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Behavior and Functional Ecology of the African Termite-Raiding Ant

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Abstract

Ants and termites play important roles in tropical ecosystems, leading to an evolutionary arms race in which diverse foraging, predation, and counter-predation strategies developed. These strategies resulted in the emergence of specialized predators of termites, such as the African termite-raiding ant, *Megaponera analis*, which organizes coordinated raids on termites of agricultural importance belonging to the subfamily Macrotermitinae. Decades of field and laboratory studies have examined the natural history of *M. analis*, describing its distribution, raiding behavior, chemical ecology, task allocation, rescue and other helping behaviors, and nursing of wounds. However, the potential of *M. analis* for the management of termites is yet to be explored. This review synthesizes the literature on *M. analis*, outlines recent progress in understanding its ecology, identifies knowledge gaps, and proposes directions for future research and possible applications of the knowledge to different fields.

1. INTRODUCTION

Ants are among the six key insect groups notable for their ecological roles as prey, predators, scavengers, indirect herbivores (100, 109, 128), soil turners (27), channelers of energy (43, 129), and dominant terrestrial fauna present in major biomes and habitats worldwide (52, 102, 109). Conservative estimates put the total number of ants at 20 quadrillion, and their dry biomass (12 megatons) is equivalent to 20% of human's and exceeds that of birds and mammals combined (12, 17, 29, 52, 109, 127–129). Their success as one of the most diverse and ecologically dominant insect species can be attributed to their ability to interact with other organisms and occupy a wide range of terrestrial habitats, from soils (subterranean) to tree canopies (arboreal) (109), and to their functional groups (12), communication systems (127), and social organization (12, 52). Adaptive ecological behaviors, such as foraging strategies, dietary diversity, and feeding preferences, have enabled ants to thrive and survive in various habitats over evolutionary time. How did these biological traits contribute to the success of ants? Initially, ants were ground-dwelling scavengers and predators that foraged individually (17, 29). However, while solitary foraging involves a single insect, it is regulated by the colony's overall fitness (16, 116) and provides access to limited food resources. This limitation, in turn, restricts colony size, growth, and development. With the rise of angiosperms during the mid to late Cretaceous Period (125–80 Mya), which provided additional food sources, ants evolved cooperative foraging (46, 52, 129). Unlike individual foraging, cooperative, group, or social foraging involves a combination of individual efforts, caste and colony demography, communication, cooperation in food retrieval, resource assessment, and the regulation of foraging at the colony level (116). Predatory ants are primarily solitary foragers, though cooperative foraging is displayed in groups that organize subterranean raids on other arthropods, often specializing on specific genera or species (17).

One of the major predatory ant groups that radiated during the primary expansion (mid to late Cretaceous Period) is the subfamily Ponerinae, which fed primarily on freshly killed arthropods, predominantly insects, with most specializing on a certain prey species (31, 52, 129). Diet specialization resulted in the development of morphological and behavioral adaptations to overcome prey defenses (52) and the synchronization of colony dynamics with the abundance and distribution of prey (135). One such ponerine species is the African termite-raiding ant, *Megaponera analis* Latreille, a termitophagous species known for organizing coordinated group raids on termites of economic importance within the subfamily Macrotermitinae. Over the past five decades, a considerable amount of research has been carried out both in the field and in the laboratory to understand the fascinating behavior and functional ecology of *M. analis*, including its natural history; scouting, raiding, and foraging behaviors; trail laying; chemical communication; prey detection; helping behaviors; and genetics (7, 21, 34–40, 50, 65, 66, 69, 77, 87, 95, 110, 119, 122, 133–136). This review consolidates the available literature on *M. analis*, bringing to the fore its ecology, unique raiding and helping behaviors, and prospects for the management of termites, as well as identified knowledge gaps and directions for future research.

2. THE AFRICAN TERMITE-RAIDING ANT, *MEGAPONERA ANALIS*

2.1. Taxonomy and Distribution

Megaponera analis is a termite specialist (termitophagous) ponerine species that organizes military-like group raids on termites, earning the common name Matabele ants after the warriors of the Matabele tribe (15, 67) of Southern Africa who were known for their fierce war tactics in the 1800s. Widely distributed throughout most of tropical sub-Saharan Africa, between 10°N latitude and 30°S latitude (125), *M. analis* has been reported in 27 countries (**Figure 1*a***), mirroring the

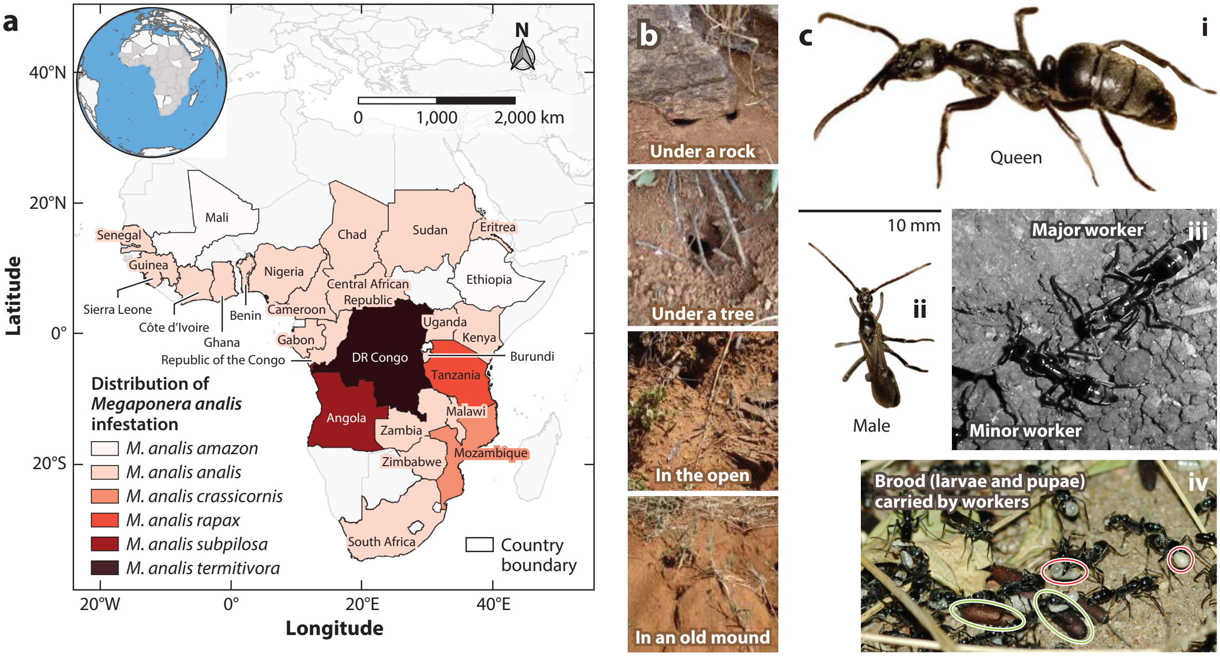

Figure 1

(*a*) Distribution of *Megaponera analis* and its subspecies reported across Africa. (*b*) *M. analis* nesting behavior under a rock, under a tree, in an open field, and in an old termite mound at Mpala, a savanna in Kenya. (*c*) Castes and reproductives of *M. analis*: (*i*) ergatoid queen, (*ii*) male, (*iii*) major worker and minor worker, and (*iv*) workers carrying larvae (*red circles*) and pupae (*green circles*) during a nest migration. Subpanels *i* and *ii* supplied by Erik T. Frank; subpanel *iv* supplied by Markus Stueben.

distribution of its termite prey (60). However, this diversity brings complexity to its taxonomy, with six subspecies (*M. analis amazon*, *M. analis analis*, *M. analis crassicornis*, *M. analis rapax*, *M. analis subpilosa*, and *M. analis termitivora*) reported on the basis of their habitats, the regions where they are found, or their raiding behavior (73) (**Figure 1*a***; **Table 1**). This complexity in taxonomy, coupled with the difficulty in delineating species or subspecies on the basis of morphological traits and genetics (28), poses a significant challenge for researchers to accurately identify this ant species. Especially within the Hymenoptera (97), as has been documented in the African honey bee (*Apis mellifera*) (42), taxonomic complexities have led most references to this species in the literature to be restricted to the species level. The naming of this species has also undergone several revisions over the years. It was first known as *Formica foetens* Fabricius 1793, then as *Formica analis* Latreille 1802 and *Megaponera foetens* Mayr 1862, and thereafter as *M. analis* (74). The ant was given the epithets *foetens* (smelly) due to its stinky smell and *analis* (anus) due to the shape of the gaster (enlarged abdomen). One hundred and thirty years later, with the relegation of *Megaponera* to a junior synonym by Brown (11), the name changed to *Pachycondyla analis*. In 2014, using ecology and behavioral tools, Schmidt & Shattuck (106) revised the classification of Ponerinae by reinstating the species to *M. analis*.

2.2. Nesting and Nest Migration Behavior

Megaponera analis ants nest in shallow ground, approximately 0.7 m deep. They do not construct the nests themselves but modify those built and abandoned by other arthropods (34, 135). These nests are often found in old inactive termite mounds, in partially rotten logs (66, 73), under rocks

Table 1 Summary of nesting, raiding dynamics, and predation behavior of *Megaponera analis* on termites reported from field and laboratory studies

Nests				Raiding dynamics				Predation on termites			
Location(s)	Subspecies	Habitat; nesting behavior; density of nests	Nest sizes (size of raiding parties)	Time of raids (number of raids per nest per day)	Foraging distance; velocity	Duration of scouting	Duration of raids (hunting time)	Termite species predated	Predation rates per nest per day	Termites carried per ant; termites carried per raiding party	Reference(s)
Cameroon[a,b]											
The Dja Biosphere Reserve Obala savanna	*Megaponera analis analis*	Tropical rain forest and savanna; inactive termite mounds, underground; ND	600 ants (237 ants)	After dawn and before dusk (ND)	53.34 m; 2.6–3 cm/s	ND	15.33 min (ND)	*Macrotermes* sp, *Cubitermes* sp.	ND	ND	20, 87
Côte d'Ivoire[a,b]											
Comoé National Park Lamto Ecology Station	*M. analis analis*	Guinea and Sudan savanna; inactive mounds and ground; 5–22 ha^{-1}	900–2,300 ants (200–500 ants)	0600–1100 h, 1500–1900 h, 2000–2400 h (1–5 raids)	40–75 m; 1.9–3.4 cm/s	ND	40–85 min (5–15 min)	*Pseudocanthotermes militaris*, *Macrotermes bellicosus*	ND	ND	34, 35, 37, 38, 66
DR Congo[a]											
Several locations	*M. analis termitivora*	Grassland; underground; ND	ND; (100–300 ants)	0800–1200 h (1–4 raids)	ND	15 min	21 min (15 min)	*Odontotermes sladdeni*, *O. planiceps*, *Microtermes calvus*, *Pseudocanthotermes militaris*	ND	6–7 termites; ND	122, 125
Kenya[a,b]											
Kajiado Mpala Research Center, Nanyuki	*M. analis analis*	Savanna; inactive termite mounds, under trees, ground, (open); 4–17 ha^{-1}	270–1,475 ants (150–550 ants)	0700–1100 h, 1600–1930 h, 2000–2400 h (1–4 raids)	3–40 m; 6.7–13.0 cm/s	5–120 min	4–99 min (2–65 min)	*Odontotermes* sp., *Microtermes* sp., *Macrotermes* sp., *Synacanthotermes* sp., *Trinervitermes* sp.	653 termites/($m^2 \cdot$day)	1–3 termites; 200–1,000 termites	51, 65, 133, 135, 136

(*Continued*)

Table 1 ***(Continued)***

Nests				Raiding dynamics				Predation on termites			
Location(s)	**Subspecies**	**Habitat; nesting behavior; density of nests**	**Nest sizes (size of raiding parties)**	**Time of raids (number of raids per nest per day)**	**Foraging distance; velocity**	**Duration of scouting**	**Duration of raids (hunting time)**	**Termite species predated**	**Predation rates per nest per day**	**Termites carried per ant; termites carried per raiding party**	**Reference(s)**
Nigeria[a,b]											
Mkowa	*M. analis analis*	Guinea savanna; inactive termite mounds, under trees, bushes; 9 ha^{-1}	320–856 ants (200–446 ants)	0700–1000 h, 1630–1930 h (1–2 raids)	30–95 m; 3.0–4.50 cm/s	ND	9 min	*Odontotermes* spp., *Ancistrotermes cavithorax*, *Macrotermes bellicosus*, *Macrotermes subhyalinus*, *Microtermes* spp.	141 [0.5285 termites/ $(m^2\cdot day)$]	ND	69, 70–73
South Africa[a,b]											
Nature reserves in Limpopo Dunstable Farm, Limpopo	*M. analis analis*	Savanna; under rocks, inactive termite mounds, ground (open); ND	200–2,000 ants (ND)	0630–1100 h 1600–1930 h, 2000–2400 h (2 raids)	ND	ND	9–120 min	*Trinervitermes* sp., mostly ND	ND	ND	23, 77, 119
Tanzania[a]											
Namakutwa-Nyamuete Forest Reserve	*M. analis rapax*	Coastal dry forest; under trees; 4 ha^{-1}	ND (16–792 ants)	Only reported as bimodal (1–10 raids)	1–44 m; 2.98–3.20 cm/s	ND	7–87 min (2–25 min)	*Odontotermes* spp., *Macrotermes subhyalinus*	932 termites/ $(m^2\cdot day)$	1–4 termites; 490–5,000 termites	7, 110
Zambia[a]											
Near Lusaka	*M. analis analis*	Savanna; ND	ND	Within 2 h of sunrise and sunset (1–2 raids)	ND	ND	17–25 min (2.5–5 min)	*Odontotermes* sp., *Pseudocanthotermes militaris*, *Hodotermes mossambicus*	ND	1–12 termites; 471 termites	110

[a] Field observation.

[b] Observation on laboratory colonies.

Abbreviation: ND, no data.

and trees, or in the open (135), and they may have two or more entrances and one brood (eggs, larvae, and pupae) chamber (**Figure 1*b***). The ants share their nest with myrmecophiles (rove beetles; Staphylinidae: *Degalliera megaponerae*, *D. peetersi*, and *Ponerilla hoelldobleri*) (62); with fungi (*Ophiocordyceps australis* and *O. unilateralis*) (112); and sometimes with the Accra snake-necked frog, *Phrynomantis microps*, commonly found in Ghana, which has evolved skin secretions that inhibit aggression by *M. analis* workers (100, 101). Nests are commonly found in savannas and forests, can be close together (~2 m) or far apart (~30 m), and can reach a density of 4 to as many as 22 nests per hectare (**Table 1**) depending on habitat type (7, 65, 66, 73, 135). Colony sizes for *M. analis* vary significantly among regions and subspecies, with some colonies consisting of a few hundred (100–300) to as many as 2,300 individuals (**Table 1**), as reported from Kenya, Nigeria, Côte d'Ivoire, and Mozambique (34, 50, 65, 66, 71, 135).

Megaponera analis displays seminomadic behavior, with migrations from an old to a new nesting site observed every 2–3 months (7, 70, 135). Migrations are initiated by scout ants, usually in the evening, and can cover distances ranging from 10–15 m (lasting 2–4 h) to 30 m (with some pit stops every 5–10 m) but not farther than observed maximum foraging distances (approximately 95 m) (71, 135). The ants can reuse a previous nesting site by returning to it after a few months (37; A.A.Y., personal observation), suggesting that they may rely on sensory cues such as chemical signals to locate old nests. During nest migration, the workers carry the queen, brood, and other colony resources, including its associated parasites (77, 125, 135). Conflicting hypotheses have been proposed for this seminomadic behavior, which fits into the general ecology of nest movement by social insects, and have been reviewed by McGlynn (75). One such hypothesis suggests that frequent migration is driven by dwindling prey and nest densities, forcing the ants to move in search of new areas and avoid competition from conspecifics. An alternative hypothesis attributed the migration to parasite loads or predation pressure from *Dorylus* spp. (driver ants) on the colony (73). A third hypothesis attributes the frequent migrations to ecological phenomena built on instinctive nomadic behavior independent of food or prey. The first two hypotheses are debatable, as migrations have been observed even in areas with low nest densities and high termite prey densities (135) as well as in locations where driver ants have not been observed as predators of *M. analis* (7, 77). Thus, it appears that the evidence for this subject is too limited to accept or reject the third hypothesis, making the basis of the frequent migrations by *M. analis* unclear and necessitating the need for more research toward understanding this behavior.

2.3. Colony Members

Colonies of *M. analis* are headed by a single ergatoid (primarily wingless) queen (79, 89–92), the only egg-laying individual with 28–64 ovarioles (119). There are two main worker types: major workers and minor workers. Morphologically, the queen can be distinguished from major workers by her more expansive gaster, denser pilosity, deeper metanotal grove, and slanting petiole (6, 51, 89, 92) (**Figure 1*c*, subpanel *i***), making her the largest individual in the nest at ~20 mm. Workers are sterile; are between 5 and 18 mm in length (100, 119), exhibiting overlap in size (monophasic allometry) (23); are polymorphic; and are grouped into majors and minors (**Figure 1*c*, subpanel *iii***) and sometimes medias (71, 119), with clearly allocated tasks (**Supplemental Table 1**). Major workers are larger and darker with fine pubescence, which is reduced in the much smaller shiny minor workers. Although the males (drones) are winged, they are smaller than the workers, with small heads and large eyes (72, 111) (**Figure 1*c*, subpanel *ii***). Males fly out to mate throughout the year and locate queens using trail pheromones left by raiding parties. Sometimes they follow raiding parties to raids (72, 111). Mating with the queen usually takes place inside the nest, with

Supplemental Material >

new colonies formed through the fission of old ones or through dependent colony foundation, in which the new queen sets out with some workers to establish her own nest (52). Eggs and larvae are white and the pupae are enclosed in brown cocoons (**Figure 1*c*, subpanel *iv***). Unlike for workers, little is known about the biology and behavior of the males and queens, or about reproduction in *M. analis*, as these topics have not been the focus of previous studies.

3. FORAGING AND RAIDING BEHAVIORS

The ecology of foraging in ants is dependent on their diet, colony requirements, differences between the energy yield (investment versus expenditure), timing, environment, and foraging range (16, 107, 116). Foraging behavior and eusociality in ant societies make them retrieve and gather food at a central place (nest), following the principle of central place foraging and optimally (16, 55, 96, 116) utilizing resources for colony fitness. Because searching for food is critical for colony fitness (89), most especially for a specialist group forager with mass recruiting (16, 29) like *M. analis*, the synchronization of foraging behavior with prey availability (8, 21, 88) is important to ensure optimal foraging (30, 35, 37, 38, 46, 58, 65, 73, 87, 135). Foraging behavior in *M. analis* aligns with Charnov's (18) marginal value theorem, which states that an optimal predator will accept an item if it does not provide less energy than that available in the same time from a different diet. The foraging and raiding behaviors of *M. analis* were first described by Livingstone in 1857 (67). Since then, these behaviors have caught the attention of many researchers (**Table 1**) because of their complexity, coordination, organization, specialization (on target prey), and the pronounced division of labor displayed.

3.1. Raids

Raiding behavior by *M. analis* can be divided into the following phases: scouting, recruitment, arrival at termite sources, attack, retrieval of termites, collection (of termites and injured nestmates), and return journey (**Figure 2*a***; **Supplemental Video 1**). Raids occur in the mornings (0600–1100 h) and evenings (1600–1930 h) (7, 73) (**Table 1**). Although a bimodal foraging pattern is commonly reported, less frequent nocturnal (2000–2400 h) raids (**Table 1**) have been observed (135) during summer when temperatures are high. This adaptive behavior could align with termite activity or serve to avoid the risk of losing track of the trail chemical signals reported as pheromones (chemicals used for communication within the same species) (25, 56, 99), which can disorient raiding columns, as observed when trails are washed away by rain or removed artificially (70, 73; A.A.Y., personal observation).

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3.1.1. Scouting. Foraging activity begins with scouting when scouts (10–19) (usually major workers) leave their nest in search of termite foraging sites. The search can last for a few minutes or up to 1 h, covering a mean distance of 30 m to a maximum of 95 m (**Table 1**). However, little is known about a scout's behavior after finding a food source, especially because the foraging patch is often heterogeneous with the risk of encountering predators (77). Some researchers have suggested that decisions made by individual scouts determine raids and their frequencies, especially in areas with high prey availability, as observed when ants are reared in the laboratory (38, 51, 132). However, it is highly unlikely that foraging in such a group-raiding species is determined by an individual's decision rather than by the fitness and needs of the colony (38, 41, 116). Colonies from South Africa have been observed to release scouts every 10 min when initial scouts were removed, with scouting lasting up to 120 min (77) (**Table 1**). The use of starvation to predict hunger states led to a threefold increase in scouting in colonies found in Côte d'Ivoire (38). Further studies of path choices (34) and mechanisms regulating scout behavior are needed.

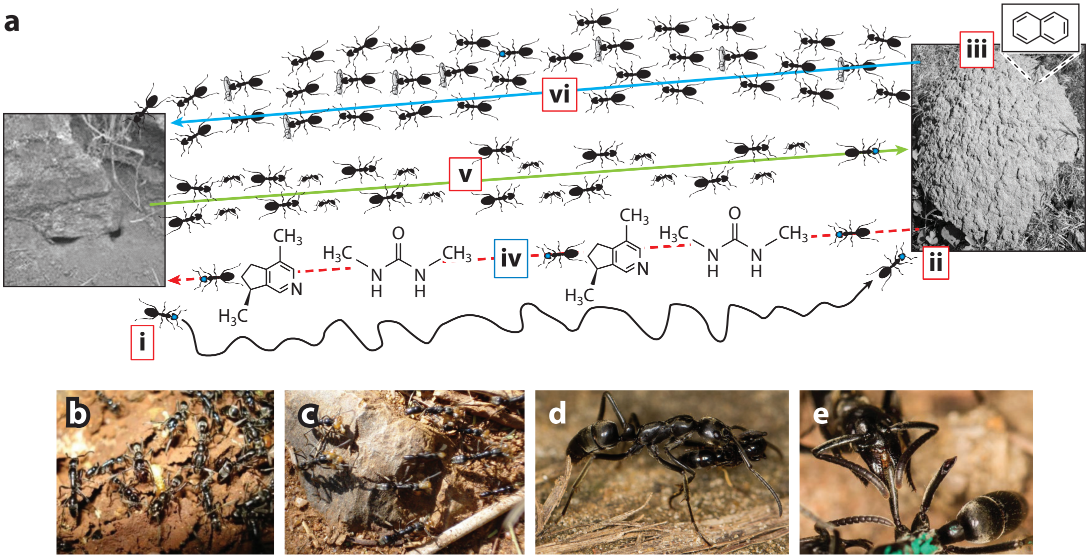

Figure 2

(*a*) The sequence involved in the raiding behavior of *Megaponera analis*. (*i*) A scout leaves the nest and randomly searches for termites (*black trail*). (*ii*) A scout detects termites using kairomone (*iii*) and vibrations and then returns (*iv*) to the nest using the shortest possible route (*red dotted line*), laying trail pheromones (*N*,*N*-dimethyl uracil and actinidine). Thereafter, she recruits nestmates (*v*) that march in a column formation toward the termite source following the trail (*green line*). (*b*) At the termite source, the major workers break open the galleries while the minor workers enter and raid the termites and pile them at the surface. (*c*) After the raids, the raiding column returns back to the nest (*a*, subpanel *vi*) using the same path (*blue line*) carrying termites in their mandibles. (*d*) Injured workers during raids are carried back to the nest by nestmates (*e*) where their wounds are nursed with antimicrobial compounds secreted by the metapleural glands. Panels *d* and *e* supplied by Erik T. Frank.

3.1.2. Recruitment. Upon detecting and assessing a termite source using attractive chemicals (kairomones; see Section 4) (57, 59, 70, 133), the scout returns to the nest via the quickest route (35), laying trail pheromones (see Section 4) in the process (possibly to expend less energy) (50, 81) by lowering its gaster to the ground as it walks along the route, and recruits nestmates within 1–5 min (110). After recruitment, it leads the outward journey toward the termite source in a column formation. However, if the scouting is unsuccessful, the scout returns to the nest in a meandering route (135). This behavior by an unsuccessful scout has not been studied but could be a measure to avoid or ward off predators.

The size of a raiding party is determined by factors such as colony size, colony requirements, richness of the food source, and termite defenses (7, 35, 65, 71, 135). Typically, raiding parties consist of between 20 and 500 ants (**Table 1**), or approximately 30–75% of the total nest population.

3.1.3. Attack and retrieval. A few centimeters away from the termite source, the raiding party stops, spreads out in a formation, and attacks using a clear display of task allocation (20, 21, 119). The major workers break up the termite galleries while the minor workers invade them (7, 38, 73, 87, 122, 135). The ant workers attack and sting termites (workers and soldiers), paralyzing them in the process (21). Paralyzed ants are carried to the surface and piled up near the termite's foraging gallery (**Figure 2*b***) until the signals to stop the attack in the form of chemical (see Section 4) and visual cues are received (134). The attack takes the form of an arms race, with the termites resisting and inflicting injuries on the ants using their mandibles (which they use to bite and cling onto the ants) and defensive chemicals (allomones secreted by the labial glands); the severity of the injuries depends on the termite species raided (38, 135). The attack and retrieval process can last between 5 and 30 min (7, 38, 135) (**Table 1**), after which the workers stop hunting and return to the pile of paralyzed termites (135).

3.1.4. Collection of termites and return journey. After the attack, the major workers collect between 1 and 12 termites between their mandibles, while minor workers carry 1 to 3 (depending on the size and species of termite prey) (**Figure 2*c***; **Table 1**). Some workers carry injured nestmates (**Figure 2*d***), while others carry none as they follow the raiding column as runners (135) (see **Supplemental Table 1**). The return journey usually starts immediately in a clear formation and at a faster pace, using the same route as that of the outward trip (71, 135). The return trip is led by the raid leader followed by other scouts, with major workers in the front and rear serving as lead and rear guards (37). This type of foraging behavior in *M. analis*, in which raids on social insects are led by scouts, could be the very first step in the evolution of army ant behavior (52), characterized by obligate collative foraging, nomadism, and a specialized queen caste. While the presence of guards in the formation during the return journey may serve to protect the raiding party, it is not yet known why other scouts join the raids or serve as leaders (**Supplemental Table 1**). A possible explanation for this behavior could be the quality and quantity of combined odors released by ants, captured termite prey, and other associated cues (25, 56, 81, 96, 133–136). When ants are disturbed during either outward or return journeys, they make audible stridulatory sounds to deter predators (135) (see Section 4).

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Colonies of *M. analis* can send out more than one foraging party in a day, with the frequency of raids varying from 1 to 10 raids per nest per day (7, 65, 119, 135) (**Table 1**), whereas some colonies stay dormant for days without going on raids (135). Like most of the behaviors described here, it remains speculative as to what determines the raiding frequencies or the dormant periods of *M. analis*. Attributing this behavior to food reserves or their absence is challenging because *M. analis* kills and consumes its termite prey fresh (132), and no evidence of food reserves has been found in its nests (132, 133, 136).

3.2. Preferences and Predation Rates on Termites

Ants and termites share similar habitats and have engaged in an evolutionary arms race, with ants evolving predatory tactics and termites evolving defensive strategies (17, 26, 32, 44, 52). Predation by ants of the subfamilies Ponerinae and Myrmicinae is thought to have resulted in the evolution of a termite soldier caste specialized in chemical and physical defense (120). Indeed, the presence of ants in ecosystems can increase predation and control pests and fungi (93, 94).

Megaponera analis predates termites of the genera *Macrotermes*, *Odontotermes*, *Microtermes*, *Ancistrotermes*, *Cubitermes*, *Pseudocanthotermes*, *Synacanthotermes*, and *Trinervitermes* (**Table 1**). In habitats where more than one genus of termite prey is available, preferences of and choices by ants depend on the presence, abundance, foraging behavior, size (reward), and defenses of the termites (7, 38, 73, 87, 135). Predation rates differ depending on habitat, nest, season, and prey type. In savannas, they range from 200 to 1,000 termites per nest per day (65, 73, 135), and in forests (7), up to 5,000 termites per nest per day (**Table 1**). Although predation rates of 42 to 141 termites/($m^2 \cdot ha$) may seem negligible, the overall impact on a habitat becomes significant when considering the frequency of raids per nest and the number of ant nests per hectare, which has been estimated to range from 1 to as many as 22 (**Table 1**).

3.3. Rescue Behavior and Care for Injured Nestmates

One of the key drivers for the success of eusocial insect societies lies in altruistic behaviors displayed by workers caring for offspring that are not their own (13), much to their detriment. Worker

Table 2 Semiochemicals used by *Megaponera analis*, their sources, and the behaviors and activities they regulate

Behavior type	Semiochemical	Source	Activity	Reference(s)
Nestmate recognition	Methyl-branched alkenes	Secretions from the Dufour's and mandibular glands found on the cuticle	Nestmate recognition	135, 136
Task allocation	Short-chain hydrocarbons (C_{10}-C_{13})	Cuticular hydrocarbons	Task allocation and communication during raids	134, 136
Alarm/help	*n*-undecane, *n*-tridecane	ND	Alerting nestmates of danger	131, 134
Raid coordination/ organization	Pyrimidone (*N*,*N*-dimethyluracil), monoterpene alkaloids (actinidine, valerian)	Pygidial and poison glands	Trail following and recruitment	50, 59, 69
Scouting	Hydrocarbon (naphthalene), aromatic ketone (2-acetonaphthone)	Termite soil galleries	Detection of termites before raids	70, 133
Identification of injured nestmates	Hydrocarbons and proteins	Metapleural glands	Solicitation for help removing termite soldiers and wound treatment	36
Retinue	Compounds not identified	Intersegmental glands	Worker attraction and retinue behavior	51

Abbreviation: ND, not determined.

ants provide help to nestmates that are in distress, putting themselves at risk—a helping behavior known as rescue (83). The adaptive value of rescue behavior outside the nest by ants was first observed in *M. analis* when raiding parties were attacked by driver ants (*Dorylus* spp.) and the major workers were seen assisting minor workers remove the attacking *Dorylus*, with some even returning to assist other workers (58). Rescue and helping behaviors are observed after raids, when *M. analis* workers (helpers) carry nestmates that have reduced mobility (**Figure 2*d***) resulting from injuries by termites or exhaustion (14, 39, 135). Despite suffering injuries, including limb loss, nearly half of the injured ants had a termite clinging to them (39). Nestmates are attracted to injured workers through the release of pheromones from the mandibular glands (**Table 2**) of the injured worker, which elicits inspection and assessment of the injury by nestmates. If help is not received, the injured ant succumbs to her injuries or becomes easy prey to predators (34). Back in the nest, clinging termites are removed and wounds are treated aseptically (**Figure 2*d***) by grooming and applying antimicrobial compounds secreted by the metapleural glands (36, 39, 40). Injured ants requiring treatment are distinguished from healthy nestmates by their cuticular hydrocarbon profiles, with treatment of wounds reducing mortality by 90% (36). Although the mechanism of wound healing in *M. analis* has not been studied extensively, wound healing in some insects has been previously described (63, 115, 126). The complex secretions from the metapleural glands, which contain 112 compounds that include proteins, are used for the treatment of wounds (36). It would be interesting to identify the wound-healing proteins. Comparative studies of wound treatment by other ants (9) are required in order to understand its evolution and potential application in entomotherapy.

4. COMMUNICATION IN *MEGAPONERA ANALIS*

Communication is central to the regulation of eusociality (52), in which chemical signals (pheromones) from exocrine glands (5, 10, 118) play a key role in mediating behaviors (49) and visual and acoustic cues are used mainly for navigation (123), orientation (108), and distress calls (53). Group raiding by *M. analis* is coordinated with the use of semiochemicals comprising pheromones released from the mandibular, poison, Dufour's, metapleural, and pygidial glands of ant workers and allelochemicals (interspecific chemical signals) in the form of kairomones from termite prey (36, 50, 51, 59, 69, 70, 133–136). The semiochemicals used by *M. analis* are from different chemical classes and vary according to behavior, activity, and context/audience (**Table 2**).

Nestmate recognition, task allocation, and identification of injured workers are facilitated by short-range cues made up of cuticular hydrocarbons (36, 134, 136) from the Dufour's gland and secretions of the mandibular glands (69). Cuticular hydrocarbons from *M. analis* workers have an interesting chemistry, with the long chains varying between populations and the shorter chains, including the candidate alarm pheromones *n*-undecane and *n*-tridecane, conserved among populations (131, 134). These cues are usually volatile, facilitating ease of detection by nestmates during raids or in the hive where rapid and fast communication is needed.

Earlier work identified the pyrimidone *N,N*-dimethyluracil and the monoterpene alkaloid actinidine [also a plant metabolite found in the silver vine (*Actinidia polygama*) and valerian (*Valeriana officinalis*)], produced by the pygidial and poison glands, as trail following and recruitment pheromones, respectively (50, 59, 69) (**Table 2**). These semiochemicals are less volatile, enabling detection during trail following by raiding ants that have to follow the path laid by the scout on the outward journey, and by the raiding party after the raids (see Section 3.1). The persistent nature of these pheromones also ensures the consistency of trails so that the ants are not lost, thus preventing disorientation during the raids.

Scouts eavesdrop on termite communication (124) by using chemicals (naphthalene and 2-acetonaphthone) embedded in termite soil sheeting (**Table 2**) as long-range host-finding cues and vibrations as determinants of short-range cues during foraging (70, 133), without needing to take samples of prey back to the nest as an indication of successful scouting.

While most chemical communication work was centered on workers, queens of *M. analis* have been observed attracting retinues using pheromones emitted from their intersegmental glands that are surrounded by sclerites (51). Little is known about the use of acoustic signals by *M. analis* besides the fact that it stridulates when disturbed or during raids (50).

Stridulation is hypothesized to deter predators, with no established role in communication because it is transmitted through substrates (33, 48) and is usually loud (50–70 dB by *M. analis*). Although this is the general view among myrmecologists, the adaptive role of acoustic communication (45, 53) in many ant species is debatable in the context of ant behavior and sensory physiology.

5. PROSPECTS OF *MEGAPONERA ANALIS* AS A NATURAL SOURCE OF BIORATIONALS FOR MANAGING TERMITES

Termites play a vital role in the stability of ecosystems, especially in the tropics, by facilitating soil fertilization, bioturbation, formation, and decomposition of organic matter (47, 82). Despite these positive attributes, they are also notorious for the damage they inflict on wooden structures and agricultural products (47, 113), causing annual losses amounting to $40 billion globally (2, 3, 103). In the tropics, the damage caused by termites could lead to crop losses of 5–100% (76, 80). Synthetic chemical insecticides, the mainstay for termite management, are harmful to human health, damage the environment, and cause insecticide resistance in termites. Insecticide resistance has already been demonstrated for several species of termites at different tropic levels (85, 105, 114). These negative effects of synthetic chemical insecticides call for the use and adoption of safer alternative management strategies, including biorationals for termites in an integrated pest management (IPM) approach (2, 24, 64, 68). Such IPM tactics should include the use of semiochemical-based baits to attract or repel termites. Knowledge from studies of *M. analis* semiochemicals, especially those of compounds used during raids, in alarm pheromones, and for detecting termites (133, 134), can be explored to develop attractants and repellents similar to those from other dolichoderine ants (22, 44).

Predation by ants and the significant impact it has on different tropic levels in tropical agroecological systems make them viable tools for pest regulation and integration into IPM strategies (93, 94, 104, 121). Some of the favorable attributes that make use of ants as suitable biocontrol agents include their abundance, responsiveness to prey densities, ability to store food in their nests, deterrence of large predators, wide habitat range, and ability to be manipulated for the purpose needed (98, 121). Prey specialization on termites of economic importance makes *M. analis* a good candidate for inclusion in an IPM program against termites that will reduce the use of toxic chemicals. Knowledge of raiding dynamics and impacts of predation on termites can be explored in a way similar to that for *Oecophylla*, *Dolichoderus*, *Formica*, *Azteca*, *Wasmannia*, *Anoplolepis*, and *Solenopsis* species used as predators in different habitats worldwide (84, 121). Unlike the use of baits, IPM approaches will be viable only in habitats that are suitable for *M. analis*; as such, these methods may be restricted to the tropics. The possibility that the introduction of the ants into new habitats could result in the displacement of native termite predators and or other beneficial ant species, including the beneficial species becoming a pest, must be addressed prior to their introduction into new landscapes. Another consideration is the challenge of removing the ants if they are not needed in the system, as their defensive strategies include painful bites and stings (6). A similar challenge has been observed in which *Oecophylla* spp. are used to control pests in orchards (84).

6. KNOWLEDGE GAPS AND DIRECTIONS FOR FUTURE RESEARCH

Five decades of research on the African termite-raiding ant, *M. analis*, have examined and revealed its natural history, raiding behavior, chemical communication, wound treatment, and helping behaviors (23, 35–40, 50, 51, 65–67, 69, 70–73, 77, 87, 122, 133–136). Despite these advances, genetic information on *M. analis* is still poorly understood. Only one study exists, conducted by Pohl et al. (95) on social and population genetics, which revealed monogyny and monandry and evidence of gene flow between four subpopulations found in Comoé National Park, Côte d'Ivoire. Its genome is yet to be sequenced, nor are there any comparative studies of the genetics of the six known subspecies found on the continent. Given the diversity and wide distribution of the species and the availability of high-throughput sequencing capability, such a continent-wide study should include males and focus on genetics, which would not only proffer insights into behavior but also help identify specific genes and/or enzymes of importance for the development of termite control methods. Comparative studies of nesting, scouting behavior, reasons for frequent migration, reproduction, and termites' dietary preferences will be useful in developing region-specific IPM strategies against termites. Such studies can apply stable isotope techniques to determine diets and modeling to determine habitat suitability and the optimal number of nests required for effective biocontrol. Habitat suitability studies should include modeling that incorporates present prey distributions and future scenarios amid climate change, which has been forecasted to affect subterranean termites (54, 86).

To ensure the development of effective target-specific semiochemical-based management, bioprospecting studies should look at differences in the composition of chemical signals between subspecies and regions. This is important considering the wide distribution of *M. analis* in different habitats and its display of differences in raiding behavior and prey choices. Indeed, regional differences have been shown in the composition of pheromones from the mandibular gland of African honey bees (137, 138) and for different populations of *Nesidiocoris tenuis*, the predator of the South American tomato pinworm, *Tuta absoluta*, a pest of economic importance in tomato production (1). Compounds released by the metapleural gland for treating wounds (36) need to be further explored to identify active compounds/fractions that could be applied in entomotherapy for wound healing and possible antimicrobial activity against antimicrobial-resistant human pathogens. Concepts of organization, communication, and division of labor in ant societies have been used to develop models for application in neural networks (130), engineering design problems (61), control system coordination (117), optimization of static mobile sensor networks (19), swarming behavior, and artificial intelligence (4, 78). Raids and the way they are conducted with precision, clear division of labor, optimized energy cost, and synchronization with prey foraging behavior have potential applications in computer networking and allocation of computing resources for maximum output.

7. CONCLUDING REMARKS

The fascinating behavior of the African termite-raiding ant, *M. analis*, gave rise to the interest in this species, with a resultant growing body of literature covering its biology and functional ecology in tropical African savannas. To date, we are privileged to know some aspects of how raids are organized, from foraging to conducting the actual raids, including division of labor and communication within and outside the nests. However, we still do not know what governs some of these behaviors in the different subspecies or how these subspecies differ from each other. There are no efforts to apply the knowledge to practical termite management. Fundamental questions on the functional ecology of *M. analis* remain unanswered. By answering these questions, we may better understand this fascinating ant and ant evolution and apply this knowledge to different fields.

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LITERATURE CITED

1. Adams B, Khamis FM, Yusuf AA, Torto B. 2025. Zoophytophagous predator sex pheromone and visual cues of opposing reflectance spectra lure predator and invasive prey. *J. Adv. Res.* 70:15–27

2. Ahmad F, Fouad H, Liang S-Y, Hu Y, Mo J-C. 2021. Termites and Chinese agricultural system: applications and advances in integrated termite management and chemical control. *Insect Sci*. 28:2–20
3. Ahmad SK, Dawah HA, Khan MA. 2018. Ecology of termites. In *Termites and Sustainable Management*, Vol. 1: *Biology, Social Behaviour and Economic Importance*, ed. MA Khan, W Ahmad. Springer International
4. Alhammadi A, Shayea I, El-Saleh AA, Azmi MH, Ismail ZH, et al. 2024. Artificial intelligence in 6G wireless networks: opportunities, applications, and challenges. *Int. J. Intell. Syst.* 2024:8845070
5. Ali MF, Morgan ED. 1990. Chemical communication in insect communities: a guide to insect pheromones with special emphasis on social insects. *Biol. Rev.* 65:227–47
6. Arnold G. 1915. A monograph of the Formicidae of South Africa. Part I. Ponerinae, Dorylinae. *Ann. S. Afr. Mus.* 14:1–159
7. Bayliss J, Fielding A. 2002. Termitophagous foraging by *Pachycondyla analis* (Latreille) (Formicidae, Ponerinae) in a Tanzanian coastal dry forest. *Sociobiology* 39:103–22
8. Bernstein RA. 1975. Foraging strategies of ants in response to variable food density. *Ecology* 56:213–19
9. Beydizada NI, Abels A, Schultheiss P, Frank ET. 2024. Injury-dependent wound care behavior in the desert ant *Cataglyphis nodus*. *Behav. Ecol. Sociobiol.* 78:97
10. Billen J, Morgan ED. 1998. Pheromone communication in social insects: sources and secretions. In *Pheromone Communication in Social Insects*, ed. RK Vander Meer, MD Breed, ML Winston, KE Espelie. CRC Press
11. Bolton B. 1994. *Identification Guide to the Ant Genera of the World*. Harvard University Press
12. Borowiec ML, Moreau CS, Rabeling C. 2021. Ants: phylogeny and classification. In *Encyclopedia of Social Insects*, ed. CK Starr. Springer Nature
13. Bourke AF, Franks NR. 1995. *Social Evolution in Ants*. Princeton University Press
14. Burgeon L. 1929. Une organisation sanitaire chez les fourmis *Megaponera*. *Rev. Zool. Bot. Afr.* 16:94–95
15. Carnegie D. 1894. *Among the Matabele*. Religious Tract Society
16. Carroll CR, Janzen DH. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4:231–57
17. Cerdá X, Dejean A. 2011. Predation by ants on arthropods and other animals. In *Predation in the Hymenoptera: An Evolutionary Perspective*, ed. C Polidori. TransWorld Research Network
18. Charnov EL. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9:129–36
19. Chen X, Yu L, Wang T, Liu A, Wu X, et al. 2020. Artificial intelligence-empowered path selection: a survey of ant colony optimization for static and mobile sensor networks. *IEEE Access* 8:71497–511
20. Chittka L, Muller H. 2009. Learning, specialization, efficiency and task allocation in social insects. *Commun. Integr. Biol.* 2:151–54
21. Corbara B, Dejean A. 2000. Adaptive behavioral flexibility of the ant *Pachycondyla analis* (= *Megaponera foetens*) (Formicidae: Ponerinae) during prey capture. *Sociobiology* 36:465–83
22. Cornelius ML, Grace JK, Ford PW, Davidson BS. 1995. Toxicity and repellency of semiochemicals extracted from a dolichoderine ant (Hymenoptera: Formicidae) to the Formosan subterranean termite (Isoptera: Rhinotermitidae). *Environ. Entomol.* 24:1263–69
23. Crewe R, Peeters C, Villet M. 1984. Frequency distribution of worker sizes in *Megaponera foetens* (Fabricius). *S. Afr. J. Zool.* 19:247–48
24. Culliney T, Grace J. 2000. Prospects for the biological control of subterranean termites (Isoptera: Rhinotermitidae), with special reference to *Coptotermes formosanus*. *Bull. Entomol. Res.* 90:9–21
25. Czaczkes TJ, Grüter C, Ratnieks FL. 2015. Trail pheromones: an integrative view of their role in social insect colony organization. *Annu. Rev. Entomol.* 60:581–99
26. Daly-Schveitzer S, Beugnon G, Lachaud J-P. 2007. Prey weight and overwhelming difficulty impact the choice of retrieval strategy in the Neotropical ant *Gnamptogenys sulcata* (F. Smith). *Insectes Soc*. 54:319–28
27. Dauber J, Wolters V. 2000. Microbial activity and functional diversity in the mounds of three different ant species. *Soil Biol. Biochem.* 32:93–99
28. De Queiroz K. 2007. Species concepts and species delimitation. *Syst. Biol.* 56:879–86
29. Dejean A, Orivel J, Cerdá X, Azémar F, Corbara B, Touchard A. 2025. Foraging by predatory ants: a review. *Insect Sci.* 32:1096–118
30. Dejean A, Schatz B, Orivel J, Beugnon G, Lachaud J-P, Corbara B. 1999. Feeding preferences in African ponerine ants: a cafeteria experiment (Hymenoptera: Formicidae). *Sociobiology* 34:558–68

31. Dejean A, Suzzoni JP, Schatz B. 2001. Behavioral adaptations of an African ponerine ant in the capture of millipedes. *Behaviour* 138:981–96
32. Deligne J, Quennedey A, Blum MS. 1981. The enemies and defense mechanisms of termites. In *Social Insects*, ed. HR Hermann. Academic
33. Ferreira RS, Cros E, Fresneau D, Rybak F. 2014. Behavioural contexts of sound production in *Pachycondyla* ants (Formicidae: Ponerinae). *Acta Acust. United Acust.* 100:739–47
34. Frank ET. 2021. Matabele ant (*Megaponera analis*). In *Encyclopedia of Social Insects*, ed. CK Starr. Springer Nature
35. Frank ET, Hönle PO, Linsenmair KE. 2018. Time-optimized path choice in the termite-hunting ant *Megaponera analis*. *J. Exp. Biol.* 221(Part 13):jeb174854
36. Frank ET, Kesner L, Liberti J, Helleu Q, LeBoeuf AC, et al. 2023. Targeted treatment of injured nestmates with antimicrobial compounds in an ant society. *Nat. Commun.* 14:8446
37. Frank ET, Linsenmair K. 2017. Flexible task allocation and raid organization in the termite-hunting ant *Megaponera analis*. *Insectes Soc.* 64:579–89
38. Frank ET, Linsenmair KE. 2017. Individual versus collective decision making: optimal foraging in the group-hunting termite specialist *Megaponera analis*. *Anim. Behav.* 130:27–35
39. Frank ET, Schmitt T, Hovestadt T, Mitesser O, Stiegler J, Linsenmair KE. 2017. Saving the injured: rescue behavior in the termite-hunting ant *Megaponera analis*. *Sci. Adv.* 3:e1602187
40. Frank ET, Wehrhahn M, Linsenmair KE. 2018. Wound treatment and selective help in a termite-hunting ant. *Proc. R. Soc. B* 285:20172457
41. Franks NR, Pratt SC, Mallon EB, Britton NF, Sumpter DJ. 2002. Information flow, opinion polling and collective intelligence in house-hunting social insects. *Philos. Trans. R. Soc. B* 357:1567–83
42. Frazier M, Muli E, Patch H. 2024. Ecology and management of African honey bees (*Apis mellifera* L.). *Annu. Rev. Entomol.* 69:439–53
43. Frouz J, Jilková V. 2008. The effect of ants on soil properties and processes (Hymenoptera: Formicidae). *Myrmecol. News* 11:191–99
44. Fujiwara-Tsujii N, Cheong C, Maryati M, Yamaoka R. 2006. Identification of a potent termite repellent from the Bornean dolichoderine ant *Dolochoderine sulcaticepus* (Hymenoptera: Formicidae). *J. Trop. Biol. Conserv.* 2:71–78
45. Golden T, Hill P. 2016. The evolution of stridulatory communication in ants, revisited. *Insectes Soc.* 63:309–19
46. Gordon D. 2019. The ecology of collective behavior in ants. *Annu. Rev. Entomol.* 64:35–50
47. Govorushko S. 2019. Economic and ecological importance of termites: a global review. *Entomol. Sci.* 22:21–35
48. Hickling R, Brown RL. 2000. Analysis of acoustic communication by ants. *J. Acoust. Soc. Am.* 108(4):1920–29
49. Hölldobler B. 1995. The chemistry of social regulation: multicomponent signals in ant societies. *PNAS* 92:19–22
50. Hölldobler B, Braun U, Gronenberg W, Kirchner WH, Peeters C. 1994. Trail communication in the ant *Megaponera foetens* (Fabr.) (Formicidae, Ponerinae). *J. Insect Physiol.* 40:585–93
51. Hölldobler B, Peeters C, Obermayer M. 1994. Exocrine glands and the attractiveness of the ergatoid queen in the ponerine ant *Megaponera foetens*. *Insectes Soc.* 41:63–72
52. Hölldobler B, Wilson EO. 1990. *The Ants*. Harvard University Press
53. Hunt JH, Richard F-J. 2013. Intracolony vibroacoustic communication in social insects. *Insectes Soc.* 60:403–17
54. Istifanus AP, Abdelmutalab AG, Pirk CW, Yusuf AA. 2023. Predicting the habitat suitability and distribution of two species of mound-building termites in Nigeria using bioclimatic and vegetation variables. *Diversity* 15:157
55. Iwasa Y, Higashi M, Yamamura N. 1981. Prey distribution as a factor determining the choice of optimal foraging strategy. *Am. Nat.* 117:710–23
56. Jackson DE, Martin SJ, Ratnieks FL, Holcombe M. 2007. Spatial and temporal variation in pheromone composition of ant foraging trails. *Behav. Ecol.* 18:444–50

57. Jaffe K, Issa S, Sainz-Borgo C. 2012. Chemical recruitment for foraging in ants (Formicidae) and termites (Isoptera): a revealing comparison. *Psyche J. Entomol.* 2012:694910
58. Jan B, Britta K. 2007. Cooperative self-defence: Matabele ants (*Pachycondyla analis*) against African driver ants (*Dorylus* sp.; Hymenoptera: Formicidae). *Myrmecol. News* 10:27–28
59. Janssen E, Bestman HJ, Hölldobler B, Kern F. 1995. *N*,*N*-dimethyluracil and actinidine, two pheromones of the ponerine ant *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae). *J. Chem. Ecol.* 21:1947–55
60. Jones DT, Eggleton P. 2011. Global biogeography of termites: a compilation of sources. In *Biology of Termites: A Modern Synthesis*, ed. D Bignell, Y Roisin, N Lo. Springer
61. Kaveh A, Talatahari S. 2010. An improved ant colony optimization for constrained engineering design problems. *Eng. Comput.* 27:155–82
62. Kistner D. 1993. Some myrmecophiles (Coleoptera: Staphylinidae) associated with *Megaponera foetens* (Hymenoptera: Formicidae). *Sociobiology* 23:71–93
63. Lai-Fook J. 1966. The repair of wounds in the integument of insects. *J. Insect Physiol.* 12:195–226
64. Lenz M, Sunden-Bylehn A, Thorne B, Lewis V, Haverty M. 2003. *Finding Alternatives to Persistent Organic Pollutants (POPs) for Termite Management*. United Nations Environment Programme. **https://www.informea.org/en/finding-alternatives-persistent-organic-pollutants-pops-termite-management**
65. Lepage M. 1981. Étude de la prédation de *Megaponera foetens* (F.) sur les populations récoltantes de Macrotermitinae dans un ecosystème semi-aride (Kajiado-Kenya). *Insectes Soc*. 28:247–62
66. Lévieux J. 1966. Noté préliminaire sur les colonnes de chasse de *Megaponera foetens* F. (Hymenoptera: Formicidae). *Insectes Soc*. 13:117–26
67. Livingstone D. 2004. Missionary travels and researches in South Africa. In *Nineteenth-Century Travels, Explorations and Empires*, Part II Vol. 7: *Writings from the Era of Imperial Consolidation, 1835-1910*, ed. PJ Kitson, W Baker. Routledge
68. Logan JW, Cowie RH, Wood T. 1990. Termite (Isoptera) control in agriculture and forestry by non-chemical methods: a review. *Bull. Entomol. Res.* 80:309–30
69. Longhurst C, Baker R, Howse PE. 1979. Termite predation by *Megaponera foetens* (FAB.) (Hymenoptera: Formicidae) coordination of raids by glandular secretions. *J. Chem. Ecol.* 5:703–19
70. Longhurst C, Howse P. 1978. The use of kairomones by *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae) in the detection of its termite prey. *Anim. Behav.* 26:1213–18
71. Longhurst C, Howse P. 1979. Foraging, recruitment and emigration in *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae) from the Nigerian Guinea Savanna. *Insectes Soc*. 26:204–15
72. Longhurst C, Howse P. 1979. Some aspects of the biology of the males of *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae). *Insectes Soc*. 26:85–91
73. Longhurst C, Johnson R, Wood T. 1978. Predation by *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae) on termites in the Nigerian southern Guinea savanna. *Oecologia* 32:101–7
74. Mayr GL. 1862. Myrmecologische studien *Megaponera*; (diagnosis in key) as genus; *Megaponera* in Ponerinae [Poneridae]. *Verh. K-K. Zool. Bot. Ges.* 12:649–776
75. McGlynn TP. 2012. The ecology of nest movement in social insects. *Annu. Rev. Entomol.* 57:291–308
76. Mitchell JD. 2002. Termites as pests of crops, forestry, rangeland and structures in southern Africa and their control. *Sociobiology* 40:47–69
77. Modiba RV, Pirk CW, Yusuf AA. 2024. Temporal dynamics of scout release-behavior of termitophagous ponerine ant, *Megaponera analis*. *J. Insect Behav.* 37:233–42
78. Mohan CB, Baskaran R. 2012. A survey: ant colony optimization based recent research and implementation on several engineering domain. *Expert Syst. Appl.* 39:4618–27
79. Molet M, Wheeler DE, Peeters C. 2012. Evolution of novel mosaic castes in ants: modularity, phenotypic plasticity, and colonial buffering. *Am. Nat.* 180:328–41
80. Mora P, Rouland C, Renoux J. 1996. Foraging, nesting and damage caused by *Microtermes subhyalinus* (Isoptera: Termitidae) in a sugarcane plantation in the Central African Republic. *Bull. Entomol. Res.* 86:387–95
81. Morgan ED. 2009. Trail pheromones of ants. *Physiol. Entomol.* 34:1–17
82. Muvengwi J, Witkowski ET. 2020. Cascading effects of termite mounds in African savannas. *N. Z. J. Bot.* 58:167–93

83. Nowbahari E, Hollis KL. 2010. Rescue behavior. *Commun. Integr. Biol.* 3:77–79
84. Offenberg J. 2015. Ants as tools in sustainable agriculture. *J. Appl. Ecol.* 52:1197–205
85. Osbrink WL, Lax AR, Brenner RJ. 2001. Insecticide susceptibility in *Coptotermes formosanus* and *Reticulitermes virginicus* (Isoptera: Rhinotermitidae). *J. Econ. Entomol.* 94:1217–28
86. Ozsahin E, Ozdes M, Smith AC, Yang D. 2022. Remote sensing and GIS-based suitability mapping of termite habitat in the African Savanna: a case study of the Lowveld in Kruger National Park. *Land* 11:803
87. Patel D, Uhlyarik A, Sheldon A, Fomekong Lontchi J. 2018. A free meal: foraging behaviour and opportunistic tendencies of the termite-raiding ant *Megaponera analis* in the Dja Biosphere Reserve of Cameroon. *J. Entomol. Zool. Stud.* 6:182–87
88. Pearce MJ, Bacchus S, Logan J. 1993. *What termite? A guide to identification of termite pest genera in Africa*. Technical Leaflet 4. Natural Resources Institute
89. Pearce-Duvet JM, Elemans CP, Feener DH Jr. 2011. Walking the line: search behavior and foraging success in ant species. *Behav. Ecol.* 22:501–9
90. Peeters C. 1997. Morphologically 'primitive' ants: comparative review of social characters, and the importance of queen-worker dimorphism. In *The Evolution of Social Behavior in Insects and Arachnids*, ed. JC Choe, BJ Crespi. Cambridge University Press
91. Peeters C. 2021. Nonflying reproductives in ants. In *Encyclopedia of Social Insects*, ed. CK Starr. Springer Nature
92. Peeters C, Ito F. 2001. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu. Rev. Entomol.* 46:601–30
93. Philpott SM, Armbrecht I. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecol. Entomol.* 31:369–77
94. Philpott SM, Perfecto I, Vandermeer J. 2008. Effects of predatory ants on lower trophic levels across a gradient of coffee management complexity. *J. Anim. Ecol.* 77:505–11
95. Pohl M, Frank ET, Gadau J. 2023. Socio- and population-genetic analyses of two West-African ponerine species (*Megaponera analis* and *Paltothyreus tarsatus*) with winged and wingless queens (Hymenoptera: Formicidae). *Myrmecol. News* 33:77–89
96. Pokorny T, Sieber L-M, Hofferberth JE, Bernadou A, Ruther J. 2020. Age-dependent release of and response to alarm pheromone in a ponerine ant. *J. Exp. Biol.* 223:jeb218040
97. Qiu L, Dong J, Li X, Parey SH, Tan K, et al. 2023. Defining honeybee subspecies in an evolutionary context warrants strategized conservation. *Zool. Res.* 44:483–93
98. Risch SJ, Carroll CR. 1982. The ecological role of ants in two Mexican agroecosystems. *Oecologia* 55:114–19
99. Robinson E, Green K, Jenner E, Holcombe M, Ratnieks F. 2008. Decay rates of attractive and repellent pheromones in an ant foraging trail network. *Insectes Soc.* 55:246–51
100. Rödel M-O, Braun U. 1999. Associations between anurans and ants in a West African savanna (Anura: Microhylidae, Hyperoliidae, and Hymenoptera: Formicidae). *Biotropica* 31:178–83
101. Rödel M-O, Brede C, Hirschfeld M, Schmitt T, Favreau P, et al. 2013. Chemical camouflage—a frog's strategy to co-exist with aggressive ants. *PLOS ONE* 8:e81950
102. Room P. 1971. The relative distributions of ant species in Ghana's cocoa farms. *J. Anim. Ecol.* 40:735–51
103. Rust MK, Su N-Y. 2012. Managing social insects of urban importance. *Annu. Rev. Entomol.* 57:355–75
104. Sanders D, van Veen FJF. 2011. Ecosystem engineering and predation: the multi-trophic impact of two ant species. *J. Anim. Ecol.* 80:569–76
105. Scharf ME, Lee C-Y. 2024. Insecticide resistance in social insects: assumptions, realities, and possibilities. *Curr. Opin. Insect Sci.* 62:101161
106. Schmidt CA, Shattuck SO. 2014. The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa* 3817:1–242
107. Schoener TW. 1971. Theory of feeding strategies. *Annu. Rev. Ecol. Syst.* 2:369–404
108. Schönrogge K, Barbero F, Casacci L, Settele J, Thomas J. 2017. Acoustic communication within ant societies and its mimicry by mutualistic and socially parasitic myrmecophiles. *Anim. Behav.* 134:249–56

109. Schultheiss P, Nooten SS, Wang R, Wong MKL, Brassard F, Guénard B. 2022. The abundance, biomass, and distribution of ants on Earth. *PNAS* 119:e2201550119
110. Sheppe W. 1970. Invertebrate predation on termites of the African savanna. *Insectes Soc*. 17:205–18
111. Shik JZ, Donoso DA, Kaspari M. 2013. The life history continuum hypothesis links traits of male ants with life outside the nest. *Entomol. Exp. Appl.* 149:99–109
112. Shrestha B, Tanaka E, Hyun M, Han J, Kim C, et al. 2017. Cordyceps species parasitizing hymenopteran and hemipteran insects. *Mycosphere* 8:1424–42
113. Su N-Y. 2019. Development of baits for population management of subterranean termites. *Annu. Rev. Entomol.* 64:115–30
114. Su N-Y, Ban P, Scheffrahn RH. 2003. Resistance of insecticide-treated foam board insulation against the eastern subterranean termite and the Formosan subterranean termite (Isoptera: Rhinotermitidae). *J. Econ. Entomol.* 96:1526–29
115. Theopold U, Schmidt O, Söderhäll K, Dushay MS. 2004. Coagulation in arthropods: defence, wound closure and healing. *Trends Immunol*. 25:289–94
116. Traniello JF. 1989. Foraging strategies of ants. *Annu. Rev. Entomol.* 34:191–210
117. Valckenaers P, Hadeli, Saint Germain B, Verstraete P, Van Brussel H. 2006. Emergent short-term forecasting through ant colony engineering in coordination and control systems. *Adv. Eng. Inform.* 20:261–78
118. Vander Meer RK, Alonso LE. 2019. Pheromone directed behavior in ants. In *Pheromone Communication in Social Insects*, ed. RK Vander Meer, MD Breed, ML Winston, KE Espelie. CRC Press
119. Villet MH. 1990. Division of labour in the Matabele ant *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae). *Ethol. Ecol. Evol.* 2:397–417
120. Waller DA, La Face J. 1987. Unpalatability as a passive defense of *Coptotermes formosanus* Shiraki soldiers against ant predation. *J. Appl. Entomol.* 103:148–53
121. Way MJ, Khoo KC. 1992. Role of ants in pest management. *Annu. Rev. Entomol.* 37:479–503
122. Weber N. 1964. Termite prey of some African ants. *Entomol. News* 75:197–204
123. Wehner R, Cheng K, Cruse H. 2014. Visual navigation strategies in insects: lessons from desert ants. In *The New Visual Neurosciences*, ed. JS Werner, LM Chalupa. MIT Press
124. Wen X-L, Wen P, Dahlsjö CA, Sillam-Dussès D, Šobotník J. 2017. Breaking the cipher: ant eavesdropping on the variational trail pheromone of its termite prey. *Proc. R. Soc. B* 284:20170121
125. Wheeler WM, Bequaert JC, Bailey IW, Santschi F, Mann WM, et al. 1922. Ants of the American Museum Congo Expedition: a contribution to the myrmecology of Africa. *Bull. Am. Mus. Nat. Hist.* 45:1139
126. Wigglesworth VB. 1937. Wound healing in an insect (*Rhodnius prolixus* Hemiptera). *J. Exp. Biol.* 14:364–81
127. Wilson EO. 1963. The social biology of ants. *Annu. Rev. Entomol.* 8:345–68
128. Wilson EO. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conserv. Biol.* 1:344–46
129. Wilson EO, Hölldobler B. 2005. The rise of the ants: a phylogenetic and ecological explanation. *PNAS* 102:7411–14
130. Wilson RI. 2023. Neural networks for navigation: from connections to computations. *Annu. Rev. Neurosci.* 46:403–23
131. Yusuf AA. 2021. Allomones in social insects. In *Encyclopedia of Social Insects*, ed. CK Starr. Springer Nature
132. Yusuf AA, Crewe RM, Pirk CWW. 2013. An effective method for maintaining the African termite-raiding ant *Pachycondyla analis* in the laboratory. *Afr. Entomol.* 21:132–36
133. Yusuf AA, Crewe RM, Pirk CWW. 2014. Olfactory detection of prey by the termite-raiding ant *Pachycondyla analis*. *J. Insect Sci.* 14:53
134. Yusuf AA, Frank ET, Fombong AT, Pirk CWW, Crewe RM, et al. 2020. Odor-mediated group organization and coordination in the termite-raiding ant *Megaponera analis* (Mayr). *Chem. Senses* 45:635–44
135. Yusuf AA, Gordon I, Crewe RM, Pirk CWW. 2014. Prey choice and raiding behaviour of the ponerine ant *Pachycondyla analis* (Hymenoptera: Formicidae). *J. Nat. Hist.* 48:345–58

136. Yusuf AA, Pirk CW, Crewe RM, Njagi PG, Gordon I, Torto B. 2010. Nestmate recognition and the role of cuticular hydrocarbons in the African termite raiding ant *Pachycondyla analis*. *J. Chem. Ecol.* 36:441–48
137. Yusuf AA, Pirk CWW, Crewe RM. 2015. Mandibular gland pheromone contents in workers and queens of *Apis mellifera adansonii*. *Apidologie* 46:559–72
138. Zheng H-Q, Dietemann V, Crewe RM, Hepburn R, Hu F-L, et al. 2010. Pheromonal predisposition to social parasitism in the honeybee *Apis mellifera capensis*. *Behav. Ecol.* 21:1221–26