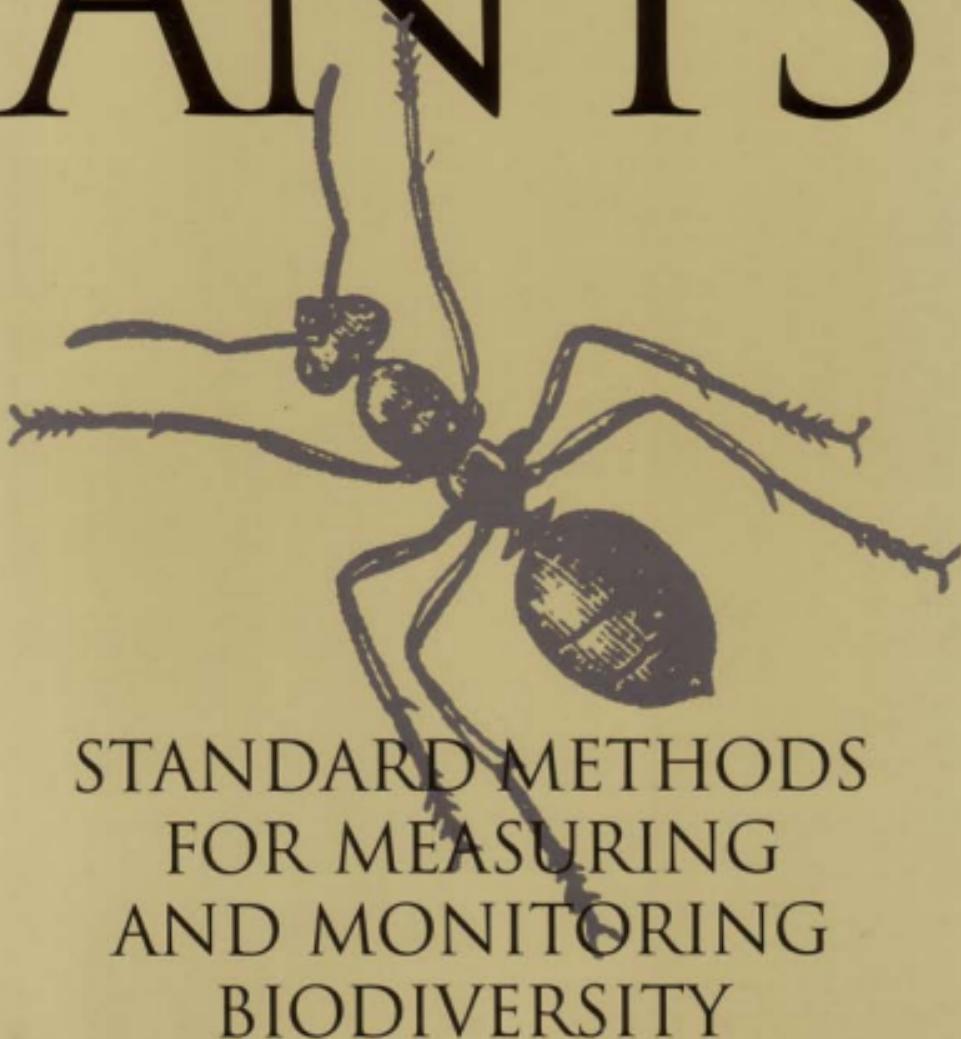


ANTS



STANDARD METHODS
FOR MEASURING
AND MONITORING
BIODIVERSITY

EDITED BY DONAT AGOSTI, JONATHAN D. MAJER,
LEEEANNE E. ALONSO, AND TED R. SCHULTZ

FOREWORD BY EDWARD O. WILSON



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BIODIVERSITY



Biological Diversity Handbook Series

Series Editor: Don E. Wilson

This series of manuals details standard field methods for qualitative and quantitative sampling of biological diversity. Volumes focus on different groups of organisms, both plants and animals. The goal of the series is to identify or, where necessary, develop these methods and promote their adoption worldwide, so that biodiversity information will be comparable across study sites, geographic areas, and organisms, and at the same site, through time.

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This book is dedicated to the memory of William L. Brown Jr.,
with affection, respect, and gratitude. For the inspiration you provided,
for the firm foundation you built for ant systematics, and especially
for your generous soul and irreverent good humor, we will never forget you, Bill.

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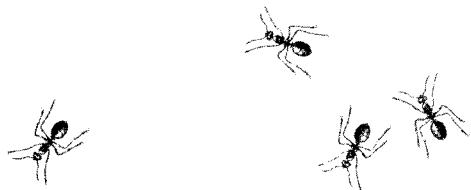
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The Interactions of Ants with Other Organisms

Ted R. Schultz and Terrence P. McGlynn



There is little doubt that the common ancestor of all ants was eusocial and that it maintained some sort of stable nest environment. From this auspicious groundplan a broad variety of complex behaviors has evolved. Coupled with the sheer abundance of the Formicidae, this behavioral diversity has produced a spectacular array of interactions between ants and other organisms. Properly understood, these interactions could be used to predict ecological conditions within a given habitat by the presence of a particular ant species, with the goal of using ground-dwelling ants as indicators of biodiversity.

Two broad factors work against the realization of this goal. First, given our current understanding of ecological processes, we are unable to draw reliable inferences about general ecological conditions from knowledge of particular

interactions between species. A more direct approach would be to establish empirically correlations between the presence of particular ant species and particular ecological conditions, and to use these correlations as predictors. This practical goal will likely be expedited if we pay special attention to ant species that participate in precise, obligate interactions with other species, or in which interactions are very complex, since we might expect such species to be most sensitive to general ecological conditions.

A second factor that mitigates against using the interactions of ants with other organisms for inferring biodiversity is our poor understanding of these interactions. Knowledge of ant biology relies heavily on the intensive study of only a few species. In many cases the diets of entire genera are unknown. Many plants are known to

possess specialized structures for the housing of ants, yet the identities of their ant guests remain mysterious. What knowledge there is exists mostly in the form of brief notes in the literature, although repeated attempts have been made to collate subsets of this information (see references cited later in this chapter).

This chapter serves as a brief and limited introduction to the complex and fascinating subject of interactions between ants and other organisms. In discussing such interactions, we will employ two broad categories: trophic interactions, in which one organism is eaten by the other, and symbioses, in which the organisms coexist for an extended period of time. We will respect the traditional subdivisions of the latter category: (1) parasitism, in which one partner benefits at the expense of the other; (2) commensalism, in which one partner benefits and the other is neither harmed nor benefited; and (3) mutualism, in which both parties benefit. Symbioses may be further distinguished as either facultative or obligate on the part of one or both symbionts, depending on whether it is possible for that partner to survive outside the relationship. Our ability to place the variety of interactions described in the following sections into these categories is limited by our ignorance of the details of particular cases as well as by the artificiality of these groupings.

Interactions with Plants

Trophic Interactions

Myrmecological orthodoxy regards ants as carnivores, and certainly few ants are entirely herbivorous. However, as pointed out by Tobin (1994), nectar and other plant products play an important and generally underappreciated nutritional role in the diets of many ant species, especially those of the adults. Certainly many otherwise carnivorous ants are attracted to floral and extrafloral nectaries, and some (e.g., species of *Solenopsis* [Tennant and Porter 1991]

and *Atta* [Quinlan and Cherrett 1979]) are known to feed on plant sap and fruit juices. Some ants (e.g., the North American *Messor pergandei*) rely entirely on seeds for nourishment, and many more (including species in *Monomorium*, *Pheidole*, and *Pogonomyrmex*) rely heavily on seeds. Aside from such obligate “harvesting ants,” many ant species are occasional seed consumers (e.g., Beattie 1985; Kaspari 1993b), and many more forage for seeds bearing elaiosomes, ant-attractive nutritive attachments manufactured by the plant to encourage seed dispersal (Handel et al. 1981; Handel and Beattie 1990a, 1990b). As discussed in more detail subsequently, ants also consume specialized food bodies produced by plants, such as Beltian bodies in the New World *Acacia* and Müllerian bodies in the New World *Cecropia*.

From the standpoint of ecological energetics, the Neotropical leaf-cutting ants could be regarded as herbivorous (Stradling 1978), since they harvest an estimated 15% of all fresh vegetation (Cherrett 1986) in the Neotropics. Likewise, ants that rely on homopteran-produced honeydew could be regarded as essentially herbivorous, since homopteran tending is bioenergetically comparable to collecting plant fluids directly (Tobin 1994). However, both leaf-cutting and homopteran-tending ants acquire their nutrition via symbiotic intermediates (fungi and homopterans)—an important consideration from the species interaction perspective taken here.

Symbiotic Interactions

Ants participate in symbioses with over 465 plant species in over 52 families (Jolivet 1996) and, not surprisingly, the literature of ant-plant symbioses is vast (for reviews, see Bailey 1922b; Bequaert 1922; Wheeler 1942; Buckley 1982a, 1982b; Beattie 1985; Hölldobler and Wilson 1990; Huxley and Cutler 1991; Jolivet 1996). Whether the majority of these symbioses

are mutualisms, in which both partners benefit, or whether they are beneficial only to the ants was formerly a matter of argument among both myrmecologists and botanists (e.g., Belt 1874; Schimper 1888, 1898; von Ihering 1891; Rettig 1904; Wheeler 1913, 1942; Skwarra 1934; Brown 1960). Largely because of recent experimental work (e.g., Janzen 1966, 1967; Davidson et al. 1988), the majority of ant-plant symbioses are currently regarded as true mutualisms, in which ants obtain shelter, nourishment, or both and plants obtain protection against both arthropod and vertebrate herbivores. In some cases, plants may also obtain nutrients from ant waste materials and soil, gain protection from competing plants (which are removed by the ants), have their seeds dispersed, and, in rare cases, even get pollinated.

Cases of commensalism, in which ant colonies gain shelter but neither harm nor benefit the host, certainly exist. For instance, many ants occupy hollow stems (e.g., *Camponotus* and *Crematogaster* species), abandoned insect galls (e.g., *Leptothorax* species), and the tangled roots of epiphytes (e.g., *Anochetus* and *Strumigenys* species). Such associations presumably served as evolutionary precursors for mutualisms in which plants receive protection from herbivory in exchange for supplying cavities favoring ant occupation, including hollow branches, stems, and thorns; hollow pseudobulbs; or pouchlike domatia on leaves and petioles. In many cases, plants provide food as well as shelter, including carbohydrate-laden extrafloral nectaries and fatty or proteinaceous pearl bodies. According to O'Dowd (1982), the latter are produced by American, Asian, and African plants in over 50 genera in 19 families. Alternatively, plants may provide food but not shelter, encouraging frequent visitations by a variety of ant species and, presumably, many of the herbivore-repelling benefits that such visitations afford. Schupp and Feener (1991) showed

that more than a third of the plants in a Panamanian forest may practice such a strategy.

The classic case of ant-plant mutualism is that of the New World members of the genus *Acacia* (Leguminosae), which produce both extrafloral nectaries and proteinaceous Beltian bodies. Known for their painful stings, ants in the genus *Pseudomyrmex* occupy the hollow thorns, repelling arthropods (Coleoptera, Hemiptera, Homoptera, Lepidoptera) as well as large browsing mammals. The ants also kill other plants growing within a certain radius around the occupied *Acacia* (Janzen 1966, 1967). Another relatively well-studied case of mutualism is that of *Cecropia* (Moraceae), in which ants (primarily *Azteca* species, including six obligate *Cecropia*-dwellers, but also species of *Camponotus*, *Crematogaster*, *Pachycondyla*, and other genera) occupy the plants' hollow stems, excavating entrance holes in preformed, weakened areas present in the walls of internodes. *Cecropia*-dwelling *Azteca* species are particularly well known for their ferocity, reacting aggressively to any disturbance to their host plant. The plant provides nourishment to the ants in the form of glycogen-rich Müllerian bodies growing on a pad (trichilium) at the base of the leaf petiole (Bailey 1922a; Rickson 1971; Longino 1991). A third example is that of the hollow pseudobulbs of *Hydnophytum*, *Myrmecodia*, and other species of the Hydnophytinae (Rubiaceae) of the Far Eastern tropics. These plants possess swollen tubers with preformed, often complex chambers that in some species are nearly always occupied by ants (usually *Iridomyrmex* species). The plants obtain nutrition from ant excrement and debris absorbed by "warted" surfaces found in some of the chambers (Miehe 1911a, 1911b; Bequaert 1922; Huxley 1978; Jebb 1991).

Some ants cultivate and occupy "ant gardens," clusters of epiphytes planted in the branches of trees on soil and carton provided by the ants (Ule 1902; Kleinfeldt 1978, 1986;

Buckley 1982a; Davidson 1988). The ants, predominantly species in the genera *Camponotus*, *Crematogaster*, and *Solenopsis*, obtain nutrition from extrafloral nectaries, elaiosomes, and fruit sap; the plants gain protection from herbivores, including leaf-cutting attines (Weber 1943). Some ant species—including *Camponotus femoratus*, *Crematogaster parabiotaica*, and *Monacis debilis*—may be obligate ant-garden nesters.

As already mentioned, ants are important dispersers of seeds (Beattie 1985) and are frequently encouraged in this role by attractive and nutritious elaiosomes provided by plants (Handel et al. 1981; Handel and Beattie 1990a, 1990b). Ants may also exercise an underappreciated influence on seed germination. Oliveira et al. (1995) showed that the South American fungus-growing ant *Mycoceropurus goeldii* (Myrmicinae) significantly enhanced germination of the seeds of the tree *Hymenaea courbaril* (Caesalpiniaceae) by removing fruit pulp and thereby reducing fungal infestation. Although ant pollination may be important for some plants in some habitats (Peakall et al. 1991), it has been suggested that, because the antibiotic secretions of the metapleural gland demonstrably inhibit normal pollen function, ants are unlikely to be recruited into insect-plant pollination symbioses (Iwanami and Iwadare 1978; Beattie et al. 1984, 1985, 1986).

Interactions with Animals

Trophic Associations

ANTS AS PREDATORS. The ancestral ant was very likely a generalized predator. Arising from this lifestyle, highly specialized predation has evolved in many ant groups. For instance, diverse groups of ants—including *Acanthostichus*, *Cylindromyrmex*, and *Eurhopalothrix heliscata*—have independently specialized on termites (Brown 1975; Wilson and Brown 1984;

Overal and Bandeira 1985). Some myrmicine ants in the genera *Carebara*, *Carebarella*, *Erebomyrma*, *Liomyrmex*, *Paedalgus*, and *Solenopsis* are known to make their nests in close proximity to those of termites, and it is assumed that they steal termite eggs and brood for food (Forel 1901; Wheeler 1914, 1936; Wilson 1962b; Ettershank 1966). Species of *Discothyrea*, *Proceratium* (Ponerinae), and *Stegomyrmex* (Myrmicinae) prey on arthropod eggs (Brown 1974f, 1979; Diniz and Brandão 1993). A variety of species in the Dacetonini (Myrmicinae) prey on *Collembola* (Wilson 1953; Masuko 1984). Species of the Neotropical genus *Thaumatomyrmex* use their bizarre, pitchfork-like mandibles to remove the repellent hairs of what is apparently their sole prey item, millipedes in the family Polyxenidae (Brandão et al. 1991). A number of *Leptogenys* species specialize on isopods (pillbugs); at least one specializes on Dermaptera (earwigs) (Steghaus-Kovac and Maschwitz 1993). Adult workers of the Japanese myrmicine species *Myrmecina graminicola nipponica* and *M. flava* capture oribatid mites, skillfully tearing a hole in the highly sclerotized integument; the larvae then feed by inserting their peculiarly elongate heads into these holes (Masuko 1995). Finally, some ant species are specialized predators on other ants, including species of *Cerapachys* and *Neivamyrmex* (Wheeler 1918; Rettenmeyer 1963).

ANTS AS PREY. Many ant species represent predictable food sources for predators because of their large numbers, their tendency to forage in trails, and their long-lived, stable, usually stationary nests. In what is no doubt a continuing evolutionary arms race, ants have adopted numerous defenses, including repellent chemicals and soldier castes, to discourage predators, while predators have acquired methods of overcoming such defenses, becoming increasingly specialized in the process. Such predators

include assassin bugs (Reduviidae), ground beetle larvae (Carabidae), rove beetles (Staphylinidae), ant lions (Myrmeleontidae), and worm lions (Diptera: Rhagionidae: *Vermileo*). Sphecid wasps in the genera *Aphilanthops* and *Clypeadon* provision their nests exclusively with ants (Evans 1962, 1977). In Costa Rica, windscorpions (Solifugae) run along and within nocturnal foraging columns of the leaf-cutting ant *Atta cephalotes*, probably preying on single workers (Bukowski 1991). Spiders that specialize on ants are often striking visual mimics of their prey, presumably as camouflage against small vertebrate predators that have learned to avoid the ants (Oliveira and Sazima 1984; Oliveira 1988). Although most vertebrates studiously avoid ants because of their stings and noxious chemical deterrents, vertebrate ant specialists include anteaters and some toads, lizards, snakes, and birds (Bequaert 1922; Weber 1972b).

Symbioses

Symbioses between ants and other animals (particularly arthropods) constitute a vast and fascinating subject, the far-flung literature of which has yet to be exhaustively catalogued (but see Kistner 1979, 1982, and Hölldobler and Wilson 1990 for excellent reviews).

ANT-HOMOPTERAN ASSOCIATIONS. The tending of homopterans by ants is well known, no doubt because of the striking parallel with the husbandry of cattle by humans. The majority of homopteran-tending ant species occur in the subfamilies Dolichoderinae, Formicinae, and Myrmicinae, although some ponerines (notably in the Ecitonini) also obtain significant nutrition through such interactions. In addition to Aphidae, ants also tend homopterans in the families Cercopidae, Cicadellidae, Coccidae, Fulgoridae, Membracidae, Pseudococcidae, and Psyllidae. Ants feed on "honeydew," a by-product of homopteran phloem-feeding consisting

largely of carbohydrate but also containing amino acids that in some cases are added by the homopteran (Dixon 1985). In return, the ants protect homopterans from predators and parasitoids.

Most ant-homopteran associations are facultative mutualisms. However, ants in the North American genus *Acanthomyops* (Formicinae) appear to be obligately dependent on their root coccid symbionts (Wing 1968), as are species of the pantropical genus *Acropyga* (Formicinae). A virgin queen of an *Acropyga* species departs on her nuptial flight carrying in her mandibles a coccid symbiont to serve as the parthenogenetic progenitor of a future "herd" (Silvestri 1925; Wheeler 1935; Bünzli 1935; Brown 1945; Buschinger et al. 1987). This behavior has also been observed in a Sumatran *Cladomyrma* species (Roepke 1930). The Malaysian ant *Hypoclinea cuspidatus* (Dolichoderinae), an obligate symbiont of the mealybug *Malaicoccus formicarii* (Pseudococcidae), is a true "nomadic herdsman." The entire colony (which can consist of more than 10,000 workers and 5000 pseudococcids) is constantly on the move as old feeding sites are depleted and new ones required (Maschwitz and Hänel 1985).

Ants also tend caterpillars in the butterfly family Lycaenidae (Hinton 1951; Atsatt 1981; Pierce 1987). In this case, nourishment is provided to the ants via specialized glands, and, as in the homopteran case, protection from predation and parasitism is provided by the ants (Malicky 1969; Pierce and Mead 1981; Pierce and Easteal 1986).

GUESTS IN ANT NESTS. Many thousands of arthropod species make their homes and/or earn their livings in the stable environment afforded in or near ant nests, including members of the Acari (Cheliceraata), Araeneae, Collembola, Diplopoda, Isopoda (Crustacea), Pseudoscorpionida, and, within the insects, of the orders Blattaria, Coleoptera, Diptera, Homoptera, Hymenoptera,

Lepidoptera, Neuroptera, Orthoptera, Psocoptera, and Thysanura. Some parasitic symbionts simply steal food from ant foragers. For example, species of the Old World calliphorid fly genus *Bengalia* dart into columns and snatch away the food of various ant species (e.g., *Bothroponera*, *Camponotus*, *Dorylus*, *Leptogenys*, *Technomyrmex* species) (Bequaert 1922; Maschwitz and Schöenegger 1980). Mosquitos of the genus *Malaya* (= *Harpagomyia*) are able to solicit regurgitated droplets from various Asian and African *Crematogaster* species (Jacobson 1909; Farquharson 1918; Wheeler 1928).

Many symbionts live inside ant nests, gaining their nourishment by feeding on refuse in the nest middens, by stealing the food of the ants, by preying on adult ants or brood, or by preying on other symbionts. In the very large nests of some ant species, remarkably large numbers of such "ant guests" can be found. For example, in one large refuse chamber within a four-year-old nest of *Atta sexdens rubropilosa*, Autuori (1942) found adult forms of 1491 Coleoptera, 56 Hemiptera, 40 Mollusca, 15 Diptera, 4 Reptilia, and 1 pseudoscorpion. In a study of 150 army ant colonies, Rettenmeyer (1962) collected 8000 mites, 2400 phorid flies, 1100 limulodid beetles, 300 staphylinid beetles, 300 Collembola, 170 Thysanura, 150 Diplopoda, 140 histerid beetles, and 6 diapriid wasps.

Facultative ant-nest symbionts, which are also found living without ants, are typically species that are predisposed to soil and leaf litter environments, such as oribatid mites and Collembola. For example, pyrgodesmid millipedes are frequently found in the refuse piles of the nests of lesser attines, e.g., *Mycetarotes parallelus*. In contrast, obligate symbionts of ants, presumably derived from facultative ancestors, are found only in ant nests, and often only in the nests of particular ant species. Mites of the genus *Antennophorus* (Antennophoridae), for example, live on the body surfaces of ants in the closely related genera *Acanthomyops* (Formi-

cinae) and *Lasius* and obtain nourishment by stealing drops of food during trophallaxis or by actively soliciting such droplets by mimicking the tactile signals used by ants for this purpose (Janet 1897; Wasmann 1902; Karawajew 1906; Wheeler 1910). Many other ant-nest symbionts, including the thysanuran *Atelura formicaria* and the histerid beetle *Hetaerius brunneipennis*, steal or successfully solicit regurgitated food (Wheeler 1908).

The pseudoscorpion *Sphenochernes schulzi* lives in nests of the Argentinean fungus-growing ant *Acromyrmex lundi*, where it apparently feeds on worker ants by first immobilizing them with injected poison, then imbibing their hemolymph (Turk 1953). The third instar of the lycaenid caterpillar *Maculinea teleius* (Lepidoptera) follows ant pheromone trails and enters nests of *Myrmica rubra*, where it feeds on the brood (Chapman 1920; Malicky 1969; Schroth and Maschwitz 1984). Other examples of nest symbionts that have acquired the ability to follow ant pheromone trails include the milichiid fly *Pholeomyia decorior*, a symbiont of the fungus-grower *Trachymyrmex septentrionalis* (Sabrosky 1959) and the cockroach *Attaphila fungicola*, resident in nests of *Atta texana* (Moser 1964). In an example of extreme integration, the staphylinid beetle *Lomechusa stumosa* (Staphylinidae: Aleocharinae) possesses specialized "appeasement glands" at the tip of its abdomen containing a proteinaceous substance that seems to exercise a calmative effect on its ant host, the European *Formica sanguinea*. Once incorporated into the nest, it preys on the ant brood and obtains regurgitated liquid food from workers (Hölldobler 1967, 1968; Hölldobler and Wilson 1990).

Numerous parasitoid species prey upon ants, including species of the hymenopteran families Diapriidae (Masner 1976; Huggert and Masner 1983) and Eucharitidae (Clausen 1940a, 1940b, 1940c, 1941; Heraty and Darling 1984; Heraty 1985, 1986). Flies (Diptera) of the family

Phoridae are particularly important ant parasitoids (Borgmeier 1963; Feener 1981; Feener and Moss 1990; Brown 1993); most phorid larvae are internal parasites of their ant hosts, but larvae of at least one species are free-living in nests of the European *Plagiolepis pygmaea*, receiving regurgitated liquid from worker ants (LeMasne 1941).

Predatory velvet worms (Phylum Onychophora) have been discovered in rainforest *Pheidole* nests, but it is unknown whether they feed upon the ants (McGlynn and Kelley 1999). In what may be a mutualistic association, the earthworm *Dendrodrilus rubidus* (Phylum Annelida) is found in nests of the European red wood ant *Formica aquilonia* (Laakso and Setälä 1997). Adult snakes in the families Colubridae, Elapidae, and Leptotyphlopidae, and lizards in the families Amphisbaenidae and Teiidae, live in nests of species of the leaf-cutting ant genera *Acromyrmex* and *Atta* and/or use the nests as oviposition sites. In some cases these associations are obligate. Some of these snakes are capable of following ant pheromone trails and may utilize the ants or brood as food (Goeldi 1897; Autuori 1942; Gallardo 1951; Vaz-Ferreira et al. 1970, 1973; Weber 1972b; Brandão and Vanzolini 1985).

Internal metazoan parasites of ants are known to include nematodes, trematodes, and cestodes. Protozoan ant parasites include (class) Microsporidea (phylum Cnidosporea), known from *Leptothorax*, *Myrmecia*, *Pheidole*, and *Solenopsis* species, and (class) Neogregarinida (phylum Apicomplexa), known from *Leptothorax* and *Solenopsis* species (Hölldobler 1929, 1933; Gösswald 1932; Allen and Buren 1974; Allen and Silveira-Guido 1974; Jouvenaz and Anthony 1979; Espadaler 1982; Buschinger and Winter 1983; Jouvenaz 1986; Crosland 1988; Buschinger et al. 1995).

SYMBIOSSES BETWEEN ANTS. Finally, ant species may enter into varying degrees of symbiosis

with each other. For instance, "thief ants" of *Solenopsis* subgenus *Diplorhoptrum* live in the walls of the nests of larger ant species and steal their food and larvae. In a more derived case, *Megalomyrmex symmetochus* is found within the nests of the fungus-growing ant *Sericomyrmex amabilis* (Wheeler 1925) and has also been reported from the nest of an unidentified *Trachymyrmex* species. The queen and brood occupy the fungus gardens, ignored by their hosts and apparently feeding on the fungus. The closely related *M. silvestrii* and an undescribed *Megalomyrmex* species parasitize other fungus-growing ants (Brandão 1990; J. Wetterer, pers. comm.).

In cases of social parasitism, ants of one species utilize the work force of another colony in order to raise their own brood. Workers of "slavemaking" species raid colonies, steal brood, and raise them as slaves. In other cases, parasitic foundress queens enter established colonies and take over, by either killing or dominating the host colony queen. Thereafter, the host workers aid in raising the interloping queen's offspring, which ultimately supplant the former inhabitants. In the most extreme cases, the parasite queen produces only sexual brood, having lost the ability to produce a worker caste. For example, the attine ant *Pseudoatta argentina* parasitizes nests of *Acromyrmex lundi*. Its exclusively sexual brood is reared by the *Acromyrmex* workers, and upon maturity they depart and mate, and the queens find new *A. lundi* nests to parasitize (Gallardo 1929).

Associations with Fungi

In general, ants avoid associations with fungi. Indeed ants have evolved at least two important characteristics for discouraging the presence of fungi (as well as bacteria) in their nests: elaborate grooming behaviors (Wilson 1962a) and the antiseptic-secreting metapleural gland (Maschwitz et al. 1970; Maschwitz 1974; Beattie

et al. 1986). Little is known of fungal diseases of ants, although ant-pathogenic fungi have been described in the families Clavicipitaceae (Thaxter 1888; Rogerson 1970), Hyphomycetales (Balazy et al. 1986), and Laboulbeniales (Thaxter 1908; Bequaert 1922); an unidentified unicellular fungal pathogen has been reported from the hemolymph of *Solenopsis wagneri* (Jouvenaz et al. 1977).

Outside the tribe Attini (Myrmicinae), no confirmed examples of fungivory are currently known in ants. Although the infrabuccal pockets of many ant species contain fungal filaments, the digestive tract does not; rather, the infrabuccal pocket serves as a temporary repository for fungi accumulated during the cleaning of the body, and the infrabuccal pellet is discarded in the refuse heap (Bailey 1920). In a rare exception, fungal filaments have been discovered within the digestive tracts of ants in the myrmicine tribe Cephalotini, *Cephalotes atratus* and *Zacryptocerus clypeatus* (Caetano and Cruz-Landim 1985; Caetano 1989; Kane 1995), but in this case the fungus is thought to serve as a digestive tract symbiont.

The northern European *Lasius fuliginosus* (Formicinae) constructs carton nests in hollow tree trunks and in the soil, cementing the carton with regurgitated sugary liquid. The fungus *Cladosporium myrmecophilum* is found growing only on this cemented carton (Lagerheim 1900); however, the ants do not consume it (Maschwitz and Hölldobler 1970). Fungi have been reported growing in epiphytic Rubiaceae that are inhabited by *Iridomyrmex* ants (Miehe 1911b; Bequaert 1922; Huxley 1978), within hollow stems of South American *Hirtella* (Chrysobalanaceae) occupied by *Allomerus* ants (Dumpert 1981), and on carton nests constructed by *Crematogaster* species in Nigeria (Farquharson 1914), but, again, there is little reason to believe that any of these ants is fungivorous.

Ants are thought to disperse the spores of mycorrhizal fungi in the order Glomales, fami-

ly Endogonaceae, including those of the genus *Glomus* (McIlveen and Cole 1976; Allen et al. 1984; Friese and Allen 1988, 1993; Janos 1993). Since glomalean spores are large (50–800 µm in diameter) and rich in lipids, and since spores are often found associated with roots in the chambers of soil-nesting ants, it has been suggested that some ants may consume them (D. P. Janos, pers. comm.). Went et al. (1972) found mycelium of various fungi in the refuse chambers of desert harvester ants in the genera *Veromessor* and *Manica*, and they reported that *M. hunteri* larvae consumed an unidentified fungus offered to them in artificial culture. Perhaps the best support for ant fungivory outside the Attini comes from observations made in Malaysia and Indonesia. In one case, a Malaysian *Prenolepis* species was photographed carrying off pieces of an unidentified basidiomycete fruiting body (Rosciszewski 1995). In a second case, fungal tissue fragments made up 50–80% of all food items carried to the nest by the giant forest ant *Camponotus gigas* in Borneo (Orr and Charles 1994; Levy 1996; S. Yamane, pers. comm.)

One group of exclusively New World ants, the Attini (Myrmicinae), are obligately fungivorous, with the fungus constituting the sole source of nourishment for the larvae and the dominant source for the adults (Barrer and Cherrett 1972; Littledyke and Cherrett 1976; Quinlan and Cherrett 1979). Attine ants possess an elaborate array of behaviors for cultivating fungus gardens. The less-derived species cultivate their fungi on insect frass, seeds, and other organic detritus obtained from foraging in the leaf litter. The derived "higher" attines, including *Acromyrmex* and *Atta* species, cultivate their fungi on fresh vegetation, including leaves and flowers cut for that purpose. The identity of the attine fungal symbiont has been the source of speculation for over a century, although most researchers agreed that attines cultivated one or more species within the families Agaricaceae or

Lepiotaceae (subdivision Basidiomycotina, order Agaricales). It is now known that most Attini cultivate lepiotaceous fungi, although some species within the genus *Apterostigma* cultivate a distantly related fungus in the Agaricales, closely related to the genus *Gerronema* in the family Tricholomataceae (Chapela et al. 1994; Moncalvo et al. 2000).

In a striking parallel with the ant-coccid association of *Acropyga* and *Cladomyrma* species already described, virgin attine queens carry a pellet of the natal nest fungus garden within their infrabuccal pockets and use this to start their new gardens following colony founding. This clonal propagation leads to the expectation of fungal lineages that closely parallel the lineages of their ant hosts. However, at least in the lower attines, this expectation is not borne out. Instead, the fungal cultivars of many lower attine ants are more closely related to free-living species than they are to other attine fungi, indicating that some fungus-growing ants occasionally replace their resident fungal cultivars with free-living stocks. Furthermore, within a given geographic area distantly related ants—in some cases species in different genera—may cultivate the same fungal clones, indicating that some fungus-growing ants occasionally replace their resident cultivars with cultivars acquired from the gardens of other ant colonies (Mueller et al., 1998).

Introduced Ant Species

The most widespread ants have been called “tramp” species; their geographic spread is tied with human activity (Table 4.1; Passera 1994). The ants belong to a variety of functional groups (Chapter 3) and use a variety of strategies to fit into widely variable habitat types. They are most frequently encountered in urban environments, in disturbed areas, and on oceanic islands (Lieberburg et al. 1975; Clark et al. 1982; Brandão and Paiva 1994; Passera 1994).

Table 4.1 Major Exotic Tramp and Invasive Ant Species^a

Species	Tramp Species	Invasive Species
Subfamily Dolichoderinae		
<i>Linepithema humile</i> (Mayr)	Yes	Yes
<i>Tapinoma melanocephalum</i> (Fabricius)	Yes	
<i>Technomyrmex albipes</i> (Smith)	Yes	
Subfamily Formicinae		
<i>Anopolepis gracilipes</i> (F. Smith)	Yes	Yes
<i>Paratrechina fulva</i> (Mayr)		Yes
<i>P. longicornis</i> (Latreille)	Yes	Yes
<i>P. vaga</i> (Forel)	Yes	
Subfamily Myrmicinae		
<i>Cardiocondyla emeryi</i> Forel	Yes	
<i>C. nuda</i> (Mayr)	Yes	
<i>C. venustula</i> W. M. Wheeler	Yes	
<i>C. wroughtoni</i> Forel	Yes	
<i>Monomorium destructor</i> (Jerdon)	Yes	
<i>M. floridana</i> (Jerdon)	Yes	
<i>M. pharaonis</i> (Linnaeus)	Yes	
<i>Pheidole megacephala</i> (Fabricius)	Yes	Yes
<i>Quadrstruma emmae</i> (Emery)	Yes	
<i>Solenopsis geminata</i> (Fabricius)		Yes
<i>S. richteri</i> Forel	Yes	
<i>S. wagneri</i> (<i>invicta</i>) Santschi		Yes
<i>Tetramorium bicarinatum</i> (Nylander)	Yes	
<i>T. caespitum</i> (Linnaeus)	Yes	
<i>T. lanuginosum</i> Mayr	Yes	
<i>T. pacificum</i> Mayr	Yes	
<i>T. simillimum</i> (Smith)	Yes	
<i>Trichoscapa membranifera</i> (Emery)	Yes	
<i>Wasmannia auropunctata</i> (Roger)	Yes	Yes
Subfamily Ponerinae		
<i>Hypoponera eduardi</i> (Forel)	Yes	
<i>H. opaciceps</i> (Mayr)	Yes	
<i>H. punctatissima</i> (Roger)	Yes	

^aTramp ants are closely associated with human activity and often nest in human structures. Invasive species move into natural habitats (either disturbed or undisturbed) and outcompete native ant species. From McGlynn (1999b).

Although they are not as frequently encountered in undisturbed continental habitats, in tropical and subtropical areas they can be encountered anywhere.

The five most widespread ant species are the pharaoh's ant (*Monomorium pharaonis*), Argentine ant (*Linepithema humile*), crazy ant (*Paratrechina longicornis*), ghost ant (*Tapinoma melanocephalum*), and big-headed ant (*Pheidole megacephala*). Although these are the only species known to appear in every nonpolar biogeographic region (McGlynn 1999a), they have no functional group or taxonomic commonalities but do excel as human commensalist species. Although some species are dominant and have been known to maintain absolute territories (Haskins and Haskins 1965; Crowell 1968; Lieberburg et al. 1975; Holway 1995), others are opportunistic or cryptic, and are capable of coexisting with nondominant ant species (Hölldobler and Wilson 1990; Delabie et al. 1995).

Where dominant species (for example, *P. megacephala*, *L. humile*, *Wasmannia auropunctata*) are introduced, their impact upon native ants is obvious and drastic. Invasive ants exclude competing species from food resources and are known to raid heterospecific nests (Clark et al. 1982; de Kock and Giliomee 1989; Brandão and Paiva 1994). Studies of invaded areas show that noncryptic aboveground foraging ants are the most severely affected (Holway 1995; Human and Gordon 1996). In at least one instance, invasive ants have disrupted ant-plant mutualisms (Bond and Slingsby 1984). Clearly the areas that contain these ants will have a reduced native ant diversity. At the ecosystem level, at least one invasive ant (*Solenopsis wagneri* Santschi, formerly *S. invicta* Buren) has

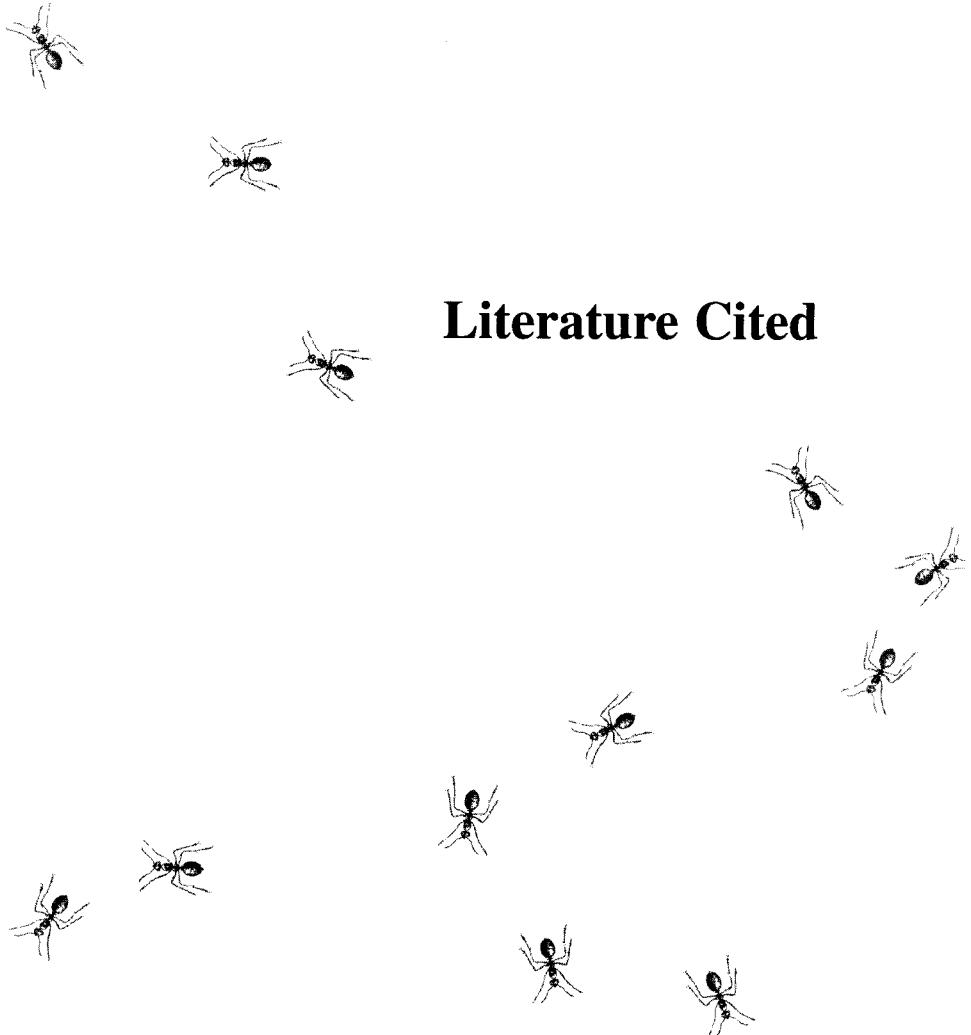
decimated areas where it is introduced, affecting ecological interactions at the levels of soil cycling, fruit decomposition, and the biodiversity of the terrestrial arthropod community in general (Porter and Savignano 1990; Vinson 1991).

The long-term effects of introduced ants are not well understood. Accounts from the West Indies of invasions of exotic ants dating back to the early nineteenth century demonstrate that there is a turnover in the species composition of the introduced ant fauna (Haskins and Haskins 1965). Wilson and Taylor (1967) suggest that the species composition of invasive ants on a given island changes over time. Invasive species are generally more successful in disturbed areas and do not create a monospecific stand of ant colonies in most localities.

Introduced ant species can serve as an excellent bioindicator for assessing the status of an ant community. The impact of human use may be indicated by the presence of introduced ants before any long-term community effects are observed. An excellent case study is in the Galápagos Islands (Clark et al. 1982), where the foci for the spread of the invader *W. auropunctata* were located in cities and campsites. As activity spreads throughout many of the Galápagos Islands, the introduced ant is marching in file with human activity.

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