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REVIEW ARTICLE

Foraging by predatory ants: A review

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Abstract In this review, we show that predatory ants have a wide range of foraging behavior, something expected given their phylogenetic distance and the great variation in their colony size, life histories, and nesting habitats as well as prey diversity. Most ants are central-place foragers that detect prey using vision and olfaction. Ground-dwelling species can forage solitarily, the ancestral form, but generally recruit nestmates to retrieve large prey or a group of prey. Typically, ants are omnivorous, but some species are strict predators preying on detritivorous invertebrates or arthropod eggs, while those specialized on termites or other ants often have scouts that localize their target and then trigger a raid. They can use compounds that ease this task, including chemical insignificance, mimicry, and venoms triggering submissive behavior. Army ants include 8 Dorylinae and some species from other subfamilies, all having wingless queens and forming raids. Dorylinae from the Old World migrate irregularly to new nesting sites. The foraging of most New World species that prey on the brood of other ants is regulated by their biological cycle that alternates between a “nomadic phase” when the colony relocates between different places and a “stationary phase” when the colony stays in a bivouac constituting a central place. Among arboreal ants, dominant species forage in groups, detecting prey visually, but can use vibrations, particularly when associated with myrmecophytes. Some species of the genera *Allomerus* and *Azteca* use fungi to build a gallery-shaped trap with small holes under which they hide to ambush prey.

Key words ants; foraging modes; oophagy; prey attraction; termite prey; trap construction

Introduction

Ants, which belong to the family Formicidae, likely appeared during the early Cretaceous (145–110 Mya), are extremely diverse with an extant 16 subfamilies, 343 genera, and 14 380 species representing ≈12 million tons of dry biomass, exceeding that of both wild birds and

mammals. This diversity and abundance is related to their ability to occupy most terrestrial environments from the Equator to subpolar regions and from the soil to the tree crowns of rainforests (Borowiec *et al.*, 2021; Schultheiss *et al.*, 2022; AntWiki, 2024a).

Historically, ants were firstly ground-dwelling predators or scavengers foraging solitarily, with a highly-specialized mandible shape adapted to predation as in the Haidomyrmecines, before numerous cases of cooperative foraging evolved (Reeves & Moreau, 2019; Barden *et al.*, 2020). They diversified alongside the rise of angiosperms that drove the explosive expansion of terrestrial diversity during the “Cretaceous terrestrial revolution” (mid- to

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late Cretaceous: 125–80 Mya), causing the extinction of stem-group Cretaceous ants and the rise of crown group ants (Moreau *et al.*, 2006; Benton *et al.*, 2022; Jouault *et al.*, 2024). Compared to the ground, the three-dimensional structure of forests permits a stratification enabling better ant species coexistence. Yet, arboreal ants are limited to wet and warm tropics with less seasonality compared to their ground-dwelling counterparts (Nelsen *et al.*, 2023).

While foraging for prey on vegetation, some species incorporated sap, resin, gums, mucilage, and oils into their diet, marking the onset of plant protection through their predatory activity that then developed further with plants producing food rewards (*i.e.*, extrafloral nectar and food bodies). Moreover, many ants attend sap-sucking hemipterans – inside or mostly outside their nest – to feed on their sugar-rich honeydew (trophobiosis) that, in natural conditions, do not then proliferate as the ants consume a part of them. Thus, the loss of sap by host plants is counterbalanced by the protection provided by ants from defoliating insects (Davidson *et al.*, 2003; Styrsky & Eubanks, 2007; Nelsen *et al.*, 2018; Pringle, 2021).

Nesting first in the crevices of bark or under epiphytes, arboreal ants began to build carton or silk nests by the late Cretaceous (≈ 66 Mya), while mutualistic relationships with myrmecophytes that shelter ant colonies in cavities appeared later. Note that non-predatory arboreal ants consume protein-rich fungus or are associated with nitrogen-fixing bacteria (Blatrix *et al.*, 2012; Nelsen *et al.*, 2018; Ramalho & Moreau, 2023).

Some ant species are defoliators, cutting up leaves to cultivate fungi to feed on them or that they use to build their nests (Dejean *et al.*, 2023), or are granivorous, certain being rather seed dispersers while others are seed “predators” (Penn & Crist, 2018). However, many species are predators with a generalist diet, able to scavenge and to feed on sugary substances, while others have different degrees of specialization on certain types of prey. In this review that is partly an updated version of Cerdá and Dejean (2011), we present information on foraging by predatory ants divided into three main cases: (1) Ground-dwelling species that can forage actively or ambush, certain species even attracting their prey; they can forage alone or are able to recruit nestmates. (2) Among them, species grouped in the “army ant syndrome” that forage in groups or raids; some species are able to forage on trees. (3) Arboreal species that generally ambush in a group, with certain species able to build gallery-shaped traps.

Active foraging

Foraging in ants is directly related to learning and memory, as foraging workers need to return to their nests and in many cases to favorable feeding areas.

During foraging, scavenging desert ants of the formicine *Cataglyphis* or *Melophorus* use path integration permitting them to continuously monitor their position via a “pedometer” and are able to return directly to their nest (Wittlinger *et al.*, 2006). This is also associated with a celestial compass (they respond to polarized light) and information from the surroundings permitting a straight return path to the nest and, thanks to a good memory, to return to areas with large food sources. This also permits *Melophorus* workers to learn changes in the landscape since the first exploration. Olfactory, vibrational and magnetic cues also provide guidance, particularly around the nest (“learning walks” prior to foraging) (Freas & Schultheiss, 2018). They also learn how to avoid a trap on their route by following a detour after an unfortunate experience (Wystrach *et al.*, 2020).

Formica fusca (Formicidae) possesses a lateralized memory based on odors that can be easily learned: the right and the left antennas are the centers of short- and long-term memory, respectively (Piqueret *et al.*, 2019; David Fernandes & Niven, 2020).

Among the ants that are mostly predators, the workers of the Australian *Myrmecia pyriformis* that forage on trees learn their landscape; they slow down and become disoriented if a change occurs (Freas & Schultheiss, 2018). The foragers of another *Myrmecia* showed good learning and memory after being captured and then released in the same location. During new foraging trips they made a detour to avoid the place where they were manipulated (Lionetti *et al.*, 2023). The workers of the African ponerine *Paltothyreus tarsatus* orient themselves in the canopy via the memorization of tree silhouettes (Hölldobler, 1980). After capturing large prey, workers of this species retrieve them by walking backward. From time to time, they leave the prey to walk in a small loop to update their position (reorientation circuit). This behavior, noted in several ponerines (Lachaud, 1985; Dejean *et al.*, 1993a; Lachaud & Dejean, 1994), was then analyzed in *Cataglyphis* (Schwarz *et al.*, 2017). In the Neotropics, the ponerine *Dinoponera quadriceps* uses both chemical and visual cues to return first to their nest and then to a food source (Azevedo *et al.*, 2022). Workers of the ectatomine *Ectatomma ruidum* learn quickly and remember long-lasting chemotactile and visual stimuli that are used during hunting rather than

olfactory and mechanical ones (Riveiros *et al.*, 2021). Those of the formicine *Gigantiops destructor* forage alone in the forest canopy where they navigate in this three-dimensional space by sequentially learning visual landmarks (Beugnon & Macquart, 2016).

A form of teaching (a high level case of social learning) during recruitment through tandem running was noted in European *Temnothorax* spp. (Myrmicinae), the recruited workers learning their route and even improving it (Leadbeater *et al.*, 2006; Franklin & Franks, 2012; Glaser & Grüter, 2023).

Optimal foraging theory and central-place foraging

The theoretical framework concerning predation (or food acquisition) by animals was widely built around “optimal foraging”, where the ratio of energy plus nutrients acquired to the energy needed to expand the search for the capture and consumption (or the amount of time during foraging and handling) of prey/food is maximized. The optimal prey or food will correspond to the highest ratio, or prey/food profitability (“maximization of energy theory”). As prey/food tend to be patchily distributed in the environment, terrestrial animals will forage in a favorable patch with dense prey/food using an “area-concentrated search” (or “area-restricted search”) characterized by a decrease in speed and an increase in sinuosity. The “marginal value theorem” developed by Charnov (1976) predicts that when the predator depletes this favorable patch, the prey/food density tends to be similar to the rest of the surrounding environment, so that the predator leaves the depleted patch to look for another favorable patch (Dornhaus & Powell, 2010; Dorfman *et al.*, 2022; Ritvo, 2022).

When animals have nests, hives, burrows, or roosts they need to “return home” and so are called “central-place foragers”. The optimal framework concerning their foraging corresponds to the “central-place foraging theory” where traveling to and handling prey/food and then returning home incur costs in energy and/or time (Orians & Pearson, 1979). In the case of ants, particularly predatory species, the “marginal value theorem” considers the decisions that a worker has to make in the field: should it collect the first item found or continue looking for another item with a higher energy value? Indeed, prey can be ranked from low- to high-energy content, considering the costs related to the pursuit, capture, handling, and transport of the prey. Thus, to maximize the rate of energy gain, foragers should choose the prey with the highest energy content in terms of costs and benefits. Several factors influence the cost/profit ratio, but the

central-place foraging theory assumes that the prey collected should always be larger or have a higher energy content as distance increases (Dornhaus & Powell, 2010; see Marples *et al.*, 2018 for prey profitability). An analog to the “marginal value theorem” was recently presented as better adapted to social insects: the “diminishing returns hypothesis” as it considers their division of labor and several modes of recruitment. This approach posits that the foraging investment level increases to its maximum; afterwards, it plateaus, and this investment is a function of the size of the collective group (Roeder *et al.*, 2020).

An example is seen in the ponerine *Megaponera analis*, a group-hunting termite specialist, whose scout workers can make decisions individually because they are aware of the hunger state of the colony. In this way, they illustrate (1) the “maximization of energy theory” as raid sizes are related to termite abundance, (2) the “central-place foraging theory” as food source selectivity increases with distance from the nest, and (3) the “marginal value theorem” as the time spent at the hunting site increases with distance to the nest and prey quantity (Frank & Linsenmair, 2017a).

How do ants search for prey?

Ground-dwelling ants need to find their prey that can be scattered in their environment, being grouped (e.g., termites or other ants) or not based on their biology. Except for army ants that form raids (see below), most ants are central-place foragers living in a nest to which prey or food are retrieved to feed the queen(s), larvae, and adult nestmates. A worker that forages individually for the first time needs to learn the position of the nest using visual or olfactory parameters during a series of walks close to the nest entrance and returns to the nest. These “learning walks” also occur when experienced workers have trouble finding the nest during a previous trip, something due to changes in landmarks around the nest (Zeil & Fleischmann, 2019; Murray *et al.*, 2020; Narendra, 2021). Later, foraging workers will explore the area surrounding their nests to find prey/food. In homogeneous environments, they move with fixed speed and sinuosity, whereas in patchy environments, they change speed and sinuosity, adopting an “area-concentrated search” when they encounter a favorable patch (Fig. 1) (Dejean & Benhamou, 1993; Heinze *et al.*, 2018; Popp & Dornhaus, 2023). They then locate (detection at a distance), identify (generally through contact), and attack the prey (or collect food for non-predatory ants); this is followed by a rather direct “homing” (return path), something well noted in solitary

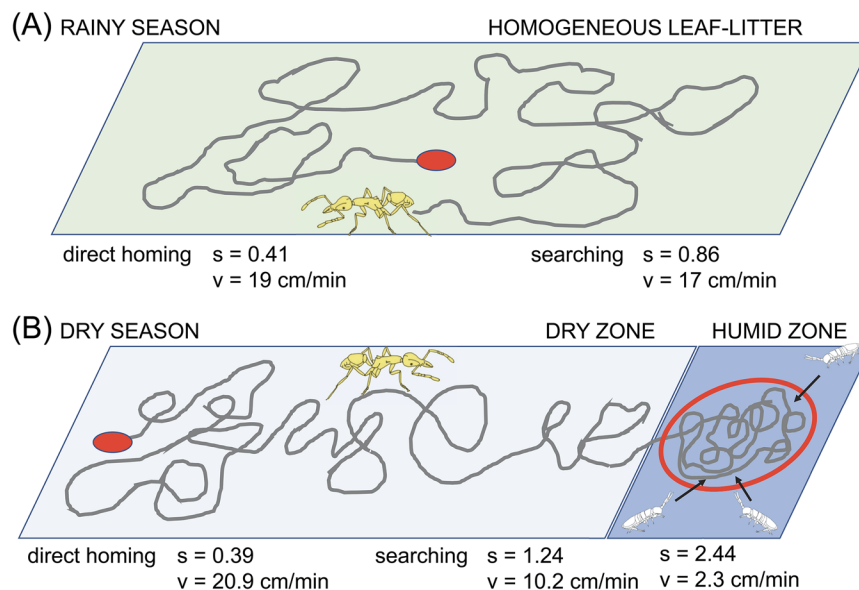


Fig. 1 Representation of the foraging paths of *Strumigenys* (*Serrastruma*) *lujae*, a solitary foraging species with trap-jaw mandibles specialized in the capture of collembolans. The red circle represents the nest entrance. (A) In a homogeneous environment (understorey of the forest during the rainy season; the humidity of the leaf-litter is homogeneously saturated), the worker conducts a random walk to look for prey (the distribution of prey is homogeneous and stochastic). (B) During the dry season, it first searches for a favorable patch (the leaf-litter is dry with humid patches) to which the collembolans are attracted (red circle); there, it adopts an area-concentrated search by increasing the sinuosity (s) and decreasing the speed (v). When the worker returns directly to the nest (direct homing), the values of s and v are similar in both seasons (data from Dejean & Benhamou, 1993).

hunting ants (Dejean & Benhamou, 1993; Dejean *et al.*, 1993a; Lachaud & Dejean, 1994).

When a prey is captured, workers take the most direct possible return paths. Indeed, while searching for prey/food, the workers update their position relative to their nest by integrating their direction and speed (path integration), which is primordial for workers foraging underground or under the leaf litter (Heinze *et al.*, 2018). For ants, foraging in areas where vision plays a role, polarized light is used to obtain the direction, whereas visual landmarks can be recalled (Narendra, 2007; Rodriguez & Oliveira, 2014; Narendra, 2021). Tree silhouettes are used as orientation cues for ants foraging under forest canopies with less polarized light (Hölldobler, 1980). Although ground-nesting, *G. destructor* workers forage solitarily in trees of the understorey and on the soil surface during the daytime, detecting prey situated far from them thanks to their good vision (Fig. 2D). They can make detours to place themselves behind the prey before jumping up to 30 cm and immediately catching them with their mandibles. Workers can also jump vertically to catch flying insects (Beugnon *et al.*, 2001; for detours during predation in trees see pp. 136–137, Curio, 1976).

How ants detect their prey

Ants can detect prey visually thanks to compound eyes, through olfactory, gustatory and ionotropic receptors mostly located on the antennae and vibrations from the substrate; they can also perceive sounds (Macquart *et al.*, 2008; Aksoy & Camlitepe, 2018; Hager & Krausa, 2019; Ferguson *et al.*, 2021; Taylor & Jandt, 2021).

Arboreal-hunting ants generally have larger eyes than ground-foraging species permitting the long-distance detection of prey (Aksoy & Camlitepe, 2018; Palavallinetti & Narendra, 2018; Sosiak & Barden, 2021; Yilmaz & Spaethe, 2022). Yet, some ground-foraging species such as the ponerine *Harpegnathos* can also have good vision enabling them to be efficient predators (Gronenberg & Liebig, 1999) (Fig. 2). Also, certain ant species can see in a wide range of light intensities thanks to compound eyes with large lenses and wide rhabdoms (transparent, crystalline receptive structures lying beneath the cornea in the ommatidia) permitting them to see in relative darkness. During the daytime, pigment cells constrict the crystalline cone protecting the photoreceptors from light, acting as a pupillary mechanism (Narendra *et al.*, 2013).

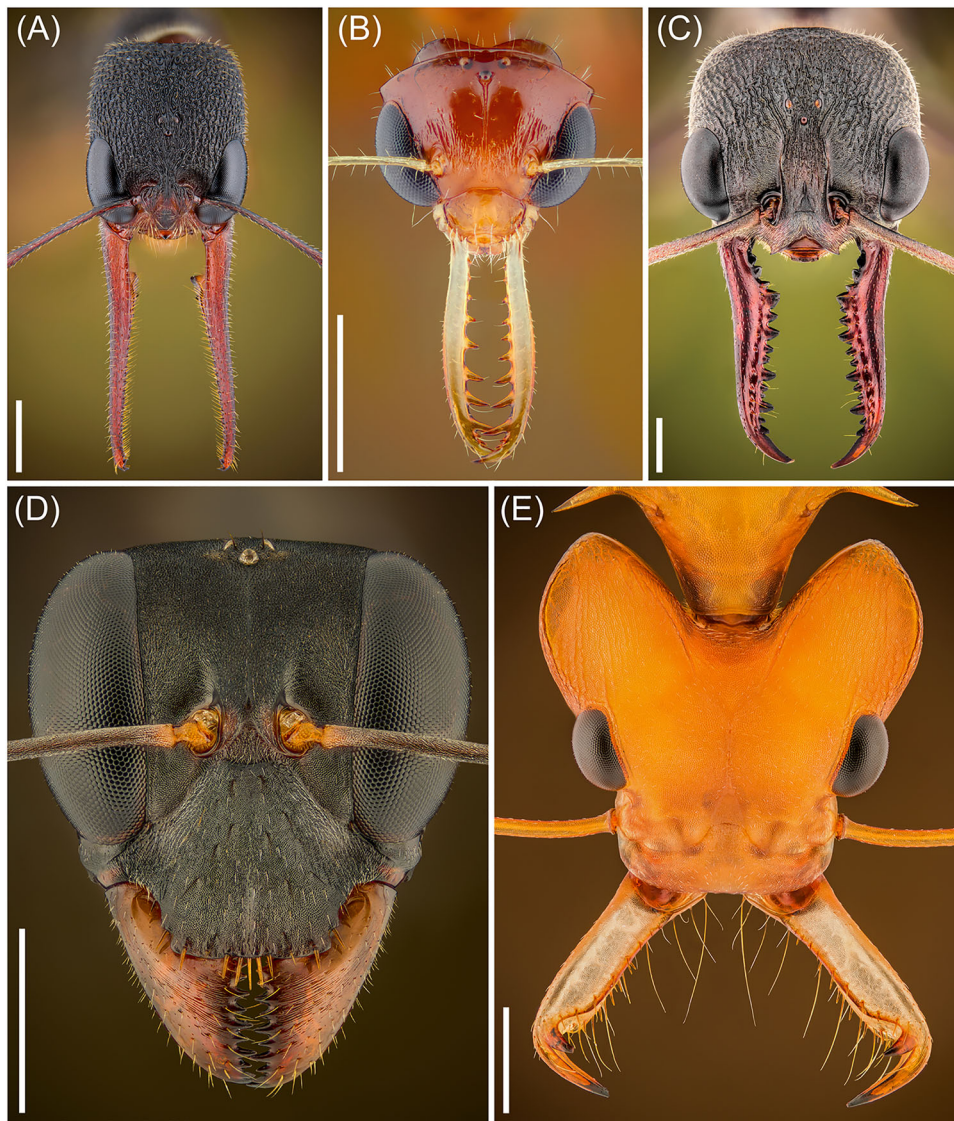


Fig. 2 Heads of different predatory ants showing their well-developed eyes (scale-bars: 1 mm). (A) *Harpegnathos saltator*, a ground-nesting ponerine whose eyes have numerous ommatidia as vision serves to detect prey and to trigger the closing of the hypertrophied mandibles when prey is within reach; they can jump to catch flying prey (Musthak Ali *et al.*, 1992). (B) *Myrmoteras* sp. (Formicinae) from the subgenus *Myagroteras*, a ground-dwelling, trap-jaw formicine with large eyes whose vision permits it to adjust its mandible closing, whereas workers from the subgenus *Myrmoteras* have “trigger” hairs whose base is situated on the labrum (Moffett, 1986). (C) *Myrmecia pyriformis* (Myrmeciinae) with well-developed eyes and long mandibles. (D) The jumping ant *Gigantiops destructor* (Formicinae) has 4 000 ommatidies per eye, likely the record among ants, permitting the long-distance detection of prey (Macquart *et al.*, 2008). (E) A *Daceton armigerum* worker, an arboreal trap-jaw Myrmicinae with “trigger” hairs situated at the base of the mandibles (Photos by Kamil Stajniak).

Still in arboreal ants, vibrations from the substrate caused by an insect landing on a leaf of a myrmecophyte where ants ambushing in the domatia can trigger group attacks, something also permitting them to hunt in relative darkness (Morais, 1994; Dejean *et al.*, 2009; Dejean *et al.*, 2010).

Finally, sound communication (*e.g.*, stridulation) is used during group raids by ants that prey on termites (Hölldobler *et al.*, 1994; Taylor & Jandt, 2021).

Olfaction concerns all ant species, as they need to distinguish nestmates from aliens through cuticular hydrocarbon profiles using the basiconic sensilla of their

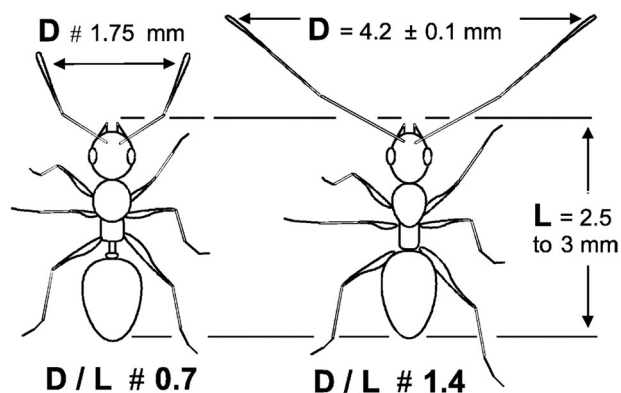


Fig. 3 Representation of workers from 2 ant species having a similar body length. The one at the right, *Paratrechina longicornis*, shows that the long length of the antennae permits a wider path to be explored during foraging (modified from Kenne *et al.*, 2005).

antenna (Sharma *et al.*, 2015). This is particularly true of ants that prey on other ants (Manubay & Powell, 2020) or on termites that also use cuticular hydrocarbons in nestmate recognition (Bednar & Silverman, 2011; Yusuf *et al.*, 2014; Buczkowski, 2023). The foreleg tarsi can be involved in olfaction, but not during predation, as they permit the ant to detect sugary substances (Falibene & Josens, 2012; Jaleel *et al.*, 2021).

Concerning foraging by predatory ground-nesting ants, we need to consider 2 main parameters. First, the greater the distance between the tips of the antennae, the better, permitting these workers to forage over the widest path (Fig. 3). Second, for many ants the range of prey detection via their antenna is relatively wide compared to their body size (Kenne *et al.*, 2005). Because they walk slowly and oscillate their body while foraging, they sweep a wider area, even more so when the path is very sinuous (Fig. 4; Dejean *et al.*, 1983). Furthermore, hypogaecic ants, which cannot adopt the former behavior, generally have a short antennal scape compared to epigaecic ants (Sosiak & Barden, 2021).

Recruitment of nestmates

Some ant species are solitary central-place foragers that search for prey in areas around their nest and are able to return to their nest in a relatively straight line after having captured a prey. This occurs for scavenging desert ants and several predatory species (Dejean & Benhamou, 1993; Dejean *et al.*, 1993a; Wittlinger *et al.*, 2006). Yet, because prey can be grouped in areas favorable to their development, predatory ants best exploit prey patches by

capturing several prey successively if their mandibles are long enough or, better, by recruiting nestmates, particularly when preying on termites or other ants.

Depending on the possibility of recruiting nestmates, 10 strategies are known in ants. (1) For solitary (or individual) foraging, the ancestral form (Reeves & Moreau, 2019), workers detect, capture and retrieve prey/food alone, something ubiquitous in ants (army ants excepted) particularly in specialist predators (Fig. 1), and frequently associated with spatial fidelity by the foragers (Pie, 2004; Guénard, 2022). (2) “Social facilitation” is an indirect type of recruitment mostly seen in solitary foragers. After a worker has deposited a captured prey in its nest, some other individuals are incited to leave the nest to forage in turn (Lachaud & Dejean, 1994; Cogni & Oliveira, 2004; Guénard, 2022). (3) “Short-distance recruitment” (also “directional recruitment” or “kinopsis”) is another type of indirect recruitment noted mostly in solitary foragers that, after having mastered a prey, walk around that prey with their gasters touching the ground. This behavior attracts nestmates foraging in the vicinity; they then cooperate to retrieve the prey (Dejean, 1991; Guénard, 2022). (4) “Prey-chain transfer” occurs when a forager captures a prey and retrieves it only along a part of the return path and then transmits it to another nestmate (Lopez *et al.*, 2000). (5) In “tandem carrying” or “adult transport” a forager that discovers a prey (or food) too large to be retrieved, returns to its nest to solicit a nestmate by drumming its antennae. In reaction, the latter adopts a pupal-like posture permitting its transport by the soliciting worker. When reaching the prey/food, the carrying worker releases the transported one. Large prey will be cut into pieces that will then be retrieved (Guénard & Silverman, 2011; Lanan, 2014). (6) In “tandem running” a forager returns to the nest where she recruits a nestmate using antennal contact and then leads her to the food; the follower keeps antennal contact with the recruiter. In some cases, the recruiter can use chemical cues from the food source. The follower can learn the path to the food source and, in turn, recruit a new worker, and so forth (Dornhaus & Powell, 2010; Franklin, 2014). (7) In “group recruitment” the recruiter that found a food source while foraging returns to the nest laying a scent trail and then leads a group of workers along this trail to the food source (Collignon *et al.*, 2014; Kolay *et al.*, 2020). A particularity is seen in *Myopopone castanea* (Amblyoponinae) and *Platythyrea modesta* (Ponerinae) that recruit nestmates to transport their larvae to the spot where they have killed a large prey (Wilson, 1958; Djiéto-Lordon *et al.*, 2001). (8) “Mass-recruitment” is the most evolved strategy where recruiters return from a food source to their nest laying a scent trail. This trail guides numerous nestmates to

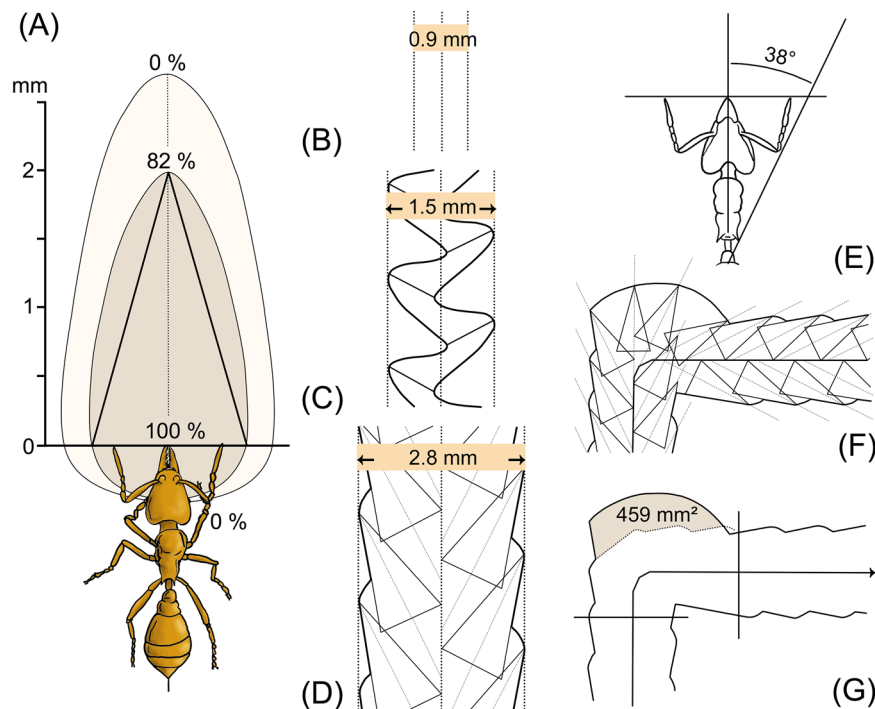


Fig. 4 Foraging by *Strumigenys* (*Serrastruma*) *lujae* workers specialized in the predation of isotomid collembolans. (A) During foraging, their antennae are spread wide; we deduced their capability of detection as they pointed them when they “located” the prey. Prey situated in front of the antennae were detected at up to 2.7 mm; 82% of them were detected at 2 mm (the total length of the ant body is ≈ 2 mm; 40 cases). Detection is nil behind the head and restricted to ≈ 0.4 mm on the external side of the antennae. The triangle represents an 82% probability of detection in front of the ant which is used for Fig. 2D and 2F. (B) Theoretical representation of a path swept when a worker walks in a straight line; the width between the antennae was ≈ 0.9 mm. (C) Movement of the workers while foraging illustrating the oscillations of the anterior part of their body with a maximum angle creating a wave of 1.5 mm (both averaged; 40 cases). (D–E) Capacity of detection by the workers (here 2 mm was retained; corresponding to an 82% probability of detection and an angle of 38°) resulting in a 2.8 mm-wide path (so more than 3 times the path represented in Fig. 4B). (F–G) When the workers turn (here representation of a 90° turn), their antennae can detect a wider area, something very frequent during a concentrated-area search. Furthermore, during their foraging path, the workers stop every ≈ 40 mm to extend their forelegs and move their body from right to left over $\approx 180^\circ$, so that the isotomid prey are detected from ≈ 4 mm in 30 cases out of 36 (modified from Dejean *et al.*, 1983).

the source (absence of a leader) who reinforce the trail in turn, creating a permanent trail and permitting them to monopolize the food source until its depletion (Price *et al.*, 2016; Kolay *et al.*, 2020; Lourenço *et al.*, 2020; Reznikova, 2021; Guénard, 2022). (9) In “leader scouting” a *Formica* worker that finds a food source can transmit information to both individuals that know the area to be foraged and, to a lesser degree, naive ones thanks to antennations (so in the absence of other cues such as scent trails) (Reznikova, 2007; Reznikova, 2008; Reznikova, 2021). (10) “Group hunting” or “army ant behavior” are organized raids characteristic of the Dorylinae and known for some non-Dorylinae species (Kronauer, 2020).

Ant workers can modulate their foraging strategy as a function of the size of the colony (Planqué *et al.*, 2010) or the size of the prey/food source, resulting in flexible for-

aging behavior. For example, when the prey is too heavy to be transported by 1 worker, they can switch from solitary foraging to social facilitation (Amor *et al.*, 2010), tandem carrying (Guénard & Silverman, 2011), tandem running (Silva *et al.*, 2021), group recruitment (Mercier & Lenoir, 1999; Cerdá *et al.*, 2009), or even group raiding (Duncan & Crewe, 1993). Also, based on the abundance of the food source or prey size, some species switch from social facilitation or tandem carrying to mass recruitment (Pratt, 1989; Cogni & Oliveira, 2004) or from group to mass recruitment (Putyatina, 2007). Yet, despite these cases, cooperative behaviors very rarely regress to solitary foraging (Reeves & Moreau, 2019).

In a field experiment, *Formica rufa* scouts were offered either 2 or 6 fly larvae per patch. When finding patches with 6 larvae, they recruited 4 times more workers and

more quickly than for patches with 2 larvae (Lenoir, 2002). Concerning prey retrieval by *P. tarsatus*, a generalist ponerine predator that hunts mostly termites and very large prey, the workers properly select single- or multiple-prey loaders based on the kind of prey discovered (Dejean et al., 1993b).

Army ant behavior

Overview

Among the 29 genera of Dorylinae, 8 genera exhibit the army ant syndrome. Remarkably, this syndrome evolved twice in the Dorylinae, with 1 originating in the Neotropics (i.e., *Cheliomyrmex*, *Eciton*, *Labidus*, *Neivamyrmex*, and *Nomamyrmex*) and the other in the Old World (*Dorylus*, *Aenictus*, and *Aenictogiton*).

Most New World species are called “phasic” as they are characterized by a nomadic phase and a stately (stationary) phase when the foraging cost for each foraging worker decreases with the number of larvae that must be fed in a context where they prey mostly on other ants. Indeed, phasic brood cycles are favored because they allow colonies to efficiently mount large-scale raids to overpower other ant colonies during brood care phases, providing abundant food for synchronized larval cohorts. This “High Cost of Entry” foraging strategy is most effective when there is a substantial initial investment required before foraging yields benefits, which aligns with the army ant’s need for large raiding parties to be successful (Garnier & Kronauer, 2017).

By contrast, as in the general case for ants, Old World species and the New World genus *Labidus* are “non-phasic” because the foraging cost increases with the number of larvae (Garnier & Kronauer, 2017). Indeed, a phylogenetic analysis of the Dorylinae shows that Old World army ants such as *Aenictus* and the clade corresponding to *Aenictogiton* and *Dorylus* are clearly separated from New World army ants, including doryline species with a non-army ant syndrome (Borowiec, 2019).

Army ants are characterized by highly specialized wingless queens (ergatoid), so-called “dichthadiiform”, and that they reproduce by colony fission (large colonies splitting into 2). The size of their large gasters varies based on the life cycle of the colony. As a result, their obligate collective foraging allows them to be key predators (Kronauer, 2009; Borowiec, 2019; Kronauer, 2020; Chandra et al., 2021). They do not have nests. Rather, they form “bivouacs” composed of numerous workers grasping each other by their legs and containing “chambers” for the queen, eggs, larvae, and food.

These bivouacs are installed in subterranean cavities, hollow logs, or tree branches and are relocated frequently due to the emigrations characterizing these nomadic ants (Kronauer, 2009).

During foraging, army ants form raids; workers walk up to the front of their column and then return toward their bivouac laying a thicker pheromone trail, some retrieving prey (Kronauer, 2020).

New World army ants

Typically, during their nomadic phase, *Eciton burchellii* colonies emigrate for 14.3 d on average permitting the larvae to develop by feeding on prey captured by diurnal swarms of workers. During this phase, the queen’s gaster is “contracted” as she does not lay eggs, permitting her to follow the swarm. Then, the stately phase lasts 20.4 d on average, beginning as the larvae pupate, so that the prey is fed quasi exclusively to the queen which, during this phase, is physogastric, laying thousands of eggs. During this phase, the colony uses the same bivouac from which they organize raids like the spokes of a wheel radiating from its center. The successive raids are separated by $\approx 123^\circ$, maximizing the different foraging paths in time and space. One raid is carried out each day and the raiding workers return with their prey to the bivouac by the principal trail, while their nestmates move out to join the front of the swarm. Indeed, this species is a “swarm raider” as this front is wider than 5 m and globally progresses in a zigzag pattern, so that the overall course of a raid is roughly a straight line. Note that the other *Eciton* species forage along narrower columns and, so, are referred to as “column raiders” (Kronauer, 2009; Cerdá & Dejean, 2011; Willson et al., 2011; Kronauer, 2020; Chandra et al., 2021).

New World doryline species prey mostly on other ants, with *Eciton dulcium*, *E. mexicanum*, and *Neivamyrmex gibbatus* foraging for ground-nesting species, while *Neivamyrmex pilosus*, *Eciton hamatum*, and *E. burchellii* rather raid arboreal-nesting ants. *E. hamatum* and *E. burchellii* are diurnal, the other species nocturnal (Hoenle et al., 2019).

When attacked by *Eciton* raids, most prey ant species evacuate their nests as soon as they perceive the propaganda of the raiders (an allomone also used by slave-making ants that triggers panic in workers of the attacked colony). Thus, prey ants lose only a part of their brood and callow workers, their queens being spared by the raiders, so that the colonies can be re-established when the workers return to their nests (Gotwald, 1995; Dejean et al., 2014).

Specialization was noted for *E. hamatum* preying mostly on *Acromyrmex* and *E. burchellii* on *Camponotus*, but the prey spectrum can sometimes be somewhat broader, particularly in *E. burchellii*, which also captures diverse arthropods. *Eciton dulcium* preys on *Pachycondyla* and *Odontomachus*, *E. mexicanum* on *Eciton* and *Pachycondyla*, and *E. vagans* on *Odontomachus* (Hoenle *et al.*, 2019; Manubay & Powell, 2020; Pérez-Espona, 2021). Among the other genera, *Nomamyrmex esenbeckii* preys mostly on *Atta*, but can raid *Odontomachus*, *Camponotus*, and *Nasutitermes* termites (Powell & Clark, 2004; Souza & Moura, 2008), *Neivamyrmex compressinodis* preys on *Wasmannia auropunctata* (Le Breton *et al.*, 2007), while *Labidus praedator* and *Cheliomyrmex andicola* are generalist predators (O'Donnell *et al.*, 2005; Monteiro *et al.*, 2008).

Old World army ants with the example of *Dorylus molestus*

Old World army ants are “non-phasic” species that migrate in an irregular manner to new nesting sites. The columns of *Dorylus nigricans* and *D. wilverthi* can reach up to 20 million individuals, but the Asian species *D. laevigatus* has smaller colonies of 30 000 to 1 million individuals. Their raids can be subterranean, in the leaf litter, or on the surface (Gotwald, 1995; Borowiec, 2016; Garnier & Kronauer, 2017).

D. molestus is a generalist predator with colonies of several million workers capturing mostly earthworms. The colonies can stay in their bivouac for 17 d on average, but this value can reach 111 d, as the cause of colony migrations is prey depletion (Gotwald, 1995; Schöning *et al.*, 2010).

Dorylus spp. are generalist predators with the exception of *D. nigricans* that attack *Macrotermes subhyalinus* termites, while *Aenictus* spp. are mostly an ant predator (Schöning & Moffett, 2007; Chandra *et al.*, 2021). Yet, they can occasionally eat plant products such as oily palm nuts and avocados (Schöning, 2008), while the Asian, subterranean *D. orientalis* is a pest attacking cultivated plant roots although it also preys on other ants (Roonwal, 1976; Bidyarani Devi *et al.*, 2022).

Non-army ant Dorylinae: prey specification

In non-army ant Dorylinae, 7 genera (*i.e.*, *Lioponera*, *Liviodopone*, *Ooceraea*, *Parasicia*, *Simopone*, *Sphinctomyrmex*, and *Zasphinctus*) raid other ants, while *Acanthostictus*, *Cylindromyrmex*, and *Eburopone* are termite predators. Only *Chrysapace*, *Leptanilloides*, and

Yunodorylus are generalist predators; however, we do not know the preferences for the 6 remaining genera (*i.e.*, *Eusphinctus*, *Neocerapachys*, *Procerapachys*, *Syscia*, *Tanipone*, and *Vicinopone*) (Feitosa *et al.*, 2012; Borowiec, 2016; Yamada *et al.*, 2019; Chandra *et al.*, 2021; Mizuno *et al.*, 2023).

Origin of army ant raids

The origin of army ant mass raiding from group raiding was shown by experimentally increasing the size of colonies of the invasive doryline non-army ant *Ooceraea biroi* (previously known as *Cerapachys biroi*), a clonal-raiding doryline species that preys mostly on other ants (Chandra *et al.*, 2021). This species is queenless, the workers producing diploid eggs via thelytokous parthenogenesis and their cycle is synchronized showing statary and nomadic phases (Tsuji & Yamauchi, 1995; Ravary & Jaisson, 2002).

It is worth noting that other Dorylinae such as *Leptanilloides* and *Zasphinctus* have ergatoid queens and their broods are synchronized (“phasic species”); this was also noted for *Eburopone* and *Syscia* whose queens can be winged or ergatoid. Brood production is not synchronized for *Lioponera* whose scouts detect other ant nests, and then recruit nestmates to raid them (Borowiec, 2016).

Army ant behavior among non-doryline ants

Other than the Dorylinae, some Ponerinae, Amblyoponinae, and Leptanillinae evolved the army ant syndrome, even showing phasic biological cycles (Garnier & Kronauer, 2017).

The Leptanillomorpha form a monophyletic unit grouping together the Leptanillinae and Martialinae (with only 1 species, *Martialis heureka*) that is the “sister” group to all other ant subfamilies (see also Borowiec *et al.*, 2019; Borowiec *et al.*, 2021; Cai, 2024). *Leptanilla japonica* specializes in capturing geophilomorph centipedes that they hunt using an army ant-like behavior. During a “larval-growing stage” the colony migrates, the workers hunt and feed themselves and their larvae with prey. The development of the larvae is synchronous and when they reach the last instar, their specialized duct organ situated on the 4th abdominal segment can secrete hemolymph. The ergatoid queens never feed on the prey; rather they grasp these organs to absorb the hemolymph (“larval hemolymph feeding”). Thus, they become physogastric (dichthadiiform as for army ants) laying 100–200 eggs; this is the “egg-laying stage” during which worker predation stops and the rate of migration is very low or nil

[Masuko, 1989; Masuko, 1990; see also Ito & Yamane (2020) for *L. clypeata*]. Here, the similarity with army ants is very high, except for possibly their hunting behavior organized via scouts to detect prey and then recruit nestmates by laying a scent trail.

In the subfamily Amblyoponinae, *Onychomyrmex hedleyi* and *Onychomyrmex doddi* have apterous, ergatomorphic (dichthadiiform) queens and are phasic. The colonies reproduce by fission and move between temporary bivouacs, the relocation distance of up to 150 cm is due to the small size of the individuals (less than 4 mm). Workers form raids to prey mostly on centipedes. A worker that detects a prey recruits nestmates from the column to kill and retrieve it, but faced with large prey the entire colony moves from the bivouac. These army ant-like characteristics were likely found in another amblyoponine, *Adetomyrma venatrix*, from Madagascar (Ward, 1994; Miyata et al., 2009).

The Neotropical ponerine genus *Simopelta* is characterized by 1 000–2 000 workers that form diurnal raiding columns of several hundred individuals foraging on the ground and on trees to prey on both the brood and adults of other ants, particularly *Pheidole*. The colonies emigrate between bivouacs or long-term nests, suggesting a nomadic lifestyle. Because their queens are ergatoid with distended gasters (dichthadiiform), the brood is produced in phases and colonies reproduce via budding, the similarity with an army ant-like lifestyle is notable (Gotwald & Brown Jr., 1966; Kronauer et al., 2011).

Still among the Ponerinae, army ant-like behavior exists in certain *Leptogenys*, something facilitated by the presence of ergatoid queens in most species in this genus and the reproduction of colonies by fission. Raids similar to those by *Dorylus* were noted in *L. nitida* in South Africa and *L. processionalis distinguenda* in Asia that prey on all sorts of arthropods, while *L. processionalis* raids mostly termites (Rajagopal & Musthak Ali, 1984; Ganeshiah & Veena, 1991; Duncan & Crewe, 1994; Witte & Maschwitz, 2000).

The myrmicine ant *Carebara diversa*, distributed from India to Southeast Asia, has large winged queens (25 mm in length) that reproduce during nuptial swarms and then are able to found a colony, producing brood constantly, 2 characteristics not found in army ants. Yet, adult colonies, which have a polymorphic worker caste from 2 mm-long minors to 20 mm-long supermajors, contain ≈50 000 individuals and form long foraging columns of ≈10 000 foragers. These trunk trails extend up to 100 m from the nest, remaining active for weeks, the ants leaving and returning along them around the clock. They are 10–30 mm in width and can be protected by walled trenches made of soil particles that can form tunnels. The ants

reaching the front of the trail spread out to expand into larger, fan-shaped swarm raids of 6 m in width. This mode of foraging behavior is comparable to that of *Dorylus* army ants, but the speed of *C. diversa* individuals during raids is much lower: 1.5–2.0 m/h versus 10–20 m/h. Furthermore, *Carebara* are generalist feeders (Moffett, 1984, 1986, 1988; Fischer et al., 2014; Moffett, 2021).

Specialized food with impact on the mode of foraging

We saw that foraging may be influenced by the environment (e.g., desert ants), but specialization can also induce adaptations among predators due to large differences in size and the means of defenses of target prey. Indeed, to prey on termites or other ants that have good defenses involves different strategies that frequently require the use of allomones while oophagy, if not related to termite or ant eggs or brood, is generally easy or implies morphological changes to open the oothecas.

Other cases of specialized termite predators

Ants specialized in the predation of termites, such as the myrmicine *Tetramorium uelense*, have cuticular hydrocarbons containing aliphatic alcohols produced by their mandibular gland permitting them to approach their prey undetected. In comparison, non-specialized congeners have repellent ketones and aldehydes on their cuticle (Longhurst et al., 1979).

Chemical mimicry was noted in the European ponerine *Hypoponera eduardi* whose hydrocarbons are similar to those of their termite prey, *Reticulitermes*, and in Mexico for an *Anochetus* whose cuticular profiles are similar to those of the *Nasutitermes* soldiers. This permits the ant workers to approach the termite trails undetected and to prey on the termite workers unmolested (Bagnères & Lorenzi, 2010).

Specialized ants detect termite presence through olfactory information from different types of semiochemicals. For instance, the ponerine *Odontoponera transversa* uses the trail pheromones produced by several Macrotermitinae termites to track them (Wen et al., 2017).

M. analis was frequently recorded as having an army ant-like behavior, particularly because the queens are wingless (Pohl et al., 2023). Its scout workers first locate a nest of termites from the subfamily Macrotermitinae using odors from the termitary gallery soil and the termites themselves (but avoid contact with them) and do not select non-Macrotermitinae termitaries, such as *Cubitermes*

(subfamily Cubitermitinae) (Longhurst & Howse, 1978; Yusuf *et al.*, 2014; Patel *et al.*, 2018). Then, the scout returns to its nest laying a scent trail to recruit both major and minor workers that form a raid of 200–500 individuals. The recruiting scout leads this raid to the chosen territory that is then besieged, the majors rather break open the protective soil while the minors enter into these openings to kill and pull out the prey. The workers sting the termites, carry them near the gallery entrance, and return to hunt until the group of paralyzed termites is large enough. Then, major workers transport up to 7 termites, the minors only three, and the column returns to its nest led by some individuals that do not carry prey (Longhurst *et al.*, 1978; Corbara & Dejean, 2000; Frank & Linsenmair, 2017b).

Similar foraging behavior was noted in Neotropical ponerine termite raiders such as *Neoponera commutata* (Mill, 1984) and those of the *laevigata* group (*i.e.*, *N. laevigata*, *N. marginata*, *N. gojira* and *N. mashpi*, frequently confused) (Leal & Oliveira, 1995; Troya & Latke, 2022). Also, in the Neotropics, scout workers of *Pheidole titanis* (Myrmicinae) recruit up to 2 000 nestmates to raid *Nasutitermes* columns. The ant workers then retrieve prey using the chemical recruitment trail laid by the scouts (Feener Jr., 1988). In Madagascar, *P. longispinosa* workers attack the foraging groups of other ant species and termites to prey on workers (Lampasona, 2015). A *Megaponera*-like behavior was recorded in Asia by the ponerine *Leptogenys cyanicatena* with wingless queens (as are many species in this genus). When encountering large millipedes during their raids, scout workers go back to their nest to recruit nestmates and all return to the prey to sting them until paralysis. Then, they form chains to retrieve them, each individual seizing a nestmate by the abdomen and walking backward, pulling the millipedes toward their nest (Peeters & De Greef, 2015; Mizuno *et al.*, 2022).

Prey robbing by ants

Cleptobiosis or food robbing by ants can involve fungi in fungus-growing species (Ronque *et al.*, 2018), sugary food including nectar and hemipteran honeydew gathered by the target colony (Richard *et al.*, 2004) or seeds robbed from the workers of other species (Grasso *et al.*, 2004). Yet, cleptobiosis is more frequent between predatory species where it represents a form of interference competition reducing the costs of searching for and handling prey (Hölldobler, 1986).

For predatory and scavenger ants, mathematical models showed that the larger the prey the higher the prob-

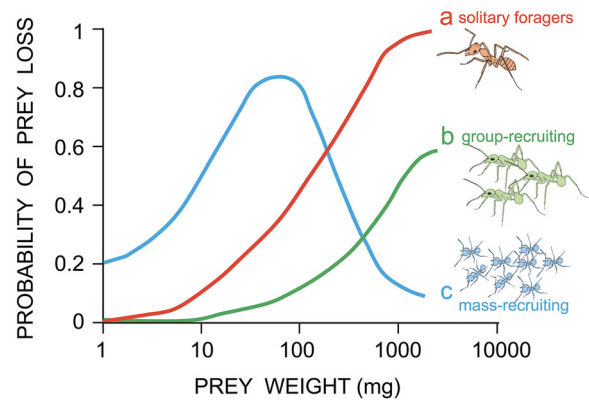


Fig. 5 Probability of prey loss through interspecific food robbing related to prey weight (in logarithmic scale) (modified from Cerdá *et al.*, 1998). Individually foraging (solitary foragers) and group-recruiting species are more likely to suffer prey interference and loss when prey are larger, whereas small-sized and mass-recruiting species show the opposite pattern, losing fewer prey to opportunistic species as prey size increases. These small ants recruit large numbers of workers on larger prey and dominate them, expelling the other species that do not have enough time to dissect and carry the prey to the nest. In Mediterranean ant assemblages, each scavenger ant species displays only 1 of these strategies, and, thus, prey size is one of the main factors determining the success of prey collection.

ability of interference competition resulting in prey robbing (Oster & Wilson, 1978). This was confirmed during empirical studies when workers from different ant species captured larger prey compared to smaller ones (Traniello, 1983; Savolainen, 1991; Cerdá *et al.*, 1998; Yamamoto *et al.*, 2009) (Fig. 5).

E. ruidum workers use the trails of *Pheidole radoszkowskii* to rob their prey (Perfecto & Vandermeer, 1993). This species frequently exhibits intraspecific cleptobiosis via deceptive means due to a lower concentration of cuticular hydrocarbons (chemical insignificance), permitting certain workers to enter a neighboring nest without injury. There, they can acquire enough chemicals to be well-tolerated (chemical mimicry). Because this process can occur for all neighboring colonies, those of the same size rob prey from each other equally, but small colonies lose more prey than they gain (Breed *et al.*, 1999; Breed *et al.*, 2012; see also McGlynn *et al.*, 2015).

Parabiotic species share their nests but live in different chambers. Their relationships are pacific but 1 species generally robs prey from the other, which is the case between the formicine *Camponotus femoratus* and the tiny myrmicine *Crematogaster levior* workers (Orivel & Leroy, 2011).

Inquiline ants are parasites of other ants of the same genus and depend on them for their development, so that they do not have to forage (De La Mora *et al.*, 2020). Comparatively, lestoproctid species nest close to or in the walls of the large nests of other ants or termites (termitolesty); their small workers can enter the nest chambers of their hosts to rob prey or brood to consume them. For example, several species of the myrmicine genus *Solenopsis* have tiny workers that dig small-diameter galleries connecting their nest to that of the targeted ants belonging to several subfamilies. During encounters, the *Solenopsis* workers avoid contact and discretely rob brood from the colonies they infiltrate (Pacheco & Mackay, 2013). In the Neotropics, some *Megalomyrmex*, also belonging to the tribe Solenopsidini, are thief ants that use chemical insignificance, while their alkaloid venom triggers submissive behavior in the host workers (Neupert *et al.*, 2018). *Megalomyrmex mondaboroides* scouts raid the fungus-growing Attini *Cyphomyrmex costatus* nests by quickly grazing the fungal garden; then they rob brood and retrieve everything to their nest [Boudinot *et al.*, 2013; see also Adams *et al.* (2012) for *M. adamsae* raiding *Trachymyrmex*]. The *Megalomyrmex* alkaloid venoms function as appeasement and repellent allomones on their host fungus-growing ants (Adams *et al.*, 2015). *Gnamptogenys hartmani* also raid *Trachymyrmex* and *Sericomyrmex* fungus-growing ants, causing them to panic and leave their nest likely due to propaganda substances as for slave-making and certain army ants. Then, *G. hartmani* usurp the host nest, feeding on the fungus and brood. When these resources are depleted, scouts will search for a new colony to raid (Dijkstra & Boomsma, 2003).

Termitolestic ants nest close to or in the walls of the termitaries. They include *Solenopsis laeviceps* and *Carebara urichi* (Crematogastrini) which rob the eggs of *Nasutitermes* or *Armitermes*, respectively (Hölldobler & Wilson, 1990). *Tropidomyrmex elianae* (Solenopsidini) live inside the chambers of *Anoplotermes pacificus* (Apicotermatinae) nests where termites and ant workers antennate each other, but we do not know if the ants prey on the termite brood (Silva *et al.*, 2009).

The workers of the African ponerine *Centromyrmex bequaerti* are blind and rarely seen outside Termitinae and Macrotermitinae mounds where the colony nests directly in the cavities, but away from the termites. They enter into the termitary galleries to reach other cavities where they capture nymphs, workers and soldiers, both latter being stung. They make temporary stockpiles of killed termites before retrieving them (Dejean & Fénelon, 1999).

Oophagy

Because arthropod eggs are generally clumped together, they are easily preyed upon by many generalist ant species (Eisawi *et al.*, 2022; Schifani *et al.*, 2023). The behavior of the myrmicine genus *Erebomyrma* suggests egg specialization as the workers frequently capture arthropod eggs among other prey (Wilson, 1986).

Proceratium spp. (Proceratiinae) are generalist egg predators, noted as preying on hemipteran, chilopod, spider and opilone eggs (Brown Jr., 1979; Masuko, 2019), while the ponerine *Plectroctena lygaria* and the myrmicine *Stegomyrmex vizottoi* prey on millipede eggs (Bolton *et al.*, 1979; Diniz & Brandão, 1993) and the myrmicine *Calypatomyrmex rectopilosus* prey on myrmecophilid cricket eggs (Ito *et al.*, 2023).

All species of the genus *Discothyrea* (Proceratiinae) are spider egg predators (Hölldobler & Wilson, 1990; Katayama, 2013; Masuko, 2020). In the African species *D. oculata*, founding queens and workers can open the spider oothecas of diverse spider species using their modified forelegs. This permits them to manipulate the crimped silk that protects the oothecas and to install their colonies in them, thus finding shelter and food in the form of eggs and newly hatched spiderlings. They can also gather and then manipulate the spider silk to line and obstruct cavities in the ground where their colonies settle (Dejean *et al.*, 1999).

Ambushing techniques

Ambush is a hunting mode permitting ants to spend less energy to capture prey. Among insects, generalist ambush predators can capture several types of prey using camouflage, by hiding, or by making traps (*e.g.*, praying mantises, assassin bugs, antlion larvae). Specialist ambushers evolved means to deceive specific prey visually or chemically by mimicking them or their pheromones (*e.g.*, reduvid of the subfamily Phymatinae, Paussinae) (Piper, 2021). We will see that ants can be generalist or specialist ambushers.

Attracting prey

In ground-dwelling species, the workers of the African myrmicine *Strumigenys truncatidens* and *S. emarginata* (former genus *Smithistruma*) do not have trap-jaw mandibles. When they detect areas where collembolans, their specific prey, form groups, they immobilize themselves, mandibles wide open. They attract these prey

likely using secretions from the labrum; the spongiform appendages of the petiole can also play a role. As the attracted collembolans climb on the ant, one of them ends up by putting one of its legs between the ant mandibles, triggering their rapid closing, and so its capture (Dejean, 1985).

A more intriguing result is seen in the ponerine *Leptogenys mexicana* preying on Bathytropidae isopods that form clusters of numerous individuals. These isopods are attracted to *L. mexicana* nests that lead them directly into its colonies, so that there is no foraging in this case (Dejean & Evraerts, 1997).

Pheidole oxyops workers place feathers around the entrance of their nest to attract mites, springtails and some other ants as a kind of trap as the prey then fall into the slippery main gallery of the nest and are subdued by the workers. Here, too, there is no foraging, although *P. oxyops* workers can also forage (Gomes *et al.*, 2019).

The prey leave their nests or emerge from a fruit

E. ruidum workers were noted ambushing stingless bees, identifying the site of a beehive entrance and waiting motionless in front of it at a short distance, their mandibles wide open. Attempts at capture are triggered by bees landing on or exiting the nest. In a rapid forward movement, the *E. ruidum* workers seize such bees and sting them immediately. Unsuccessful individuals can restart an ambush or can introduce their head inside the beehive entrance, attempting to seize any bee within reach, including guards (Schatz & Wcislo, 1999). A very similar behavior was noted for *E. tuberculatum* able to capture hovering stingless bees (Ostwald *et al.*, 2018).

In Brunei, Borneo, numerous predatory ant species belonging to the Ponerinae, Pseudomyrmecinae, Myrmicinae, Formicinae, and Dolichoderinae prey on fig wasps on *Ficus* trees. The hunting workers face the fig ostiole, ambushing exiting wasps, either individually (e.g., *Oecophylla smaragdina*) or in a group of workers (e.g., *Crematogaster* sp.). Here, in addition to being seen, wasp odor also plays a role in this process (Schatz *et al.*, 2008; Schatz & Hossaert-McKey, 2010; Zachariades *et al.*, 2010).

Ambushing in trees

The Neotropical myrmicine *Daceton armigerum* is a territorially dominant arboreal ant species characterized by very populous colonies, large and/or polydomous nests, and an absolute intra- and inter-specific territoriality. As for most arboreal species, the workers are

visual predators ambushing diurnally, their body quasi perpendicular to their host-tree branches and situated ≈ 11 cm from each other with their hypertrophied trap-jaw mandibles wide open (see Figs. 2D and 6). When a worker captures a large flying insect, it attracts nestmates through short-range recruitment to spread-eagle and sting it (Dejean *et al.*, 2012). In Africa and Asia, the arboreal formicine weaver ants of the genus *Oecophylla* are also territorially dominant species whose workers detect by sight and capture flying insects on their host trees; they also spread-eagle large prey. Yet, they show behavioral flexibility, hunting at night around artificial sources of light that attract numerous insects. They also have permanent secondary territories situated on the ground in areas rich in potential prey, such as riverbanks, where numerous workers go back and forth from their host trees as they capture many insects. On the secondary territories, workers also conceal large prey with leaves to put them out of sight of competing predators including lizards, and so avoid being robbed (Dejean, 1990; Dejean, 1991; Rastogi, 2000).

The role of vibrations during ambushing by arboreal ants

Vision forms the basis of most arboreal ants' ambushing, but some use vibrational information. The Neotropical dolichoderine *Azteca bequaerti*, whose colonies shelter in leaf pouches situated at the base of the laminae of myrmecophytic *Tococa guianensis* (Melastomataceae), react to the vibrations transmitted by an alien insect landing on their leaf, making it unnecessary for them to forage for prey. Indeed, groups of workers, likely on alert, immediately rush the prey and try to spread-eagle it (Dejean *et al.*, 2009).

Again, in the Neotropics, numerous workers of the arboreal *Azteca lanuginosa* and *Azteca andreae*, the latter associated with myrmecophytic *Cecropia* trees, ambush side-by-side under the leaf margins of their host trees, their mandibles wide open. When an insect lands on their leaf, the vibration it triggers prompts numerous workers in a simultaneous group attack who then spread-eagle this flying insect prey (Fig. 7). Then they retrieve it to their nest. This technique permits the capture of very large locusts and moths weighing up to 13 350 times the weight of a worker (Morais, 1994; Dejean *et al.*, 2010).

Construction of traps to capture prey

The walls of the leaf domatia of the Colombian Melastomataceae *Clidemia killipii* and *Tococa spadici-*

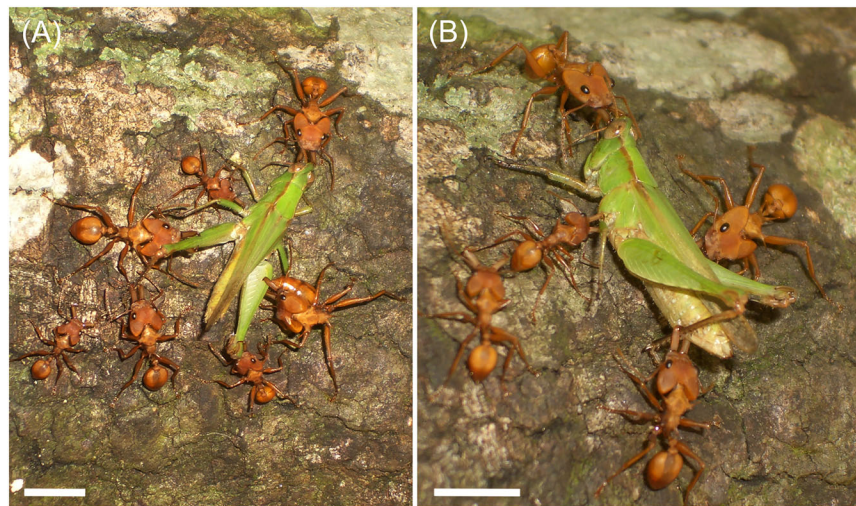


Fig. 6 *Daceton armigerum* capturing a locust (scale bars: 1 cm). A first worker attacked this prey closing their trap-jaw mandibles on its head and so stunning it. Nestmates situated in the vicinity rapidly arrived to immobilize it. (A) One of the workers situated to the right of the picture stings the hind leg of the locust. (B) Three workers seize the legs of the locust as it tries to move (photos by A. Dejean).

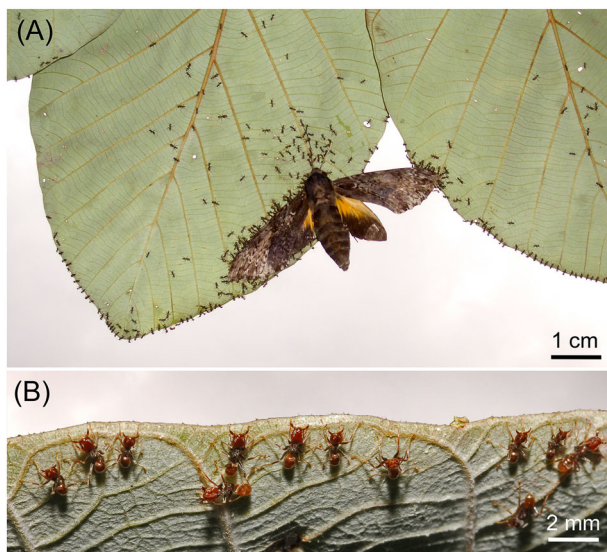


Fig. 7 (A) *Azteca andreae* hiding under the margins of the leaves of their host *Cecropia* tree have captured a sphingid moth that is exhausted after struggling in trying to escape from the ants. (B) Detail of the workers, hiding, mandibles open under a *Cecropia* leaf margin (photos by A. Dejean).

flora are verrucose, bearing a series of small protuberances pierced by small holes likely by their tiny associate ants, the myrmicine *Pheidole* sp. or the formicine *Brachymyrmex heeri*. Because their workers hide under the holes to prey on flying insects that land on these leaf

pouches, the latter constitute a kind of trap (Alvarez *et al.*, 2001; Vogel, 2012).

Also in the Neotropics, the myrmecophytes *Hirtella physophora* (Chrysobalanaceae) and *Cordia nodosa* (Boraginaceae) are, respectively, associated with the myrmicine *Allomerus decemarticulatus* and *Allomerus octoarticulatus* that build gallery-shaped traps. They use intact host-plant trichomes acting as pillars and severed trichomes reinforced by the hyphae of Chaetothyriales fungi to create a composite material that forms the vault of the gallery pierced by numerous holes from which the workers ambush prey. When a flying insect lands on the gallery, workers waiting in nearby holes seize appendages and pull backward, moving deeper into the trap, immobilizing the prey and permitting recruited workers to sting it repeatedly (Fig. 8) (Dejean *et al.*, 2005). Similarly, gallery-shaped traps formed by masticated plant material reinforced by Chaetothyrialean hyphae are built by *Azteca brevis* along the stems of trees, including the myrmecophyte *Tetrathylacium macrophyllum* (Salicaceae) (Schmidt & Dejean, 2018).

Discussion

The different types of ant foraging behavior we have described are the result of their phylogenies, the size of their colonies and their own life histories, the whole conditioned by their nesting habitats and in many cases their specific prey. They can be ground-dwelling workers



Fig. 8 (A) *Allomerus decemarticulatus* workers hidden under holes in their gallery-shaped trap built using fungi. One worker is still in a hole, while others have begun to leave the trap to retrieve the captured social wasp. (B) A locust was first captured by the *Allomerus* when a social wasp tried to rob pieces of this prey, but was captured in turn (photos by A. Dejean).

hunting solitarily, the ancestral foraging mode, or are able to recruit nestmates, in both cases specialization can occur, while army ants organize raids composed of numerous workers. Most arboreal species, if not all, hunt in groups to prevent prey from escaping in the three-dimensional space where they forage.

For a predator, the force and the speed with which the prehensile organ strikes as well as its length will determine its success at capturing prey, something enhanced when the predator has venom. In ants, the shape of the mandibles (e.g., trap-jaw mandibles) can play a large role, particularly in specialized predators that hunt solitarily. Ants have venom (or the equivalent in dolichoderine species), and their venom apparatus is determined by their subfamily. However, certain species do not use their venom during predation.

Most ground-foraging species use vision and olfaction to detect prey presence. Arboreal species, particularly territorially dominant ants, mostly use vision, but the vibrations caused when a prey lands on a leaf permits nocturnal predation by certain species, while other species build gallery-shaped traps to capture prey. Behavioral plasticity was illustrated in arboreal *Oecophylla* weaver ants able to leave their trees to ambush on prey-rich nocturnal artificial lights or on secondary ground territories where workers conceal large prey, putting them out of sight of competitors.

Because ants and termites are social insects, forming large concentrations of potential prey, numerous strategies have been developed by some predatory ants to prey on them. Most specialized termite predators have

aliphatic alcohols on their cuticles, rendering them difficult to detect. In the other cases, the ant workers mimic the cuticular compounds of the termite soldiers or, in termitolesty, can infiltrate the termitaries to rob the brood or to kill the adults. Ants that prey upon other ants also use compounds that facilitate this task; army ants use propaganda and cleptobiotic species use chemical insignificance, mimicry, or have venom that triggers submissive behavior.

In conclusion, predatory ants have a wide range of foraging behavior, something expected given their phylogenetic distance [from the primitive proceratiine *Discothyrea* to highly evolved formicines such as the arboreal *Oecophylla*; see the phylogeny of Formicidae in Antwiki (2024b)] and the great variation in their colony size, life histories and nesting habitats as well as the diversity of prey.

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Disclosure

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