, Fig. 5 The pselaphine beetle *Claviger testaceus* inspected by its host ant *Lasius niger*. This highly specialized parasite enjoys a royal treatment (grooming, transport, trophallaxis) in the nest, which is mediated by yellow trichomes exposing glandular secretions. The central cavity of the beetle's abdomen serves as a handling notch for the ants. The antennae are compacted, which is an adaptation to frequent handling and carrying by the host. (Photo by Pavel Krásenský – <http://www.macrophotography.cz>)

are also typical structures of specialized myrmecophiles. They are licked by the ant host and seemingly facilitate the complete integration of “symphiles.” Pores connected to glands are located between the trichome hairs. The trichomes probably serve as wick-like structures to expose

glandular products. Trichomes are typically found in highly specialized myrmecophilous beetles (Figs. 1 and 5), but also some termitophilous beetles and the myrmecophilous wasp *Tetramopria* carry an analogous structure of trichomes.

A unique morphological feature independently evolved in multiple lineages of termitophiles (mostly found in rove beetles, but also in phorid flies, gall gnats, and scarabaeids) is physogastry [4, 5], the swelling of the abdomen to several times its initial size (Figs. 6 and 7). Extremely enlarged abdomens are recurved and held over the body as seen in the rove beetle tribe Corticocini. The exact role of this inflated body is unknown, but it is assumed that it is associated with the production of deceiving chemicals or may favor tactile mimicry. Physogastry is typically seen in highly integrated termitophiles. Some physogastric rove beetles (*Corotocina*) went even a step further and exhibit morphological mimicry. Their swollen abdomen is strategically constricted and supports projecting appendages, resembling in that way the nymphs of their host as seen from above. Morphological mimicry is also manifested in some highly integrated myrmecophilous beetles associated with ► **army ants**. They closely resemble the body of their host through a petiolate abdomen, elongated legs and body, geniculate antennae, and in some cases similar body coloration. This myrmecoid body plan evolved at least 12 times independently in the rove beetle subfamily Aleocharinae. Mimicry of the body plan of a host is known as Wasmannian mimicry. The selection pressure acting on the beetles is still open to discussion and possibly different mechanisms act in synergy. Wasmann originally argued that the resemblance in body plan of the beetles has been selected to dupe the host, as tactile cues may play a role in colony integration as well. However, since army ants have poor vision, this cannot explain why some beetles evolved matching coloration. It seems likely that it serves in protection from visually hunting predators, especially the various birds that attend army ant columns.

Many poorly integrated termitophilous and myrmecophilous beetles (Figs. 8 and 9) and silverfish (Fig. 10) have independently evolved

a limuloid (*Limulus*: horseshoe crab) or drop-shaped body form [4]. This is an expansion of the anterior body part in concert with shortening of appendages, covering shields, and reduced head size. This smooth body form does not expose potential grasping points and permits the inquiline to slip through the mandibles of its host. Finally, the compact, robust body of some free-living arthropod lineages proved to be preadaptive to successfully integrate into social insect nests. Inquiline representatives of these groups look nearly identical to free-living relatives. Their tank-like body is well suited to withstand host aggression, especially when the appendages are also retracted (e.g., the red wood ant associates *Monotoma* and *Dendrophilus*).

Behavior

Poorly integrated species exhibit a completely different behavioral repertoire from that of specialized guests. Whereas unspecialized species are prudent and avoid direct physical interaction with their hosts, highly specialized species boldly walk among the host workers without eliciting aggression. The host will actively interact (antennating, grooming) with the guest as with a worker or larva. Even congeneric inquilines can greatly vary in their behavior, as is seen in the ant cricket *Myrmecophilus*. The generalist *M. formosanus* targets multiple unrelated hosts. It avoids physical contacts with them and escapes attack by running and jumping. The host-specific *M. albicinctus* provokes much less aggression. When detected, it displays a specific defensive behavior: It stops walking and humps its back. The host then stops chasing and antennates the cricket, which allows the cricket to escape. While *M. formosanus* feeds on food remnants in the nest, *M. albicinctus* is completely dependent on food delivered by the host through trophallaxis (Fig. 2). This transfer of food to other colony members via mouth-to-mouth (stomodeal) or anus-to-mouth (proctodeal) feeding is a key process in social insects. The specialized cricket *M. albicinctus* imitates the begging behavior of a hungry worker by tapping the ant's mouthparts with its forelegs or maxillary palps and is rewarded with regurgitated food. Many other myrmecophiles (e.g.,



Guests of Social Insects, Fig. 6 The physogastric rove beetle (Staphylinidae: Lomechusini) *Longipedisymbia* sp. associated with *Longipeditermes longipes*. (Photo by Taisuke Kanao)



Guests of Social Insects, Fig. 8 *Vatesus* are conspicuous rove beetles with a limuloid defensive body shape and are associated with army ants. The adults and larvae walk in the emigration columns of their host, here *Eciton burchellii*. (Photo by Taku Shimada – <http://www.antroom.jp/>)



Guests of Social Insects, Fig. 7 The unusual, physogastric fly *Javanoxenia* sp. (Diptera: Phoridae, Termitoxeniinae) associated with the fungus-growing termite *Odontotermes* sp. (Photo by Taisuke Kanao)



Guests of Social Insects, Fig. 9 *Discoxenus lucidus*, here with its host *Hypotermes makhamensis*, has a typical defensive limuloid body form. (Photo by Taisuke Kanao)

Antennophorus in Fig. 11, *Atelura formicaria*, *Amphotis marginata*, *Dinarda maerkelii*, *Claviger*, *Maculinea* species with cuckoo strategy, *Paussus*, subtribus *Lomechusina*, termitophiles (e.g., *Sinophilus*), and even bee guests (*Aethina tumida*) also solicit food. Many of these are highly integrated and even show a reduction in mouthparts (*Claviger*), but moderately specialized species (*Amphotis*, *Dinarda*, *Atelura*) also engage in trophallaxis. As trophallaxis facilitates the distribution of the nest colony odor among nestmates, food begging by guests may also favor their chemical integration.

Acoustic Communication

It has only recently become apparent that guests can exploit the acoustic communication found in many insect societies. They have managed to break the acoustic code, similar to what is found in chemically mimicking guests. Some ants produce low-frequency sounds through stridulation. These are used to communicate to nestmates regarding recruitment, rescue, mating, and caste identity or social status. Acoustic deception was first reported in caterpillars and pupae of *Phengaris rebeli*. The caterpillar is constantly fed by trophallaxis (cuckoo strategy) and even supplied with the host's larvae in case of food shortage. The host even rescues the caterpillar in

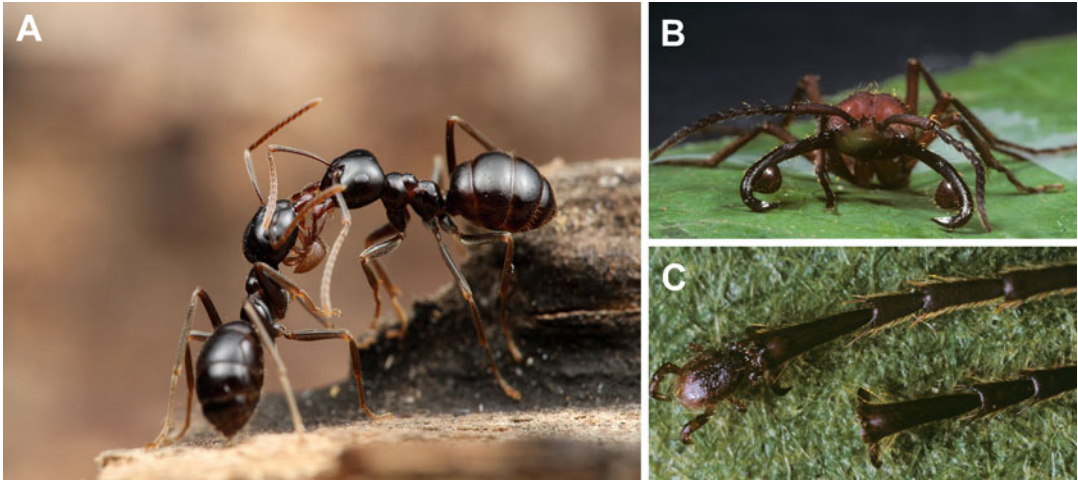


Guests of Social Insects, Fig. 10 Silverfish associated with social insects. (a) Unidentified silverfish with a limuloid body associated with the termite *Longipeditermes longipes*. (Photo by Taisuke Kanao). (b) *Neoasterolepisma* sp. associated with *Messor barbarus*. (Photo by Thomas Parmentier) (c) *Atelura formicaria* associated with *Lasius flavus*. (Photo by Thomas Parmentier)

preference to its own larvae when the nest is disturbed. Caterpillars and pupae closely mimic the larval hydrocarbon profile of its host (*Myrmica schencki*), which helps in getting adopted into the colony. However, chemical transfer experiments with dummies indicated that chemical trickery was not sufficient to achieve integration. The royal treatment appears to be achieved by acoustically mimicking the host's queens. The workers display the same benign behavior in response to the sounds of the caterpillars as those produced by their own queens. Acoustic mimicry is even more refined in the specialized myrmecophile *Pausus favieri*. This beetle is able to imitate the sound of three castes (worker, soldier, and queen) of its host ► *Pheidole pallidula*. It is suggested that this beetle can modulate its acoustic signals dependent on its needs and the caste with which it is interacting.

Dispersal

Dispersal to new nest sites is a critical but poorly studied phase in the life cycle of many guests. Given the spatial configuration of host nests as small islands embedded in an inhospitable landscape matrix, effective dispersal is fundamental. Overall, social insect associates disperse when they colonize a new host colony or when they track a mobile host colony as it moves to a new site. Guests, especially those that fly, are expected to locate new host colonies at a distance by moving toward volatiles emitted from the host workers or nest. The attractive role of long-range host cues has been clearly demonstrated in phorid flies parasitizing ants. These cues represent different types of pheromones and are produced in several glands. In addition, positive attraction to host volatile cues is reported in some other guests. The myrmecophilous isopod *Platyarthrus*



Guests of Social Insects, Fig. 11 Different ectoparasitic mites associated with ants. (a) The ectoparasitic mite *Antennophorus* sp. steals food from two *Lasius capitatus* workers in trophallaxis. These mites also directly beg for food by stimulating the worker they are riding on with its long front legs. (Photo by Taku Shimada – <http://www.antroom.jp/>). (b) Two individuals of *Circocylliba crinita*

on the mandibles of an *Eciton dulcium* army ant major. (Photo by UConn BRC/C. W. Rettenmeyer – Kodachrome database at <http://aagc.uconn.edu>). (c) *Macrocheles rettenmeyeri* on the hind leg of the army ant *Eciton vagans*. (Photo by b and c: UConn BRC/C. W. Rettenmeyer – Kodachrome database at <http://aagc.uconn.edu>)

hoffmannseggii shows positive chemotaxis to an increasing gradient of formic acid, a defensive volatile abundantly secreted by many of its host's workers. Females of the hover fly *Volucella bombylans*, of which the larvae live in bumble bee nests, are triggered to deposit their eggs when they detect the odor of bumble bee nests.

Further evidence of the attractive role of host cues comes from work on *Lomechusa*. These beetles have a remarkable life history. Larval development and pupation take place in a *Formica* nest. The emerged adult then seeks a *Myrmica* nest to hibernate (Fig. 1). In spring females locate a *Formica* nest, in which they deposit their eggs. Experiments showed that adult beetles are strongly attracted to an air flow directed over nest material of the host. Interestingly, this positive response in the adult beetles toward the *Myrmica* cues only lasted 2 weeks after leaving the *Formica* host. It was also reported that newly emerged adults of some myrmecophilous rove beetles were more active and exhibited a greater tendency to fly than older individuals. These findings suggest that dispersal propensity in guests peaks during a short period of time and may depend on specific conditions.

Host detection in *Phengaris* butterflies is more complex. Gravid females of *P. arion* are not attracted by host ant cues but rather respond to volatiles emitted by their host plant, *Origanum vulgare*. Because of the sequential host exploitation of the host plant and the *Myrmica* ants, female *P. arion* butterflies preferentially lay eggs on the host plants located near *Myrmica* nests. Females are guided to these particular plants by carvacrol, a monoterpenoid volatile emitted by oregano as a response to root disturbance by nesting *Myrmica* ants.

While little is known of the attractive role and nature of volatile cues emitted from the nest, multiple studies demonstrated that myrmecophiles can track their host's pheromone trails. Nearly all army ant symbionts tested could follow the pheromone trails of their hosts (Fig. 8). As the nomadic ants constantly move to new nest sites, it is adaptive for the guests to closely keep up with them. Poorly integrated army ant guests have been observed flying to the bivouacs, so it was suggested that they locate their host by volatile nest cues.

Trail following has also been documented in guests associated with non-nomadic ants. They

probably use these pheromone trails to find nests connected to these trails, but the localization of distantly located nests likely requires the tracking of volatile nest cues. Some ants with permanent nests, such as ► [red wood ants](#) and weaver ants, occasionally move to new sites as well. The complete colony may look for a new home when nest conditions are deteriorate. Alternatively, ► [polydomous colonies](#) with multiple queens often bud fragments of the colony. Recent observations showed that a large part of the parasitic larvae of the beetle *Clytra quadripunctata* were able to follow their red wood ant host when it moved to a new nest site. Nevertheless, the host could profit from regularly ► [relocating the nest](#) when a large part of the associated parasites is not capable of tracking the host to the new site.

Many guests climb on the body of their host to track their host or to disperse to a new nest. Such *phoresy* is especially found in mites. Phoretic mites associated with Neotropical army ants are adapted to particular positions (between tarsal claws, antennae, mandible) on the host's body (Fig. 11). The beetles *Odontoxenus* and *Doryloxenus* are equipped with special hairs that assist in holding onto their termite or ant hosts. Some phoretic mites are ectoparasitic, but most phoretic mites and beetles appear to be commensals that consume exudates or organic material on the host's body. Some myrmecophilous mites preferentially attach to virgin queens, which are the dispersing individuals in ant colonies. The wingless cockroach *Attaphila fungicola* also takes advantage of virgin queens to colonize new nests. After mating, the cockroach seems to remain with the alate queen when it enters an established nest. The queen can also found a new nest, but then the cockroach appears to separate from its vector and seeks an established nest. Some phoretic parasites also target foraging workers, which carry them into the nest. This is nicely demonstrated by *Metoecus* beetles, obligate parasites of eusocial wasps. The main host of *Metoecus paradoxus* is *Vespula vulgaris*. This strange-looking beetle lays eggs in the crevices of decaying wood. The following spring, the larvae hatch and wait for a visiting wasp worker to come collecting wood for nest construction. The larvae

cling to the bodies of the workers and are carried into the wasp nest. They crawl into cells with full-grown larvae and consume them (Fig. 12). Phoresy is especially well-developed in army ant guests. Army ants do not have a permanent nest, and most species are often on the move. Many of their associates are less mobile and can only track the fast-moving mass by hitchhiking on workers, brood, or booty. In that way, they are also protected from lurking predators during migrations. The recently discovered histereid beetle *Nymphister kronaueri* uses a stunning mechanism of phoresy. With its long mandibles, it clings to its army ant host between the petiole and postpetiole while retracting its appendages. Another exceptional mode of transport is found in the snail *Allopeas myrmekophilos*. This snail produces a foam which is highly attractive to its ► [Leptogenys](#) army ant host. The workers pick up the snail and transport it to a new nest site as they do their brood.

Synchronization of Reproduction

Our knowledge of the biology of social insect guests is fragmentary, and the life cycles of only a few species have been worked out. Nevertheless, it appears that the life cycle of guests is narrowly synchronized with the reproductive cycles in the host's colony. This is nicely illustrated in the rove beetle *Vatesus* (Fig. 8). The colony cycle of its army ant host alternates between a 2-week nomadic phase in which it migrates to a new site every day and a stary phase in which it is based in the same site for about 3 weeks. Egg maturation in the female beetles starts at the end of the nomadic phase, and egg laying occurs at the beginning of the stationary phase. As such, the beetle's eggs hatch in the temporary nest (bivouac), where the larvae can directly benefit from host's resources. Once the colony starts to move again, the larvae follow it to new sites. Mature larvae leave the colony and pupate, and the adults search for a new host colony, probably on the wing.

Reproductive synchronization can also be found in guests associated with red wood ants in Europe. The nest conditions alternate between hibernation and a phase of active



Guests of Social Insects, Fig. 12 The beetle *Metoecus paradoxus* (Ripiphoridae) in the nest of its host *Vespula vulgaris*. Soon after emergence from a larval cell of its host, the beetle will leave the nest. (Photo by Tom Wenseleers – <https://bio.kuleuven.be/ento/index.htm>)

thermoregulation from April until August. The larvae (and adults) of associated rove beetles reach peak abundance during the warmest period, which overlaps with the peak of ant brood and retrieved prey. This synchrony with the optimal temperature and maximum availability of resources promotes the beetles' rapid growth and can even lead to multiple generations in one season. When temperatures drop in autumn, larval numbers rapidly decline and hibernation takes place in the adult phase.

Niches of Social Insect Guests

Trophic Niche

Many social insect guests negatively affect their hosts. They either prey on the brood, pilfer foraged food, solicit food, or even consume cultivated fungi. However, a large fraction of guests does not seem to harm the host. They live as commensals and thrive in the refuse of the nest. It is generally assumed that the most specialized guests are strictly parasitic, whereas poorly integrated species act as scavengers, facultative parasites, or commensals. Interestingly, different trophic strategies can occur among congeneric species. *Volucella* are spectacular syrphid flies of which the larvae develop in the nests of bees and wasps and the adults resemble the host adults

(Batesian mimicry). The larvae of most European species are commensals feeding on detritus or refuse. The larvae of *V. inanis*, however, have evolved to consume the wasp larvae (Fig. 13), which is reflected in their deviating feeding apparatus.

Mutualistic interactions between guests and the host have not been demonstrated in social insects. In solitary bees, some mites have a sanitary effect in the brood cells by consuming contaminating fungi. Likewise, fungivorous social insect guests, such as springtails and mites, or guests feeding on dead corpses, may provide hygienic services to their host, although this has not yet been demonstrated.

Social insects regularly support multiple species of guests, and it can be expected that these species not only interact with their hosts but also with each other. A network of predator-prey interactions was demonstrated in the large community of myrmecophiles associated with red ► [wood ants](#) [8]. The host indirectly benefits from the presence of some predatory guests, as they also capture parasitic guests. Next to predatory interactions, interspecific competition may also drive the dynamics of symbiont communities. *Maculinea* and *Microdon* larvae can co-occur in *Myrmica* colonies, although both are brood predators that severely exploit the host's resources. Larval development of *Maculinea* caterpillars takes place during spring, whereas the *Microdon* larva growth occurs during the summer. It was suggested that larvae of both parasites can coexist due to this temporal segregation.

Spatial Niche

Nests of social insects are heterogeneous in resources, building material, climatic conditions, and worker density. Especially large nests, with a greater variety of niches, presumably harbor a richer symbiont community. The brood is typically confined to the deep and central parts of the nest and is surrounded by the greatest density of workers. Other typical niches are refuse pits and locations where prey or nectar is stored. Specialized guests circumvent host aggression using deception and so may enter the heavily protected brood chambers where they feast on



Guests of Social Insects, Fig. 13 Left: The adult hover fly *Volucella inanis* (Diptera: Syrphidae) is a Batesian mimic of the social wasp *Vespula vulgaris*. (Photo by Keith Edkins. Right: The fly's larva feeds on larvae of the wasp host. Photo by Bob Brown)

host's eggs and larvae. Unspecialized guests, rather, reside in the peripheral parts of the nest or in the refuse area, which is characterized by fewer agonistic interactions and more hiding opportunities. Exceptions are some unspecialized red wood ant inquilines that are found in highest numbers in the brood chambers. It is noteworthy that some obligate guests (apart from the typical trophobionts) live outside the nest and so are strictly speaking not inquilines. These arthropods live at the periphery of the nest, along the trails or in extranidal refuse pits. One group is harmful to the host and captures living workers (Aleocharinae: *Pella* and *Zyras* living with *Lasius fuliginosus*), feeds on aphid herds (the ladybirds *Coccinella magnifica* and *Platynaspis luteorubra*), or begs for food (*Amphotis marginata*).

Future Directions

Our knowledge of social insect guests has steadily grown in the last decades. Still, they must be regarded as poorly understood, with a great many fruitful avenues still open for both field and laboratory studies. The following are what I

consider some of the most interesting topics for the coming period:

1. While a great number of guests of social insect guests have been recorded and described, many more remain to be discovered. Their hidden existence ensures that large numbers have been overlooked. They are markedly undersampled in many parts of the world, including Australia and all tropical regions. Many unrecognized new species are undoubtedly also sitting in museum collections. The Carl W. & Marian E. Rettenmeyer Army Ant Guest Collection at the University of Connecticut contains more than 100,000 myrmecophile specimens. It recently became clear that cryptic diversity could be exceptionally high in social insect guests, with very similar-looking species specialized to different hosts. Multidisciplinary approaches integrating large-scale sampling, morphology, and emerging genetic tools could help us to resolve the complicated taxonomy of guest lineages. An improved taxonomy of social insect guests will help us to assess the pervasiveness of inquilinism in different arthropod lineages. It will give us a better understanding of community structuring in social insect-symbiont

networks across different scales, and new patterns in host specificity and host switching will be unraveled.

2. A large part of recent research on guests has focused on their chemical ecology. More specifically, manipulative adaptations to the cuticular chemical profile have been examined in different types of guests. Unfortunately, research on the glandular secretions of guests has been losing momentum. The difficult identification and isolation of glandular compounds requires expertise in advanced organic chemistry, which clearly discourages many biologists. Given the plethora of glands found in many guests, it can be expected that they play a pivotal role in appeasing, deceiving, and/or deterring the host. Guests probably require both cuticular and glandular secretions to exploit the benefits of the colony to the fullest. It would be very useful to compare glandular and cuticular compositions along a gradient of guest specialization while using glandular and cuticular composition of free-living relatives as a reference, for example, in the rove beetle subfamilies Aleocharinae or Pselaphinae. Integrating phylogeny into the study of chemical deception could help us to better understand the evolution of inquilinism. Next to the chemical deception strategies, we have little or no knowledge of the chemical cues that attract guests. It is intriguing how they can locate their host nest from a distance. Some guests are generalists with little or no host specificity, yet even these seem always to be confined to one of the four social insect groups.
3. Ecological research on social insect guests is rather scant and limited to a few local field studies. The unique spatial distribution of inquiline communities makes them very good models for small-scale studies of spatial ecology. Inquiline communities can be conceptualized as metacommunities, because the symbionts live in spatially distinct nests (patches) susceptible to colonization from other local communities and surrounded by an inhospitable landscape. Therefore, inquiline communities are among the few true terrestrial

metacommunities. Surprisingly, the mechanisms that inquilines use to disperse from one nest to another and the rate of dispersal are poorly known. It can be expected that symbionts use different strategies to persist in the metacommunity. This variation may have a profound effect on the structure and stability of the local host-inquiline networks. Field observations and experiments in concert with new molecular tools using next generation sequencing (NGS) will enable us to disclose the dynamics of these spatial networks. Next, large-scale studies focusing on patterns and processes that shape inquiline communities are completely lacking. A macroecology approach could, for example, help us to understand how host distribution patterns vary across different groups of symbionts (termitophiles vs myrmecophiles/parasites vs. mutualists). We could also gain insight into how abiotic nest conditions and features of the host affect the assembly of inquiline communities. At present there are only some vague indications that host colony size and the presence of organic nest material (cf. red wood ants, *Lasius fuliginosus*) may positively affect guest diversity. Recently it was argued that social insect guest communities are ideally suited to approach with an ecological network framework [3]. Historically, the interaction between a host and a guest was studied in separation from other interactions. However, different guests often interact directly (predation, competition) or indirectly with other guests and may target multiple host species. A community-wide approach can integrate these multispecies interactions and reveal new ecological and evolutionary patterns for comparison with other ecological networks.

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