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3. Predation by ants on arthropods and other animals

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Abstract. Ants are the most widely distributed and most numerically abundant group of social insects. First, they were ground- or litter-dwelling predators or scavengers, and certain taxa evolved to adopt an arboreal way of life. Most ant species are generalist feeders, and only some ground-nesting and ground-foraging species are strictly predators. Ants are central-place foragers (with the exception of army ants during the nomadic phase) that may use different foraging strategies. Solitary hunting is the most common method employed by predatory ants. Cooperative hunting, considered more evolved than solitary hunting, is used by army ants and other ants such as *Myrmecaria opaciventris*, *Paratrechina longicornis* or the dominant arboreal *Oecophylla*. Army ants are predators with different levels of specialization, some of which focus on a particular genus or species, as is the case for *Nomamyrmex esenbeckii* which organizes subterranean raids on the very large colonies of the leaf-cutting species *Atta colombica* or *A. cephalotes*. Arboreal ants have evolved predatory behaviors adapted to the tree foliage, where prey are unpredictable and able to escape by flying away, jumping or

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dropping. The weaver ant, *Oecophylla longinoda*, for example, hunts prey diurnally in groups. They detect prey visually from a relatively long distance and the workers adhere to the plant substrate by means of very powerful adhesive pads and claws. On some occasions, during prey retrieval, the prey can be stolen by other ants; food-robbing is more frequent in ground-dwelling than in arboreal species. Many predatory ants are engaged in a kind of arms race: they have evolved morpho-physiological adaptations to foil prey defense or escape mechanisms. Mandible shapes have changed and powerful venoms have been developed by different species. Depending on their prey specialization ants can have many different mandible shapes: trap-jaw mandibles, nutcracker mandibles adapted to hunting long prey, pitch-fork mandibles, falciform mandibles and long mandibles. Other ant species are specialized in hunting a certain prey type, but do not have a mandible shape particular to that specialization; these species are egg predators, collembolan predators, or social insect predators. Some ant species are either specialized or occasional termite predators. All of these ants play a role in the equilibrium of ground- and litter-dwelling detritivorous arthropods and the herbivorous insects living in these strata.

Introduction

Ants, which represent the family Formicidae, have a stinging apparatus and so belong to the aculeate suborder within the insect order Hymenoptera (some evolved taxa later lost the ability to sting). The oldest ant fossils date from ≈ 100 mya, meaning that ancestral ants most likely appeared during the early Cretaceous Period (144-65 mya) [1].

Ants were firstly ground- or litter-dwelling predators or scavengers, which are plesiomorphic traits. Furthermore, the first ants may have behaved much like today's army ants, based on what we know from molecular phylogenies that show that the subfamily Leptanillinae is a sister group to all other extant ants [1,2]. Initially, most ant species had spherical or ovoid heads and short mandibles with small numbers of teeth [3]. As ants evolved, worker morphology changed in two main ways: (1) their heads changed shape and their mandibles became more elongated as they became specialized in predation; and (2) their claws became well-developed and their tarsi acquired adhesive pads, thus permitting them to adopt an arboreal way of life [3,4]. Both of these changes occurred in certain taxa.

Indeed, the arrival of angiosperms created more complex habitats on the ground and in the leaf-litter when compared to the gymnosperms that had previously dominated the flora. In addition, some angiosperm species provided ants with food in the form of extrafloral nectar, food bodies and the elaiosome on their seeds. Consequently, ant diversification closely tracked the rise of angiosperms and the ecological dominance of ants was notable by the mid-Eocene (50 mya) with nearly all extant subfamilies and most genera

already in place, suggesting an explosive radiation just prior to this period [1,3]. Moreover, as the angiosperms proliferated, the “higher” termites (which comprise 84% of the species) and major herbivorous insects became more diverse, and so there was an increase in the abundance and diversity of potential prey. Hemipterans also became more diverse and numerous taxa developed mutualistic relationships with ants [3,5-6].

The family Formicidae is extremely diverse with 12,651 known ant species [7], and an estimated 3,000 to 9,000 additional species as yet unknown to science. The phylogeny of the family is clearly separated into three clades divided into 19 subfamilies [1]. Ten subfamilies are almost entirely composed of ground-dwelling predatory or scavenging ant species. Although many Myrmicinae, Formicinae and Dolichoderinae species are ground-nesting, their workers forage mostly on plants to gather exudates or attend Hemipterans, the same being true for some less diverse subfamilies such as the Paraponerinae, Myrmeciinae, Heteroponerinae, Ectatomminae and Pseudomyrmecinae [1,8]. Finally, the very abundant group of canopy-dwelling ants, here also mostly Myrmicinae, Formicinae and Dolichoderinae species, represent a large proportion of the overall animal biomass in this habitat where the irregular availability of prey means that they are omnivorous [9].

Foraging

Ants as ecosystem engineers ... and ground-dwelling predators

Ecosystem engineers are defined as “organisms that directly or indirectly affect the availability of resources for other organisms through modifications of the physical environment” [10]. Among soil dwellers, earthworms, termites and ants have been identified as the main soil engineers [11-12]. Food storage and the accumulation of feces, corpses and food remains by ants have been shown to rapidly and extensively change the soil conditions within the nest area [13] by affecting: soil texture [12]; chemical composition (i.e., C, P, N and K content) [11, 12,14,15]; and microbial and microfaunal communities [16]. As a result, ants create biogenic structures (e.g., nest, galleries and waste chambers) that influence decomposition dynamics at scales of time and space that exceed their life-span [17].

However, most soil-dwelling ant species are predators (or scavengers; see Box 1) that prey on invertebrates or arthropods participating in the cycle of litter and wood degradation: earthworms, acarids, isopods, different kinds of myriapods (e.g., iulids, chilopods, polyxenids), collembolans, termites, other ants, and “other insects” (e.g., beetles, bark lice, lepidopterans).

Box 1. WANTED...dead or alive? Scavengers or predators? A methodological commentary

In Webster's Online Dictionary (<http://www.websters-online-dictionary.org>) *predation* is defined as “the act of preying by a predator who kills and eats the prey”; and *scavenger* as “any animal that feeds on refuse and other decaying organic matter”. It seems easy to distinguish between predatory ants, which collect (and kill) live prey, and scavenger ants which collect dead items. But a problem arises because most ant species are omnivorous and generalist, meaning that, even if they are predators, they can also collect arthropod corpses and very frequently scavengers may act as predators when prey are small (e.g., arthropod eggs [21] and/or with very reduced or no mobility (e.g., pupae, small Hemiptera or injured arthropods).

In his monograph about fire ants [22], Walter Tschinkel wrote, "In fire ants, the largest portion of their animal-matter diet is insects. How important is predation, as opposed to scavenging? Again, the answer is probably a matter of opportunity. Fire ants are clearly effective predators, often suppressing prey populations, and therefore control agricultural pests. Fire ants are truly omnivorous, feeding on fluids derived from plants or animals, acting as both predators and scavengers and at times even primary consumers."

When Robert Jeanne studied the rate of ant predation along a latitudinal gradient [23], his method was to assess predation on the brood of social wasps (by using wasp larvae baits). Predation was more rapid in tropical than in temperate sites, in fields (open habitats) than in forests, and on the ground than on vegetation and these differences were much more pronounced in the temperate zone than in the tropics. Because the wasp larvae were alive, it was a study on predation (excellent, beyond all doubt), but the question is how many of the species that fed on these wasp larvae were truly predators and how many were mostly scavengers?

It might be relevant to the results of Jeanne's study if ants are scavengers or predators, but, in many other cases, it can be very important, especially when considering the role of ants in the ecosystem (e.g., nutrient cycling). Predacious species are secondary consumers; whereas, scavengers, like many detritivorous micro-arthropods, are decomposers.

Trophic relationships are fundamental to understanding the structure and function of terrestrial ecosystems. The data in most studies on ant diet are gathered in the field by collecting the prey that workers transport to the nest. However, fresh prey may come from predation or from scavenging. Very recent studies on food webs use stable isotopic analysis (N isotopic values) to assess the main type of food sources for each species [9,24]. But without direct observations, it is impossible to disentangle scavenging/predation categories because the isotopic values are the same whether the insect has been collected dead or alive.

The study of PCR-based techniques (i.e., DNA gut-content analysis) are highly efficient and sensitive, both in fresh and carrion prey detection [25]. One approach to disentangling active predation from scavenging might be to use isoenzyme electrophoresis, as this method relies on active prey enzymes which may become altered after death [25].

Ants may act as ecosystem engineers, but they can have a negative effect on other soil engineers (see sections below): the ponerine African ant *Psalidomyrmex procerus* is a specialist predator of earthworms that may have an intense impact on its prey populations [18]. The African army ant *Dorylus molestus* preys mainly on earthworms. After swarm raids, there is an immediate decrease in earthworm numbers (the estimated proportion of earthworm prey biomass extracted by driver ants and swarm-attending birds was about 2%), but 8 days later the number returned to pre-raid levels [19]. On the other hand, earthworms seem to be associated with red wood ants (*Formica aquilonia*) in Finnish forests [20]. The ant nest mound surface (the uppermost 5-cm layer) harbors a much more abundant earthworm community than the surrounding soil. Earthworms are not preyed upon by the ants because their mucus repels the ants (suggesting a chemical defense against predation) [20].

A bit of optimal foraging theory

Robert MacArthur and Eric Pianka are considered to have presented the first paper on the Optimal Foraging Theory [26] aimed at understanding the determination of diet "breadth" (i.e., the range of food types eaten by an animal) within a given habitat. These authors argued that, in order to obtain food, any predator must expend time and energy, first in searching for its prey and then in handling it (i.e., pursuing, subduing and consuming it). While searching, a predator may encounter a wide variety of food items and have different responses. Generalists collect a large proportion of the prey types they encounter, while specialists continue searching until they encounter the prey of their specifically preferred type [27]. For each foraging strategy, the predator has a "problem" to solve: if it is a specialist, then it will only pursue profitable prey items, but it may expend a great deal of time and energy searching for them; whereas, if it is a generalist, it will spend relatively little time searching, but will pursue both more and less profitable types of prey. An optimal forager must balance the pros and cons so as to maximize its overall rate of energy intake [27]. Although the consequences of individual foraging decisions on fitness are relatively straightforward in most solitary animals, they may be more complicated to disentangle in social animals. Hence, while the errors made by solitary animals have an impact on them alone (in terms of reduced fitness), those by social animals have negative consequences at both the individual and colony levels. To prevent such errors, insect societies have developed efficient, collective mechanisms for reducing the risk of error and conveying information about food sources [28].

Since ants are social insects, the decision to exploit a food source is made at two different levels: at the individual level (when the worker carries the food to the nest and communicates this to nestmates) and at the colony level (when social strategies such as recruitment using chemical trails are employed to collect the food source) (see Box 2). In many species, foragers are able to “measure” food characteristics (e.g., quality, quantity and transportability), deciding whether or not to recruit accordingly [28-31]. The social integration of individual information about food emerges as a colony decision as to whether to initiate or to continue recruitment when the food patch is rich.

Central-place foraging

With regard to animals that carry the food they find to a fixed place (i.e., central-place foragers, as is the case for ants that carry the food to the nest), the Central-Place Foraging Theory (CPFT) explains foraging behavior and food choice [32]. The CPFT predicts that if food size is independent of the costs of manipulating the item, optimal foragers will choose larger items far from the central place. CPFT also predicts that workers will be more selective in their food choice when farther away from the central place. There are four basic assumptions to this model [32]: (1) organisms behave in ways that maximize the net rate of energy gain; (2) all prey types are encountered randomly and, thus, foragers can look for different food types simultaneously; (3) there are no additional time costs in traveling with a food item; and (4) the energy costs for traveling with a load are greater than the energetic costs of traveling without a load.

Some studies on foraging in seed harvester ants have suggested that these organisms routinely violate two CPFT assumptions [see 33]. First, the energetic costs of foraging are minimal and do not appear to have a significant role in seed choice. Second, food size is not independent of time costs. Larger seeds cause an increase in the time required to return to the nest. Workers regularly choose loads that are large in relation to their body size, and this causes a substantial increase in the time required to take an item to the nest. Another unstated assumption of classical CPFT is that all foragers behave independently of one another. In individually-foraging ant species, the net energy gain of individuals may be relatively unaffected by nestmates; but in species where workers cooperate for food retrieval, individual actions are not independent of one another [33].

Most studies about optimal foraging theory and CPFT in ants have focused on seed-harvesting and leaf-cutting ants. It is easier to manipulate or to offer workers a seed or a leaf than a prey (which can escape). There are

very few studies analyzing predation by ants in a CPFT framework. This could be the case for *Pachycondyla tarsata* (formerly *Paltothyreus tarsatus*), a generalist ponerine predator that strongly prefers termites and very large prey such as giant diplopods and crickets to other choices within its diet. Its workers show an adaptive predatory strategy compatible with CPFT: CPFT predicts that single-prey loading is an extension of the optimal diet choice since the greater distance from the central place enhances selectivity, while multiple-prey loading behavior would correspond to optimal patch use. According to the kind of prey discovered, *P. tarsata* workers properly choose one of the two foraging strategies predicted by CPFT. While hunting its favorite large prey, the recruitment of nestmates enhances the efficiency of total predation (single-prey loaders). The strategy for capturing small, aggregated prey (grouped termites) is characterized by the loading of multiple prey at a single time (multiple-prey loaders) through a concentrated search in a restricted area (optimal use of patches) and by an optional recruitment of nestmates from starved colonies [34].

Another study on CPFT focused on the wood ant, *Formica rufa*, but not on its prey choice or predation behavior, but its trail use. Using experimental colonies in the laboratory, it set out to test the CPTF assumption that colony efficiency is expected to be maximized by minimizing the lengths of established trails [35]. Wood ants made clearly adaptive behavioral adjustments in their choices of foraging trail routes and tended to use the shortest route whenever possible. The conclusions of this study contradicted some previous conclusions for harvester ants [36], showing that the theory may be flawed if it cannot be extended to other groups.

Foraging strategies of predatory ants

Foraging, that is the collection of resources from the environment, has two phases: the search for the resource and its recovery. Both phases account for the costs, but only recovery produces a tangible benefit [37]. The foraging strategies of predatory ants (see Fig. 1 for different examples) fall mainly into two categories. Small prey items are captured by either single workers using their mandibles or sting (solitary hunting), or groups of ants foraging cooperatively, forming large raiding groups or swarms, thus enabling them to overwhelm large prey items or other social insects (cooperative hunting) [24].

Solitary hunting is the most common method employed by predatory ants, in some cases coupled with the recruitment of nestmates when necessary in order to transport the prey (see Box 2). The ponerine ants *Gnamptogenys moelleri* and *G. sulcata*, for example, hunt solitarily, but can retrieve both solitarily (small items) and in a group of recruited workers (large

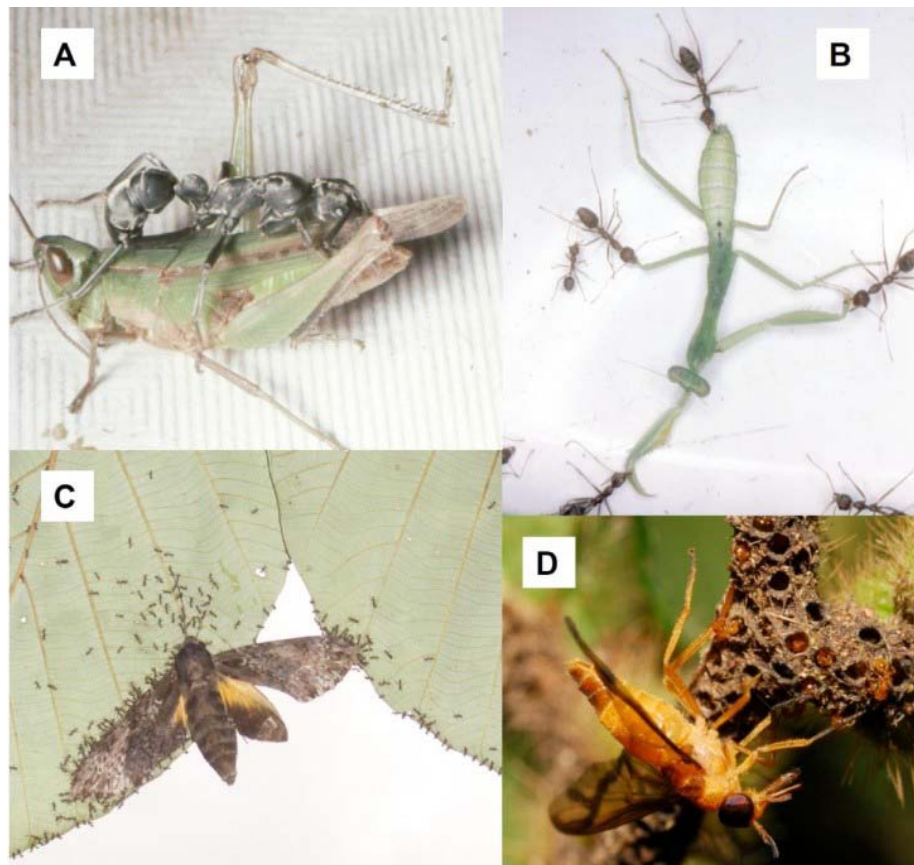


Figure 1. Examples of different ant strategies for preying on arthropods. A. Solitary hunting. A *Platythyrea conradti* worker is capturing a locust by sliding its gaster under the prey's thorax in order to sting it ventrally. This permits the venom to act on the ventral neural chain. B. Group ambushing. *Oecophylla longinoda* workers spread-eagling a praying mantid; they never use their venom during prey capture. C. Coordinated group ambush. With their mandibles wide open, *Azteca andreae* workers ambush side-by-side under the leaf margins of their host tree, the myrmecophyte *Cecropia obtusa*. Insects alighting on the leaves are seized and then spread-eagled. These workers are able to capture comparatively large prey thanks to their hook-shaped claws and the velvet-like structure of the underside of the leaves, both combining to act as a natural Velcro®. D. The use of a trap. *Allomerus decemarticulatus* workers build gallery-shaped traps by manipulating their host-plant trichomes and fungal mycelium that they use to form a composite material pierced with holes. They ambush under the holes, and seize the extremities of insects landing on their trap and pull backward, immobilizing them. Recruited nestmates then use their venom to paralyze these prey. (Photo credits: Alain Dejean).

items) [31,38]. Similarly, foragers of the ant *Formica schaufussi* search for prey individually and recruit nestmates to large arthropod prey and cooperatively transport them to the nest [39].

Cooperative hunting is considered more evolved than solitary hunting because it implies cooperation between workers and results in a greater range

of prey sizes that a species can exploit. Among generalist predatory ants, group hunting is known principally in army ants, which are swarm raiders, and in dominant arboreal ants, such as *Oecophylla*. In both cases, the colonies are very large. For army ants, workers forage in groups during swarming, while for *Oecophylla* they stalk [40]. In both cases, they have developed a system of short-range recruitment that permits numerous workers to overwhelm large prey by spread-eagling them. Army ants generally carve up large prey on the spot, while *Oecophylla* always retrieve large prey whole. *Myrmecaria opaciventris* is an African myrmicine ant with very large, polydomous and polygynous colonies. *M. opaciventris* uses a group hunting strategy enabling the species to overwhelm very large prey items [40]. *Paratrechina longicornis* (Formicinae) workers also participate in a type of group hunting. Each individual forages, surrounded by nestmates behaving in the same way and within range of a recruitment pheromone. They detect prey through contact with successful workers; then, they recruit nestmates at short range and all together they spread-eagle the prey and retrieve them whole [41].

An example of a highly-evolved cooperative strategy is army ant teams [42]. Army ants form groups, with a definite structure, to retrieve large prey. These groups have a distinct caste (worker size) distribution. They typically consist of a large front runner, often a submajor, which is assisted by smaller workers that prevent the prey item from dragging on the substrate [42-43]. The workers are able to assess their own performance and their potential contribution to a group effort, and they act as a superefficient coordinated team for optimizing large food item retrieval [43].

A foraging strategy may be modulated by the workers of the colony. Edward Wilson was one of the first to study in depth how ant colonies modulate foraging according to the food source. In his already classical study, he showed that the fire ant, *Solenopsis saevissima*, organizes worker recruitment through trails as a function of food quality [46]. From an adaptive perspective, the more flexible the foraging behavior, the more readily the colonies may adjust to environmental changes [47]. Deborah Gordon [48] considers behavioral flexibility to be the process by which an animal changes its behavioral patterns when the environment changes. In ants, for example, an individual worker may change from individual retrieving to group-recruitment. According to the weight and size of their prey, *Ectatomma ruidum* workers can employ different recruitment systems (e.g., solitary hunting, cooperative hunting and group hunting with recruitment) [47]. *Pheidole pallidula* ants shape their recruiting behavior simply according to the prey's tractive resistance [29]. Some ant species are able to "measure" food size or patch richness and recruit accordingly: *Formica rufa* scouts that find baits with six larvae recruit more workers and more rapidly than for baits

Box 2. Different prey transport strategies by ants

The transport of a prey is a crucial phase of foraging. Depending on the species and the prey size, different strategies may be employed. These strategies can be summarized as individual or social (recruitment). Social strategies are the different types of recruitment used when the worker is not able to transport the prey individually, and the different communication systems used to recruit nestmates to the food source.

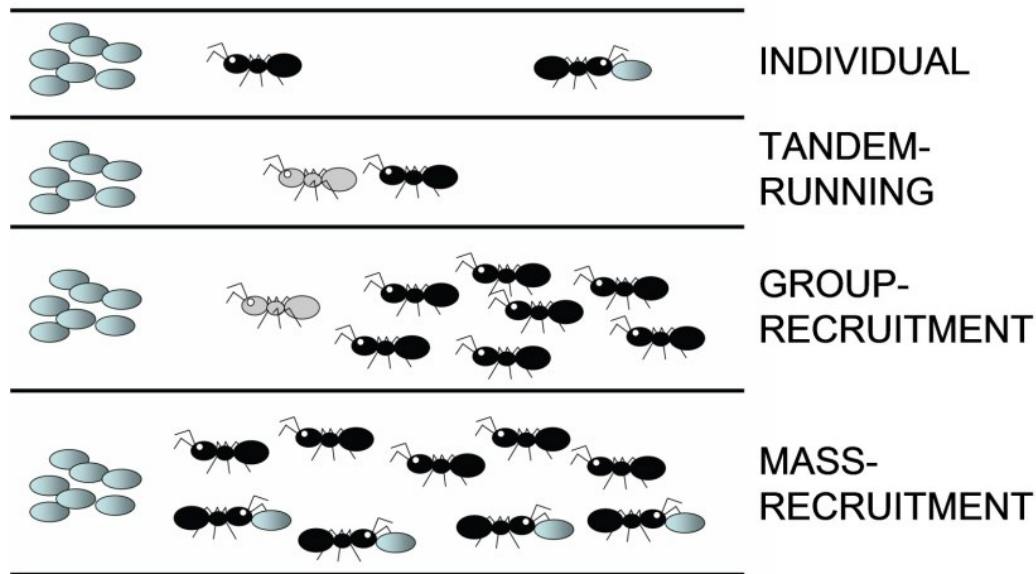


Figure 2. Main strategies employed by ants to collect and transport small prey. (Modified from [44]).

- 1. Individual:** the successful solitary forager collects the food that she is able to transport alone. There is no transmission of information about prey discovery to nestmates.
- 2. Tandem-running:** when the forager comes back to the nest, she recruits a nestmate and leads her from the nest to the food. The recruiter (in grey in the figure) and the recruit (walking behind her) keep in close antennal contact. This is considered the most primitive recruitment system because it only allows the recruitment of one worker, but it is a prey-size-dependent type of recruitment well adapted to small colonies [45].
- 3. Group-recruitment:** the recruiter (in grey in the figure) first lays a temporary chemical trail as she returns to the nest and subsequently leads a small group of recruits along this trail to the source. It is mainly used to collect solid food items by recruiting a few workers.
- 4. Mass-recruitment:** in the most evolved strategy, recruiters returning from a food source to the nest lay a chemical trail that guides their nestmates to the source. While group-recruitment involves a leader, mass-recruitment is "anonymous". Moreover, in mass-recruiting species, chemical signaling prompts the formation of a permanent trail and the recruitment of hundreds of workers that monopolize the source.

During food collection, for all the recruitment systems, the recruit may become the recruiter and activate a positive feed-back process.

(Modified from [28,44]).

with only two larvae [30]. However, the modulation of foraging behavior is not limited to recruiting species. *Decamorium decem* and *Serrastruma lujae* are myrmicine ants that hunt solitarily for collembolans and other small arthropods in the leaf litter of African rainforests. During the dry season, collembolans aggregate in wet patches in the dry litter where numerous single workers hunt from their nest. When foragers reach a wet patch, they use area-concentrated searching: they control the sinuosity and the speed of their food searching paths in order to concentrate their activity on these areas of high prey density [49,50].

Food robbing by ants

Bert Hölldobler [51] proposed that the term "food robbing" include only those cases in which prey or any other food was directly taken away from the body of the forager ants by the robber ants. Food robbing is a widespread form of interference competition by means of which many animals reduce the costs of searching for, handling, and obtaining food [52]. This behavior is relatively common in predacious and scavenger ants, but social wasps also rob food from ants; *Polybioides tabida* (Polistinae; Ropalidiini), for example, rob pieces of large prey from *Tetraponera aethiops* (Pseudomyrmecinae) whose colonies live in the hollow branches of the plant *Barteria fistulosa* [53].

Food robbing has been frequently observed in the North American desert ant *Myrmecocystus mimicus*, which waylays the returning foragers of several *Pogonomyrmex* species at their nests and takes insect prey, particularly termites, away from them [51]. The tropical ponerine *Ectatomma ruidum* also robs food, and it is able to use the foraging trails of other species (e.g., *Pheidole radoszkowskii*) to find the returning workers and remove bits of prey from their mandibles [54]. One very original case involves *Ectatomma tuberculatum* and the myrmicine *Crematogaster limata parabiotica*, both of which are sympatric arboreal ant species that forage on the same pioneer trees. Most of the *E. tuberculatum* workers coming back to the nest carrying a droplet of liquid food (of Hemiptera honeydew) between their mandibles were robbed by *C. l. parabiotica*. This is not solid prey robbing, but rather a case of sugary food robbing [52].

Georges Oster and Edward Wilson [55] inferred from elementary mathematical models that the relationship between prey size and the probability of interference (e.g., food robbing) is somewhat sigmoidal: as prey size increases, so does the probability of interference competition. This prediction has been confirmed through different field studies (see an example in Box 3) with insect prey and baits: ant species that hunt large prey are

subject to higher levels of interference during foraging than species that hunt small prey [56-59].

A recent comparative study about the prey retrieval strategy (fragmentation *vs.* transportation whole) in 44 Asian ant species [59] showed that the workers of most arboreal species cut up large prey at the site of capture, and individual workers retrieved the smaller pieces. In contrast, in ground-dwelling species, the most frequent strategy was for a group of workers to retrieve large prey cooperatively without fragmentation. Moreover, one of the most interesting results was that, on the ground, parts of the large prey item were often robbed by other ant species during transport, while such interference was rare on trees [59].

Box 3. Food robbing in a guild of Mediterranean scavenger ants

In open habitats in temperate or semi-arid ecosystems, predation by ants on arthropods is much rarer than in tropical ecosystems. In these habitats, the ant species that feed on arthropod items are mainly scavengers. This is the case for the thermophilous *Cataglyphis cursor*, *C. rosenhaueri* or *C. velox*, the group-recruiting *Aphaenogaster senilis* or *A. iberica*, and the mass-recruiting *P. pallidula*, *Tapinoma nigerrimum* or *Tetramorium semilaeve* [58,60]. Some of these species composed the guild of scavenger ants in a Mediterranean town (Canet de Mar, Barcelona, Spain) where interspecific interference interactions were studied [58]. Prey of different sizes (i.e., small: fruit flies; medium: cockroaches; large: crickets; and very large: baits) were offered to foragers from each species at different times of the day (i.e., morning, afternoon and night). For most of the species studied, prey loss (through food robbing) varied according to prey size, but dissimilarly so at the different periods of the day (when different ant species were present). Figure 3 shows the percentages of prey loss for medium and large prey for the morning and afternoon periods. First, food robbing is not only interspecific but also intraspecific: in the morning 8% of medium-sized *Cataglyphis cursor* prey and in the afternoon 20% of *Aphaenogaster senilis* were robbed by other workers from the same species. Second, prey size does matter: 38% of the cockroaches offered to *C. cursor* were snatched by *A. senilis* workers and, inversely, 14% of cockroaches offered to *A. senilis* were snatched by *C. cursor* workers; but when the prey offered were larger (i.e., a field cricket), only *A. senilis* was a successful robber, and *C. cursor* lost 56% of its prey. Third, the ecologically dominant species that were the mass-recruiting ants (i.e., *P. pallidula*, *T. nigerrimum* and *T. semilaeve*) were relatively unsuccessful facing the subordinate *A. senilis*; they lost most of the medium-sized prey (between 76 and 94%) and nearly one-third of the large prey (between 20 and 36%). *A. senilis* dissected the prey inefficiently, but transported whole prey to the nest in a single, highly cooperative and very rapid action by several workers. In contrast, dominant species were better able to defend larger prey by recruiting a large number of workers before their competitors were able to intercept and carry them to the nest. There is a trade-off between dominance at food resources and speed of food location and transport.

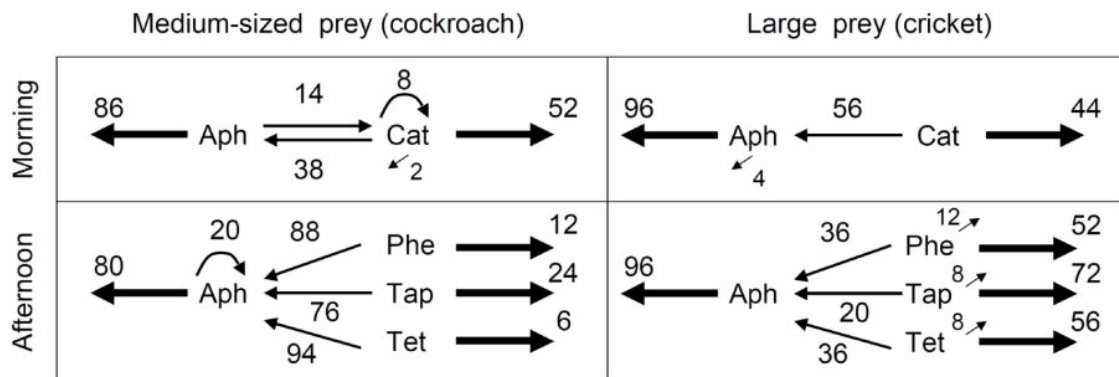


Figure 3. Percentages of thefts of medium (i.e., German cockroaches: *Blattella germanica*) and large (i.e., Mediterranean field crickets: *Gryllus bimaculatus*) items among different scavenger ants in a grassland (Canet de Mar, Barcelona, Spain). The species abbreviations are: Aph, *Aphaenogaster senilis*; Cat, *Cataglyphis cursor*; Phe, *Pheidole pallidula*; Tap, *Tapinoma nigerrimum*; and Tet, *Tetramorium semilaeve*. Thin arrows indicate the direction of prey robbing, including intraspecific robbing; tiny arrows indicate prey robbing by ant species not included in the study; thick arrows indicate the percentages of items carried back to the nest from those offered to each species. Two periods of the day were considered separately: the morning (n=50 items of each prey type) and the afternoon (n=25 items of each prey type). (Modified from [58]).

Army ant behavior

Army ant adaptive syndrome is defined as “a life-history” characterized by group predation, nomadism, permanently wingless queens, and dependent colony founding [61]. Classically, three ant subfamilies are considered “true” army ants: Aenictinae, Ecitoninae, and Dorylinae. However, none of the army ant traits are restricted to these families, as they also occur in distantly-related ant species, including members of the subfamilies Amblyoponinae, Cerapachyinae, Leptanillinae, Leptanilloidinae, Myrmicinae and Ponerinae.

Army ants are characterized by the raids they conduct on large arthropods or social insect prey (see section “Preying on social insects” below; that is, they are ants preying on ants). The adaptive value of nomadism seems clear; by continually moving into fresh hunting grounds, only predatory ants are able to build large colonies [62]. Army ant colonies have a rigid temporal pattern of activity associated with the development of their brood, which, to a large extent, dictates their foraging pattern [37,63] (see Box 4).

The relevance of most army ants to ecosystem functioning remains globally poorly understood [61]. However, in the ecologically best-known army ant species, *Eciton burchelli*, a raid triggers (by preying on other ant

colonies) a process of change, similar to succession, in the ant community and also favors the establishment of prey species colonies: incipient prey species colonies are founded in greater abundance in recently-raided areas [37].

Box 4. Foraging and migration pattern in the army ant *Eciton burchelli*

In a noteworthy study conducted at Barro Colorado Island, Panama, Nigel Franks and Charles Fletcher mapped, on a daily basis, the position of each swarm's principal trail to describe the changes in the spatial pattern and raid systems of *Eciton burchelli* colonies [63]. This species inhabits the tropical American lowland rainforest and its colonies stage the largest army ant raids: a single swarm raid may contain up to 200,000 ants and average 6 m wide [63]. The raid moves as a phalanx of ferocious workers; the swarm front proceeds in a zigzag pattern, so that the overall course of a raid is roughly a straight line [37]. Only one swarm is produced per colony per day and the raiding ants return with their prey to the nest by a principal trail, while others move out to join the swarm [63]. The colonies of this species maintain, throughout their lives, a 35-day cycle of activity (see Fig. 4). Colonies alternate bouts of central-place foraging (statory phase) with periods of nomadism. During the statory phase, the colony uses the same nest site during an average of 20 days, and produces raids like

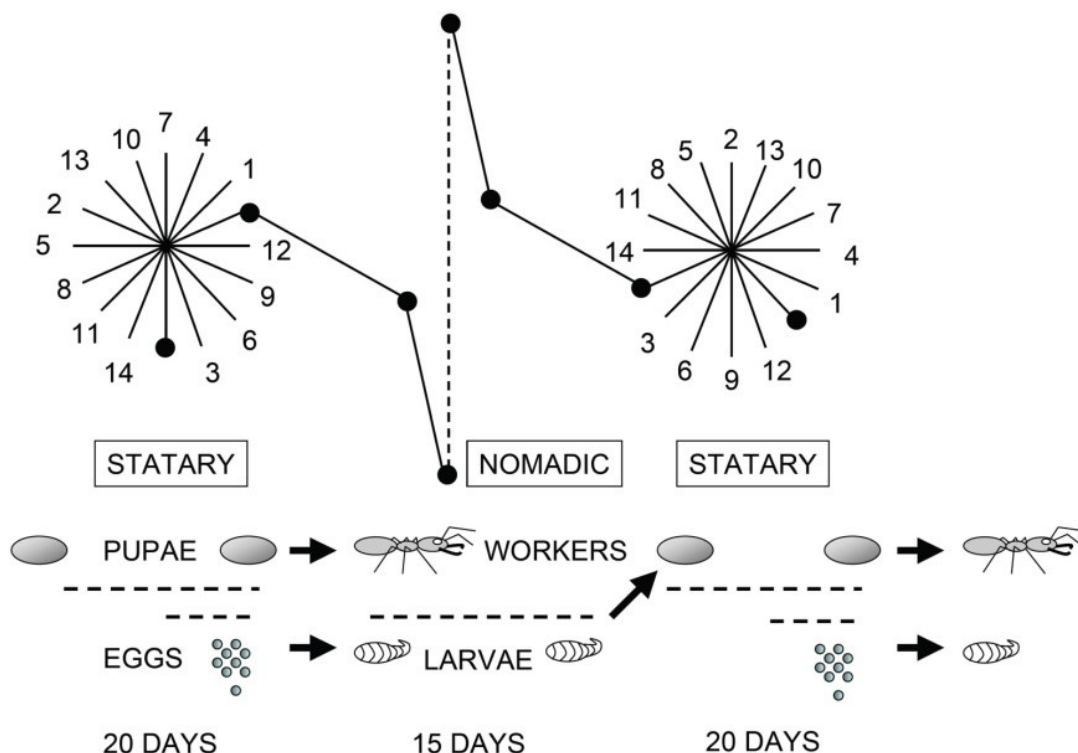


Figure 4. The 35-day behavioral cycle of *Eciton burchelli* in Barro Colorado Island, Panama. The foraging and migration pattern of the brood cycle is diagrammatically represented above. Numbers indicate the raid sequence. See text for further explanation. (Modified from [37] and [64]).

the spokes of a wheel from the hub of the central bivouac. Successive raids are separated on average by 123°. This system maximizes the separation of neighboring foraging paths in time as well as in space, allowing time for their general arthropod prey to recover before the next raid [37].

During the statory phase, the brood is mainly composed of eggs and pupae and workers have only themselves to feed. At the end of this central-place foraging phase, the eggs and pupae hatch into larvae and callow workers, respectively, and the nomadic phase begins. Emigration is constrained and determined by the foraging patterns because it follows the principal trail of the nomadic raid. To feed its voracious larvae, the colony conducts raids every day; after a 15-day nomadic phase, the larvae all pupate and the colony enters another statory phase [37,63].

Generalist predatory species

Generalist predators and biological control

Most ground-dwelling ant species are omnivorous, feeding on nectar or plant exudates, Hemiptera honeydew, and preying (or scavenging, see Box 1) on other arthropods. In a Scottish forest, the total daily colony intake for the wood ant, *Formica rufa*, was composed of 44% honeydew and 66% solid food. [65]. In other British *F. rufa* populations, caterpillars were 3-4 times more abundant on sycamore trees not explored by ants than on those where workers foraged [66]. A large colony of *F. rufa* in Germany has a daily intake of 65,000-100,000 caterpillars (Gosswald 1958 in [67]). This heavy predation of herbivores by wood ants has led to breeding them for biological control purposes [68].

The type of response that predators show towards a prey population can have a marked effect on the population dynamics of the prey. Egg predation by ants can reach 71%, and be an important mortality factor for *Cactoblastis cactorum* in South Africa. Because ants are polyphagous, their population dynamics would probably only be negligibly affected by fluctuations in the density of *C. cactorum* eggs as these would form only a small component of the ants' diet [69]. An interesting case of adaptation to prey availability is that of a North American seed harvester ant, *Pogonomyrmex rugosus*, which forages intensively on the seeds of herbaceous annuals and annual grasses, but exhibits a "pulse" of predation in response to a short-duration episodic event (e.g., the emergence of a large number of prey; in this case, grass cicadas). This pulse of predation demonstrates the importance of protein to seed harvester ant colonies [70].

Predatory ants can significantly affect the behavior of prey and depress the size of potential pest populations (see Box 5) [71]. The published literature has emphasized seven genera of dominant ant species that are either

beneficial or potentially beneficial predatory ants: *Oecophylla*, *Dolichoderus*, *Anoplolepis*, *Wasmannia*, and *Azteca* in the tropics; *Solenopsis* in the tropics and subtropics; and *Formica* in temperate environments (see reviews in [21,72]).

Box 5. Ants as biological-control agents

Victor Rico-Gray and Paulo Oliveira consider that the most important attributes of ants, which make them potentially useful biological control agents, are [71 page 217]:

1. Their diversity and abundance in most tropical and temperate ecosystems, and the fact that most can be considered predators;
2. Their response to changes in the density of prey;
3. Their ability to remain abundant even when prey is scarce because they cannibalize their brood and/or use plant and insect exudates as stable sources of energy;
4. Their ability to store food and hence continue to capture prey even if it is not immediately needed (i.e., predator satiation is not likely to limit the effectiveness of ants);
5. That they can, in addition to killing some pests, deter many others including some too large to be successfully captured; and
6. That they can be managed to enhance their abundance, distribution, and contact with prey.

Defenses against generalist predatory ants

Arthropod prey may develop different defense mechanisms to protect themselves from ant predation. Many lepidopteran larvae have chemical defenses against ants. The accumulation of sulfur amino acids in the caterpillars of the leek moth, *Acrolepiopsis assectella* (a pest moth with different economic host plants: leek, onion, garlic, etc), makes plausible the role of alkyl-cysteine sulfoxides of *Allium* in the protection of *A. assectella* from *Formica* ants [73]. In a wider study [74], Lee Dyer offered 70 species of lepidopteran larvae extracts to the predatory ant *Paraponera clavata* to examine the effectiveness of larval antipredator mechanisms and to test the assumption that diet breadth and chemistry are important predictors of predation responses. He offered caterpillar extracts paired with sugar water controls to the *P. clavata* colonies, and then measured the degrees to which the extracts and the controls were consumed. The extracts were considered unpalatable when the ants consumed more control than extract. Prey with unpalatable extracts were frequently rejected by *P. clavata*, while prey with palatable extracts were rarely rejected. He concluded that plant specialist caterpillars were better protected than generalists.

In the tropics, where the majority of social wasp species dwell and the greatest diversity in nest architecture occurs, predation by ants on the brood is believed to be a major force in nest evolution [75]. The brood of social wasps is particularly vulnerable for several reasons: it occurs in large concentrations, is exposed in open cells, and the nests have a long durability, making the chance of discovery by predators relatively high. Tropical social wasps can be divided into two major groups according to the type of nest and the evolution of the type of defensive behavior used against ants: a single comb of cells suspended from a petiole or nests enclosed by an envelope [75]. Most solitary founding species construct small uncovered nests, where the petiole is built of a tough material of glandular origin and may have ant-repellent properties [75,76]. However, nest protection is not only provided by physical or chemical barriers against ants. They have developed behavioral (e.g., different alarm signals) and ecological mechanisms such as the association with plant-ants. As a result of strong predation pressure from Ecitoninae army ants, the wasp *Parachartergus apicalis* nests mostly on *Acacia* trees occupied by *Pseudomyrmex* colonies. They benefit from the protection provided by the *Pseudomyrmex* that are very aggressive towards *Eciton* [77]. Similarly, other wasp species nest mostly on trees occupied by aggressive dolichoderine ants since this strategy is considered to be the only truly efficacious protection against army ants [78].

Specialized species and predator-prey arms race

To enhance their efficiency by reducing the time and energy necessary to overwhelm their prey, many predatory ants are engaged in a kind of arms race where they have evolved morpho-physiological adaptations to the different potential means of prey defense or escape. Potential prey in this case include animals contributing to the cycle of degradation of the leaf litter and wood fallen to the ground such as earthworms, isopods able to roll into a ball or to escape swiftly, centipedes, millipedes and polyxena among the Myriapoda, collembolans able to jump thanks to their furca, termites and other ants, and even some newly-emerged flies. Note that the phylogenetic distribution of the most specialized predatory ant species is disproportionately concentrated in the morphologically primitive subfamily Ponerinae. Yet oligophagy is a derived character as most genera in this subfamily are polyphagous predators or include both polyphagous and oligophagous species [79].

Like for other insect predators, the success of foraging predatory ants depends on several factors including prey detection (at a distance rather than by contact), effectiveness of prey seizure (i.e., the role of the mandibles) and prey immobilization (i.e., the role of the venom) increasing the speed at

which the prey are mastered. Ants have evolved in different ways in relation to their predatory activity; for example, the shape of their mandibles has changed and they have developed increasingly powerful venoms generally correlated with a specific type of behavior, whereas the group hunting strategies that some ant species use are known to be an evolved trait [79].

Mandible morphology, mechanics and neurophysiology of mandible closure

Trap-jaw mandibles

Three tribes of ants belonging to three different subfamilies – namely, the Odontomachini (Ponerinae), the Dacetini (Myrmicinae), and the Myrmoteratini (Formicinae) - have independently evolved the ability to strike prey extremely rapidly using their hypertrophied mandibles thanks to a so-called “trap-jaw mechanism” [79]. Here, the mandible closure in a fast strike is similar in design to a catapult and results from the release of stored energy that overcomes the constraints of the muscles. It is controlled by a monosynaptic pathway of giant neurons and a trigger muscle specialized in high contraction velocity.

First, by contracting their adductor muscles, which are composed almost entirely of long sarcomeres or slow-contracting fibers, the ants store mechanical energy in their mandibles. Then, a structure, which acts as a kind of “latch” (i.e., the labrum or mandible protrusion, depending on the species), is suddenly released, so that the mandibles close quickly, striking and sometimes locking onto a prey. These structures keep the mandibles blocked open at approximately 180° in *Odontomachus*, *Anochetus* and *Strumigenys*, and up to 280° in *Myrmoteras* [80,81]. The mandibles close through a reflex mechanism that is triggered when the long sensory hairs located on the inner edge of the mandibles or on the labrum make contact with the target. They in turn monosynaptically stimulate giant motor neurons (with axons that have a particularly large diameter and that conduct information very quickly) commanding muscles specialized in high speed contraction that release the latch and thus trigger the strike [82-90]. The 4-10 millisecond latency of the entire reflex corresponds to one of the most rapid movements made by an animal [83,85]. Note that *Myrmoteras toro* does not have sensory hairs, but *M. barbouri* does [80].

After leaving their nest to forage, *Odontomachus* workers open their mandibles, and are ready to react when they encounter a potential prey. Although some *Odontomachus* species can feed on sugary resources such as extrafloral nectar and the honeydew produced by Hemipterans, and even if

they can capture a large variety of small ground-dwelling arthropods, they are mostly termite predators. The mandible strike permits them to numb the termite soldiers during head-on encounters in galleries. *Anochetus* species (Odontomachini) are also mostly specialized in termite predation, while ground-dwelling Dacetini are specialized in the capture of Collembolans, something also noted in *Myrmoteras barbouri* [79,80,91,92].

Nutcracker mandibles adapted to capturing long-shaped prey and the role of snapping

Whereas, among the long-mandibled Ponerinae, the stenophagous *Psalidomyrmex* capture only earthworms, *Plectroctena* are predators of a relatively wide range of arthropods, but need millipedes in their diet for their colonies to be able to produce adult individuals [93, 94].

When they come upon small earthworms (4-cm-long individuals), *Psalidomyrmex procerus* seize and sting the anterior parts of the prey, immediately paralyzing the distal parts and enabling the ants to retrieve the entire prey. Large earthworms, in contrast, are seized by the part with which the ants first come into contact. When this is the anterior part, the workers sting the worm and - because autotomy is rather exceptional - the process is similar to the one described above, and the entire worm is retrieved. In the other cases, the worm undergoes autotomy, and the workers retrieve the part of the worm that they seized [93].

Hunting *Plectroctena minor* workers seize spirostreptid millipedes of up to 4 mm in diameter by their anterior part. The ants' mandibles slip on the exoskeletal coils of the millipede's body and are caught between two segments that are slightly separated by the strong pressure, allowing them to sting the millipede, mostly on the ventral surface in the soft intersegmentary space of the seized zone. The venom acts quickly on the ventral neural chain, immediately paralyzing the distal parts of the millipedes and thus permitting the ants to easily retrieve them. The workers seize larger millipedes by an appendage before stinging them or by wrapping themselves around the prey to form a kind of collar. Once the millipede is paralyzed, they recruit nestmates to help retrieve it. Very large millipedes (95-to-105 mm-long individuals; approximately 8 mm in diameter) can be captured only if encountered in galleries (or test-tubes during experiments). During head-on encounters, the workers grip one of the millipede's antennae or mandibles and sting the very end of its body, triggering rapid paralysis and so singly mastering and then retrieving it. This is the highest body weight ratio between a prey and a predator ever noted for ants that hunt solitarily as these millipedes weigh 94 to 117 times as much as a worker. It is difficult,

however, for the hunting worker to seize the hind part of the millipede, so that it recruits nestmates in most cases; nevertheless, the process of mastering the prey is relatively long [95].

Plectroctena (Ponerinae) [96] and *Mystrium* (Amblyoninae, another subfamily of the Poneromorphs) [97], have mandibles that are able to snap, something that is mostly known in termite soldiers and used in nest defense. The ants snap their mandibles by contracting the adductor muscles while bracing the tips of their long mandibles against one another, storing mechanical energy much as a catapult does. It is supposed that an imbalance in the energy stored in the left and the right mandibles is released when one of the mandible tips pivots, and that the strike is initiated when there is contact with the mechanosensory hairs on the mandibles [89]. Snapping can occur in *Plectroctena minor* during prey capture, especially in the case of termite soldiers that are stunned. Nevertheless, because prey are classically captured through seizure and stinging, this snapping behavior is mostly used for colony defense as intruders are snapped at if they are encountered close to the nest entrance [96].

The pitch-fork shaped mandibles of the genus *Thaumatomyrmex*

Colonies of *Thaumatomyrmex* spp. contain only a few workers equipped with slightly asymmetric, pitch-fork shaped mandibles [98,99]. They are stenophagous, specialized in the capture of Polyxenidae (Diplopoda, Penicillata, Polyxenida) and known to use a very efficacious anti-predator strategy based on the projection of detachable barbed and hooked trichomes [100]. A foraging worker encountering a polyxenid first palpates it with the tip of the antennae, and then seizes and stings it on the intersegmentary membranes, rapidly immobilizing the prey. The worker then seizes its prey at the base of the head, avoiding contact with the prey hairs, and transports it over its own head. Once inside the nest, the successful hunting worker places its paralyzed prey on the ground, and grasps it with its mandibles whose teeth penetrate through the layer of trichomes permitting the workers to get a good grip on the prey's body. Then, they strip the trichomes down to the polyxenid's integument using the short, stout setae on the tarsi of their forelegs. The worker then eats its prey, starting from the head. Sometimes it shares it with a nestmate, or feeds the entire prey or the remains to larvae. Then, using their forelegs, the workers transport the piles of polyxenid trichomes away from the nest [98,99].

Although they are not equipped with pitch-fork shaped mandibles, workers of the Asian ant *Probolomyrmex dammermani* also specifically hunt polyxenids and strip the prey's trichomes inside their nest [101].

The falciform mandibles of *Leptogenys*

Leptogenys workers are armed with long, thin, curved mandibles articulated at the extreme corners of the anterior margin of the head. Most of the species, whether they are African, American, Oriental or Indo-Australian, have small colonies with solitary foragers specialized in the capture of isopods. This stenophagy seems to correspond to a plesiomorphic character as dietetic diversity is associated with species having larger colonies and hunting in a group, two characteristics considered as derived in ants [79, 102-104]. Note that among the species with solitary hunters, *L. benghazi* is specialized in termite predation and *Leptogenys* sp. 13 in earwig predation [105,106].

Oniscoid isopods, protected by a shell and tegumental gland secretions, present three types of behavioral and morphological defenses: “rollers” can roll into a ball, “spiny forms” have long spines that stick out when they roll, and “runners” are capable of rapid escape. Based on the size of their mandibles and the size of the prey, *Leptogenys* workers can seize these prey by their body whether or not they are rolled up (they do not sting the prey) or, alternatively, by the edge of the shell; they then turn the prey over and sting it on the ventral surface. Because this ventral surface is membranous, it is easily penetrated, and the venom quickly reaches the ventral neural chain, facilitating paralysis. Species with long mandibles can easily seize their prey by the body, while large prey are more often seized by the edge of the shell [104].

Spiny isopods are easily captured as the workers can seize them by the edge of the shell, negating in this way the defensive role of the spines. Runners that generally escape swiftly from antennal contact are seized by the edge of the shell. After they have successfully escaped once, many prey are finally captured thanks to the so-called “reserve behavior” of the ants whereby excited workers find them a second time, seize them by the edge of the shell and sting their ventral surface. Bathytropid isopods are attracted to the nest of *L. mexicana* colonies. They enter the nests where they move slowly or remain immobile for a long time if not detected by the workers, and so they go “into the mouth” of their predator [104].

Among species with larger colonies, two types of group hunting have been noted. “*Megaponera*-like” foraging takes place when a scout, having successfully discovered a group of prey, lays a recruitment trail while returning to the nest; this trail is then followed by a group of nestmates [107,108]. Army ant-like mass foraging behavior is known in the Asian species *Leptogenys distinguenda* that has very large colonies (several thousands) [109,110].

Long mandibles, detection by sight and jumping

Workers of the Indian ponerine species *Harpegnathos saltator* have long mandibles equipped with trigger hairs on their inner surface. When the mandibles are open, the contact of these hairs with the prey body triggers a strike. Workers hunt by sight thanks to their compound eyes with ca. 1,600 ommatidies permitting binocular vision centered on the mandibles. This makes it possible to detect prey at relatively long distances, something that is helped by an adaptive behavior enabling them to jump. Indeed, by using both their median and hind legs, workers can jump and hence capture prey escaping by running or even flying away, such as cockroaches or dipterans. Even 10% of the prey located approximately 10 cm from the workers are captured, and the rate of successful capture attempts reaches 80% for prey detected at 3-4 cm. Furthermore, workers use their jumping ability to escape from their own enemies. In this case, they can jump distances of up to 20 cm [111,112].

Specialized predatory ants with behavior not automatically related to mandible shape

The evolution of prey specialization globally followed the diversification of ant subfamilies during the geological ages. Indeed, specialization has mostly concerned ground-dwelling species, with poneromorphs being the most represented and some Myrmicinae and dorylomorph subfamilies also concerned. The Formicinae are represented by the genus *Myrmoteras* (preying mostly on collembolans), while the Dolichoderinae are not represented [79].

Egg predators

Although they are generalist predators, several ant species can opportunistically gather arthropod eggs, but the African Ponerinae *Plectroctena lygaria*, Proceratiinae of the genera *Discothyrea* and *Proceratium* as well as the Myrmicinae *Erebomyrma* and *Stegomyrmex* can be specialized in preying on arthropod eggs [79,113,114].

Several species, such as *Plectroctena lygaria*, are specialized in gathering myriapod eggs and in storing millipede eggs in their nest chambers [115], while *Stegomyrmex vizottoi* workers are specialized in gathering diplopod eggs that they retrieve by holding them between the ventral surface of the opened, curved mandibles and the hairy anteroventral region of the head [114]. *Proceratium silaceum* tuck the slippery eggs between their opened mandibles and their downward-pointing gastral tip during transport [79].

The African species *Discothyrea oculata* is specialized in spider egg predation. Both founding queens and workers are able to open spider oothecas and even manipulate the crimped silk that protects them so as to line and obstruct cavities where the colonies settle thanks to forelegs that are equipped with parallel claws and a comb-shaped tibial spur opposite a brushlike zone on the first article of the tarsi. Furthermore, both founding queens and adult colonies can settle in the oothecas where they find both shelter and food. Yet, hunting workers can also forage for new oothecas that they open easily with their forelegs. Spiderlings emerging from eggs are stung and eaten [93,116].

Collembolan predators

The tribe Dacetini is composed, among others, of two genera, *Strumigenys* and *Pyramica*, whose representatives live in the leaf litter of subtropical or tropical countries. Although some Asian species prey mostly on soft-bodied ground- and litter-dwelling arthropods [117,118], most *Strumigenys* and *Pyramica* species are specialized in collembolan predation [92,117, 119-125]. Yet, when the colony is starved, hunting workers have a tendency to capture alternative prey [126].

Typically, hunting *Strumigenys* workers forage in a slow, erratic movement. When detecting a prey at a very short distance (a few mm), they stop, open their long mandibles to approximately 180°, exposing the pair of trigger hairs that rise up from the labral lobes and extend forward from the ant's head. Special teeth at the base of the mandibles catch on the lateral lobes of the labrum while the adductor muscles tense. Then, the workers approach the prey very cautiously and when the two trigger hairs touch the prey's body, the labrum drops, triggering a violent strike. The prey's body is generally impaled on the mandible's apical teeth. Stinging is not always necessary, but struggling prey are lifted and stung into paralysis [92,117,119].

Among the species now regrouped under the genus *Pyramica*, one can distinguish medium- from short-mandibled species. The mandibles only open to 90° maximum and the prey is seized by an appendage or, for *Pyramica benten*, even at the outer circumference of the cephalic cavity from which the mouthparts protrude, so that stinging is necessary [117-120]. Species with very short mandibles have a tendency to halt when perceiving the presence of a prey, or even ambush it. In both cases, they have a "pointing phase" where they crouch by lowering their head against the substratum, fold their antennae into their scrobe while they open their mandibles between which are the trigger hairs that protrude from the labrum. These workers approach the

detected prey very slowly, placing their mandibles on both sides of a prey appendage; seizure occurs when a prey movement makes its appendage come into contact with the trigger hairs [119,123]. Prey seizure for both medium- and short-mandibled species is followed by the struggling of the prey which is stung on the seized appendage.

Other examples include the ability of short-mandibled Asian species to camouflage themselves by smearing their bodies with organic material that they gather from the ground with their mandibles. The workers then use their forelegs to scrape the dorsum of their head and thorax with this material [118]. In African species of the former order *Smithistruma*, the workers attract collembolans. The source of the attractant, unknown, could be the spongiform appendages of the petiole or secretions from the labrum [122].

Several studies have illustrated the fact that the predatory behavior of these ants is not stereotypical. Prey anaesthetized with carbon dioxide are not stung if encountered far from the nest, but are stung if found next to the nest entrance, illustrating the influence of territoriality. They are also stung if the colony was previously starved. If, during a capture attempt, the prey successfully escapes, the worker uses the “reserve behavior” consisting of an intensive searching process where both the sinuosity of its trajectory and its speed increase, facilitating the retrieval of the prey. If the prey (or another insect) is encountered, it is immediately attacked, seized and stung [92,123,126-129]. This reserve behavior has also been found in all ground-hunting ant species studied so far [47,50,81,130,131].

Colonies of short-mandibled species that are bred in the laboratory are fed with alternative prey (Psocidae) that escape when the workers are in their pointing phase. The workers only capture these prey using the reserve behavior once the colony begins to starve. Then, as the colony ages, the workers starting to hunt for the first time will only encounter Psocidae that they attack directly, so without going through a pointing phase. Several months later when confronted with collembolans, their principal prey, these workers never go through the pointing phase. Thus, pointing is acquired only if the workers passing from the internal to the external service of the colony encounter collembolans as they begin to hunt. Otherwise, they act as generalist predators, which enables them to capture alternative prey when the dry season arrives and collembolans are more and more rarely found in the leaf litter [129].

Myriapod predators

We have already seen how, by using their pitch-forked mandibles, *Thaumatomyrmex* capture and strip polyxenids of their protective hairs.

Moreover, *Plectroctena* workers, thanks to their nutcracker mandibles, are specialized in the capture of millipedes; encounters in restricted environments such as galleries permit them to capture large items. This notion was illustrated again in a study on the dacetine ant species *Pyramica hexamerus* which is, on the other hand, a centipede predator. The workers hunt in galleries or crevices, crouching and remaining immobile when encountering a centipede. When the centipede steps on its lowered head, the worker attacks from below, and, in an upward strike of its mandibles, impales the prey trunk on its long, apical teeth [117].

Leptanilla (Leptanillinae) and *Amblyopone* (Amblyoponae) are predators that mostly capture centipedes [132]. *Amblyopone* are equipped with long mandibles placed at the extreme corners of the frontal part of the cephalic capsule, which allows them to seize the bodies of prey with a relatively large diameter. Like for trap-jaw mandibled species, two trigger hairs emerge from the clypeus, enabling the workers to adjust the degree of mandible closure [132]. Workers detect these prey from a distance and approach them cautiously so as to place themselves over the prey body and seize it. They then bend their gaster, whose extremity comes under the prey body, and sting the ventral surface where the neural chain passes. Because paralysis is not immediate, the workers move forwards along the prey body, their mandibles slightly opened and placed on both sides of the prey body, ready to seize it if necessary. Upon reaching the anterior part of the prey body, the workers bite it and sting it again. They then lick the paralyzed prey before dragging it to the nest [132,133]. In *Amblyopone* and *Myopopone*, larvae can be transported to the prey rather than the reverse [79].

Preying on social insects

Attacking a social insect colony: Importance of the Lanchester theory of combat

Unlike cases of lestoprosocial species whose colonies live in the ant hills or termitaries of their host, predatory ants must penetrate the colonies of social insects to prey on them or on their brood, while vulnerable species have developed several means of defense (e.g., walls for termitaries, the presence of soldiers or major workers blocking the nest entrances, chemical defenses).

The Lanchester theory of combat was proposed as a theoretical framework to explain combat between ants [134]. The Linear Law predicts that fighting ability contributes more towards victory than the number of combatants when a restricted combat area forces individuals to engage in a series of duels. Here, the presence of termite or ant soldiers blocking the

entrance to a gallery leading to their nest is very important, particularly for termite soldiers that generally have a large, sclerotized cephalic capsule, powerful mandibles that can snap in certain species, and defensive anti-ant chemicals produced by their frontal gland. On the other hand, the Square Law predicts that when combatants can mix freely, numerical superiority is the deciding factor.

Lestobiosis including termitolesty

The colonies of some ant species with small workers take shelter in the walls of the large nests of other ants or termites. They enter the host nest chambers to steal food, or to prey on the host eggs and/or larvae. There are no confrontations between individuals, or they are much reduced. The relationship is therefore both “parasitic” with respect to nest sharing and “predatory” with respect to the brood thief [79].

Colonies of *Solenopsis* of the subgenus *Diplorhoptrum* (Europe and North America) generally nest next to larger ant species; the workers enter the other ant species’ nests where they prey on the brood. *Diplorhoptrum fugax* workers produce repellent chemicals (trans-2-butyl-5-heptylpyrolidin) permitting them to avoid attack by workers of the host colony. Species of *Carebara*, *Caberella*, *Diplorhoptrum* and *Eberomyrma* nest in the vicinity of termite mounds if not in their walls. They enter the termitary galleries and pouches where they steal termite eggs [79,135]. Workers of the ponerine ant *Hypoponera eduardi*, whose colonies develop inside societies of *Reticulitermes* (lower termites), have a kind of chemical camouflage through similarities between their cuticular hydrocarbons and those of the termite host [136]. Workers of the termitolestic species *Tetramorium termitobium* do not trigger an alarm among different higher termite species of the subfamily Macrotermitinae thanks to secretions of the mandibular gland [137].

In the African Ponerinae *Centromyrmex bequaerti*, entire colonies settle in the chambers and galleries of the termitaries of diverse Termitinae and Macrotermitinae species instead of in the walls. In this species, several evolved traits have been noted, such as: a strong dimorphism between the queens (large) and workers, something relatively rare in the Ponerinae where queens and workers are generally of a similar size; oligogyny (multiple queens, but mutually isolated by living in different chambers of the termitary); a polymorphic worker caste, as the workers are blind (a trait related to living in the termitaries); and relatively large colonies. Although all kinds of workers can hunt, this task is mostly limited to media individuals while, on the other hand, majors act as guards, blocking the entrances of the chambers where the colony is established [138].

Moreover, *Plectroctena* workers, thanks to their nutcracker mandibles, are *Nasutitermes* spp., so that hunting workers are at least partially cryptic to their prey. They attack termite soldiers head-on, and the mandible strike numbs them in more than 60% of the cases. They sting non-numbed soldiers on the thorax, while termite workers, approached from behind, are seized and stung on the abdomen. *Anochetus* workers are therefore able to distinguish termite soldiers from workers and to adapt their capture behavior to the situation [139].

“Lower” termites (i.e., the Termopsidae, Kalotermitidae, *Prorhinotermes* in the Rhinotermitidae), are one-piece nesting or wood dwellers since they inhabit and spend their entire life cycle in pieces of wood that also serve as feeding sites. Their nesting habits indirectly protect the colonies; soldiers exist and have likely evolved to defend the colonies from other termites [140]. In “higher” termites (i.e., the Serritermitidae and Termitidae) and most Rhinotermitidae, individuals must forage outside the nest and so are exposed to ant predation. Their defensive strategy consists of their termitary structure with thick walls and chambers connected by easily-defended galleries, foraging in subterranean or covered galleries leading to food sources and investment in soldiers [140].

Occasional termite predators

The workers of many non-specialized ant species occasionally prey on foraging termites or on termite individuals exposed after their termitaries are broken open by a vertebrate or a falling tree. Consequently, to locate ant nest entrances in the tropical rainforest, researchers scatter portions of termitaries on the ground and track the ants that retrieve the termites [79]. In this case, the foraging strategy is very similar to hunting other kinds of insects, save for the fact that finding an individual termite is generally correlated to the presence of nestmates in the vicinity, resulting in concentrated searching (increased sinuosity and decreased speed) after discovering a first termite or detecting only termite tracks (acting here as kairomones), the successive capture of several individuals if the ant mandibles are long enough, and the rapid recruitment of nestmates [50,79,141,142].

Workers of the short-mandibled basicerotine ant *Eurhopalothrix heliscata* ambush solitarily in rotting wood where termites forage. They seize termite prey by an appendage and sting them [143] in a manner very similar to that described for short-mandibled Dacetini with regard to collembolans.

The defensive mechanisms of termites are generally efficacious enough against most army ants, with only subterranean African doryline ants being specialized in termite predation [64]. Nevertheless, there is the exceptional

case of the epigaeic species *Dorylus rubellus*, which successfully attacks fungus-growing termites of the genus *Macrotermes* [144].

Specialized termite predators

The elimination of termite soldiers in order to gain access to workers or brood is therefore a challenge that specialized ant predators have to surmount. Chemical crypsis has been noted in several specialized termite predators including *Crematogaster* sp.C, and *Decamorium uelense*. Like in the termitolestic species *Tetramorium termitobium*, the mandibular glands of these species produce non-repellent aliphatic alcohols, whereas unspecialized congeneric species produce repellent ketones and aldehydes [137,145].

The elimination of soldiers of the fungus-growing termite *Macrotermes bellicosus* by workers of the African ponerine ant *Pachycondyla analis* was observed in laboratory conditions by using large pieces of termitaries whose galleries, connected to chambers, were opened laterally to form a narrow window permitting direct observation [146]. These termite soldiers guard gallery entrances through phragmosis (plugging the galleries with their large sclerotized head) aided by powerful mandibles and the secretion of toluquinone by the salivary gland [147]. Detecting these guards from a distance, the ants flexed their gasters under their thoraces and heads, extending their stingers towards the counter-attacking soldiers. The latter closed their mandibles, which then slipped on the tip of the ant's fusiform, sclerotized gaster, and then remain closed due to the tetany of the adductor muscles. This behavior is effective as regards non-specialized enemies which are then killed by the chemical defenses, and, furthermore, participate in plugging the galleries. The *Pachycondyla analis* workers then, stingers extruded, deposited venom on the mouthparts of the now inoffensive termite soldiers due to the fact that their mandibles were locked in a closed position. The venom seemed to have an immediate topical effect, probably owing to the numerous, thin intersegmental membranes located there. The ants then pulled the termite soldier backward to gain access to the termite workers [146]. According to the Linear Law of the Lanchester theory of combat, minor *Pachycondyla analis* workers have developed a specific behavior that grants them easy victory during combat in galleries.

Pachycondyla analis (previously *Megaponera foetens*) has a typical foraging behavior now reported as 'Megaponera-like behavior' when noted for other ants specialized in termite predation. The scouts are major workers looking for foraging termites or even termitaries at as far as 95 m from their nests. After discovering a group of termites, thanks to the odors emanating from their foraging galleries and serving as kairomones, the scouts return to

their nests while laying a scent trail with their sting partially extruded. They recruit nestmates with 5-12 major workers and approximately 40 minor workers forming a column guided by the recruiting individual following its return path. All of the workers in the outgoing column in turn lay a scent trail while stridulating loudly enough to be audible by humans. When the column reaches the termite foraging area or the termitaries, the major workers break open the galleries. Only the minor individuals enter the galleries, and the attacks last approximately 9 minutes during which time the minor workers, in a series of exits and entrances, create piles of paralyzed termites around the gallery entrances. At the end of the raid, the major workers gather up to 10 termites that they pack between their mandibles; the minor workers gather fewer termites or none at all. The major workers, including the recruiting individual, lead the way along the return path that follows the same route as the outbound path [146-150].

Megaponera-like foraging behavior, with some variants, has been noted in other ant species such as the myrmicine ant *Decamorium uelense* that preys mostly on *Microtermes*, *Leptogenys chinensis* on *Odontotermes* or *Hypotermes*, *Pachycondyla commutata* on *Syntermes*, and *Pachycondyla marginata* on *Neocapritermes* [107,151-153].

Ant predators

Melophorus anderseni (Formicinae) prey on the brood of *Iridomyrmex sanguineus* (Dolichoderinae). During encounters with *Melophorus* workers, *Iridomyrmex* foragers cower as they do when faced with large competing ant species (but *Melophorus* are small). This enables the *Melophorus* to rub their bodies against those of the *Iridomyrmex*, and thus to acquire their cuticular hydrocarbons (colony odor). Then, the “made up” *Melophorus* individuals safely enter the *Iridomyrmex* nest where they steal larvae that they retrieve to their own nest [154].

New World army ants, or Ecitoninae, are ant predators with different levels of specialization. Some of them are even specialized in a particular genus or species [64,155,156]. When army ants begin to enter a nest, they release an allomone that triggers panic among the assaulted workers that then leave their nests, some of them carrying brood, so that fighting is avoided in most cases. The army ant workers then capture nearly all of the brood, callow workers and winged sexuals of the attacked colonies. Yet, they do not attack other workers or the queen(s), so that the attacked colony can reconstitute itself in most cases, particularly when the colonies have polydomous nests [64,155-159].

Nomamyrmex esenbeckii colonies organize subterranean raids on the very large colonies of the leaf-cutting, fungus-growing ants *Atta colombica* or

A. cephalotes. Both the perpetrator and the attacked colonies contain several million individuals. *Nomamyrmex* soldiers always attempt to penetrate the targeted colonies, while the entrance galleries of the *Atta* nests are defended by major workers that are rapidly recruited. The confrontations therefore take place in a restricted area where the ability of the fighters is primordial in a series of duels, according to the Linear Law of the Lanchester theory of combat [134]. While major *Atta* workers defend their nest entrances using their large mandibles and are helped by minor workers that attack vulnerable parts of the *Nomamyrmex* soldiers, the latter also use both their mandibles and their venom. There is, therefore, a complex distribution of tasks in the defensive strategy, so that the success or failure of a raid attempt will depend mostly on the rapidity with which the defense is organized. If *Nomamyrmex* soldiers are successful, all of the other workers will enter the *Atta* nest, so that this time the number of combatants is primordial, corresponding to the Square Law of the Lanchester theory of combat. In fact, two *Nomamyrmex esenbeckii* raids out of three are successful and approximately 60,000 *Atta* larvae are captured, representing one-third to the half of the brood in addition to the hundreds of major workers killed. In extreme cases, the *Atta* colony can die. Therefore, a two-stage strategy, where both the Linear and Square Laws come into play, exists in this case [160].

Territorially-dominant African ant species such as *Oecophylla longinoda* and *Crematogaster* spp. have workers that forage on the ground around the base of their host trees. They even prey on *Dorylus* spp. workers when a column of these army ants passes close to the base of their host tree. These arboreal ants, probably helped by allomones, lower the level of aggressiveness of the *Dorylus* that are preyed upon while surrounded by thousands of nestmates [161-163].

From ground nesting and foraging to relationships with plants

From the ground (or underground) to the trees

Initially, ants formed a group of soil-dwelling predators or scavengers, as still occurs in the vast majority of ant species belonging to "primitive" subfamilies. A second step was to have a nest on the ground and forage on plants. And the acquisition of an arboreal life in ants probably developed secondarily; strictly arboreal species belong to the most "advanced" subfamilies. Species of foliage-dwelling ants include both "true" canopy inhabitants that nest only in plant organs, and species that commonly nest on the ground, but that are also able to form colonies in hanging soil or are

associated with the epiphytes and hemi-epiphytes that abound in the canopy of a tropical forest [71].

Ants numerically dominate the canopy fauna of tropical rainforests where they are considered to be key predators. Studies of foliage-dwelling arthropods have shown that ants may represent 86% of the arthropod biomass and up to 94% of the arthropod individuals living in the rainforest canopy [71]. A conspicuously low abundance of less mobile holometabolous insects (e.g., Lepidoptera larvae) corresponds to this ant dominance. This is in contrast to temperate regions where ants are mostly absent from trees and holometabolous larvae are frequent [164].

Davidson [165] has suggested that the high abundance of liquid food sources (i.e., extrafloral nectaries and honeydew-producing Hemiptera) on foliage plays an important role in shaping the food-web structure of tropical forests by fueling costly prey-hunting activities by foliage-dwelling ants, especially if the ants are physiologically adapted to a low-nitrogen diet.

Arboreal ant species (nesting and foraging on the trees)

Predation on tree foliage and biotic protection of the plants

It is likely that ground-nesting, foliage-foraging species constitute the first line of defense in the plants' biotic protection thanks to their predatory activity. If defoliating insects have frequently developed the means for resisting plants' chemical defenses, they rarely possess successful counter-adaptations against ants, except by escaping through dropping, jumping or flying away [166,167].

Some ant lineages developed tight evolutionary bonds with plants and became arboreal-nesting and foraging. Most arboreal ants have evolved diffuse relationships with plants, the latter inducing different ant species to patrol their foliage by producing energy-rich food rewards such as extrafloral nectaries or food bodies. Furthermore, the relationship can be indirect with ants attending sap-sucking Hemipterans whose role can be similar to that of extrafloral nectaries when the host plant is not affected or only a little [79].

Nonetheless, the relationship between myrmecophytes and ants is necessary to the survival of both partners, with myrmecophytes offering a nesting place (i.e., hollow structures called domatia such as hollow twigs and thorns or leaf pouches) and frequently extrafloral nectar or food bodies to specialized "plant-ants". In return, plant-ants protect the myrmecophytes from a broad range of herbivores plus competitors and fungal pathogens, and/or provide them with nutrients [168,169].

In the exceptional cases when food bodies are protein-rich, hence rendering hunting unnecessary, the ants protect their host-tree foliage from herbivorous insects and mammals only through their territorial aggressiveness. This is, for example, the case of the association between Central American *Acacia* spp. and ants of the genus *Pseudomyrmex*, or *Piper* and *Pheidole* [170,171]. Other plant-ants are predatory, while intermediary cases have been noted in plant-ants that retrieve only a part of the insects that they capture. They discard the other individuals, but can eventually consume part of their haemolymph [172,173].

Predatory behavior in the trees

The canopies of tropical forests and tree crop plantations are occupied by “territorially-dominant” species characterized by (1) extremely populous colonies (several hundred thousand to several million individuals), (2) the ability to build large and/or polydomous nests (carton builders, carpenter ants and weaver ants), and particularly (3) a highly developed intra- as well as inter-specific territoriality that causes their territories to be distributed in a mosaic pattern in the forest canopies [163,174]. These territories are marked with persistent landmarks that can last for over a year and are recognized by other ants that avoid them or adapt their behavior so as to avoid encountering the occupying ants [163,175,176].

Since the availability of prey in tree foliage is unpredictable and most prey are insects able to escape by flying away, jumping or dropping [163], arboreal ants have evolved predatory behaviors adapted to this restricted foraging area by optimizing their ability to capture such insects.

The predatory behavior of the weaver ant, *Oecophylla longinoda*, the first species studied in this context, is well adapted to the fact that prey are likely to escape. Workers hunt diurnally in groups. Prey detected visually from a relatively long distance are seized by an appendage and immobilized by a first worker that then releases a pheromone to attract nestmates. Recruited nestmates, in turn, seize a prey appendage and pull backward, spread-eagling the prey. This behavior, used even for relatively small prey, also permits the ants to capture large insects and even other animals [79,177,178]. Entire prey are retrieved cooperatively, including, in some cases, heavy prey such as small birds [179]. This form of prey capture and retrieval requires the workers to adhere to the substrate by means of very powerful adhesive pads and claws, a characteristic that seems common in arboreal species [180].

Other dominant ants exhibit relatively similar behavior based on the spread-eagling of prey. Detection may occur at a short distance or even by

contact; venom is generally used to subdue the prey prior to cutting it up and transporting it in small pieces. This concerns African Myrmicinae *Atopomyrmex mocquerisii*, *Crematogaster* sp., and *Tetramorium aculeatum* and the Neotropical dolichoderine ant *Azteca chartifex* (the Dolichoderinae do not have a sting) [173,181-183].

Azteca lanuginosa and *A. andreae* workers possess an elaborate hunting technique consisting of ambushing side-by-side under the leaf margins of trees with their mandibles wide open. When an insect lands on their leaf and moves toward the edge, all of the members of the ambushing group attack it simultaneously, rushing onto the upper surface of the leaf to spread-eagle it [184,185].

Plant-ants can capture prey in a similar way as territorially-dominant species by spread-eagling them [173,186], but some plant-ants use a more evolved behavior. *Tetraoponera aethiops* (Pseudomyrmicinae) and *Azteca bequaerti* workers, hidden in their host plant domatia, react to the vibrations transmitted by an alien insect landing on a leaf, making it unnecessary for them to forage for prey [172,173]. Furthermore, plant-ants of the genus *Allomerus* collectively ambush prey by building galleries pierced with numerous holes serving as traps. When a prey lands on the gallery each worker waiting in a hole near the landing site seizes an appendage and pulls backward, moving deeper into the trap. With its appendages caught in the trap's different holes, the prey is immobilized and recruited workers sting it repeatedly [187].

Conclusions

This study has focused on the predatory behavior of ants, mostly on prey capture, taking into account the fact that most ant species are generalist feeders. Only ground-nesting and foraging species are strict predators (certain species are even predators specialized on one prey taxa); among them, some ecitonine species can climb trees to hunt for other ants. All of these ants play a role in the equilibrium of ground- and litter-dwelling detritivorous arthropods and the herbivorous insects living in these strata. Note that, in this general context, human perturbation, through greater agricultural activity, plays an important role in the balance between termites and army ants; for instance, in the Ivory Coast, *Macrotermes* spp. termitaries were massively destroyed by *Dorylus dentifrons* after farmers changed their agricultural methods [188].

Many ground-nesting ant species are also arboreal foraging, exploiting extrafloral nectar, sometimes food bodies, and mostly Hemipteran honeydew, while arboreal-dwelling ants rely primarily on these foods. Because they are

also predators, certain territorially-dominant species have been used as biological control agents [24,163]. Certain arboreal species do not even hunt or scavenge, so that their nitrogen requirement is provided by their host plant – as is the case for *Acacia*-associated *Pseudomyrmex* [169,171] - or through endosymbiont bacteria [189,190].

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