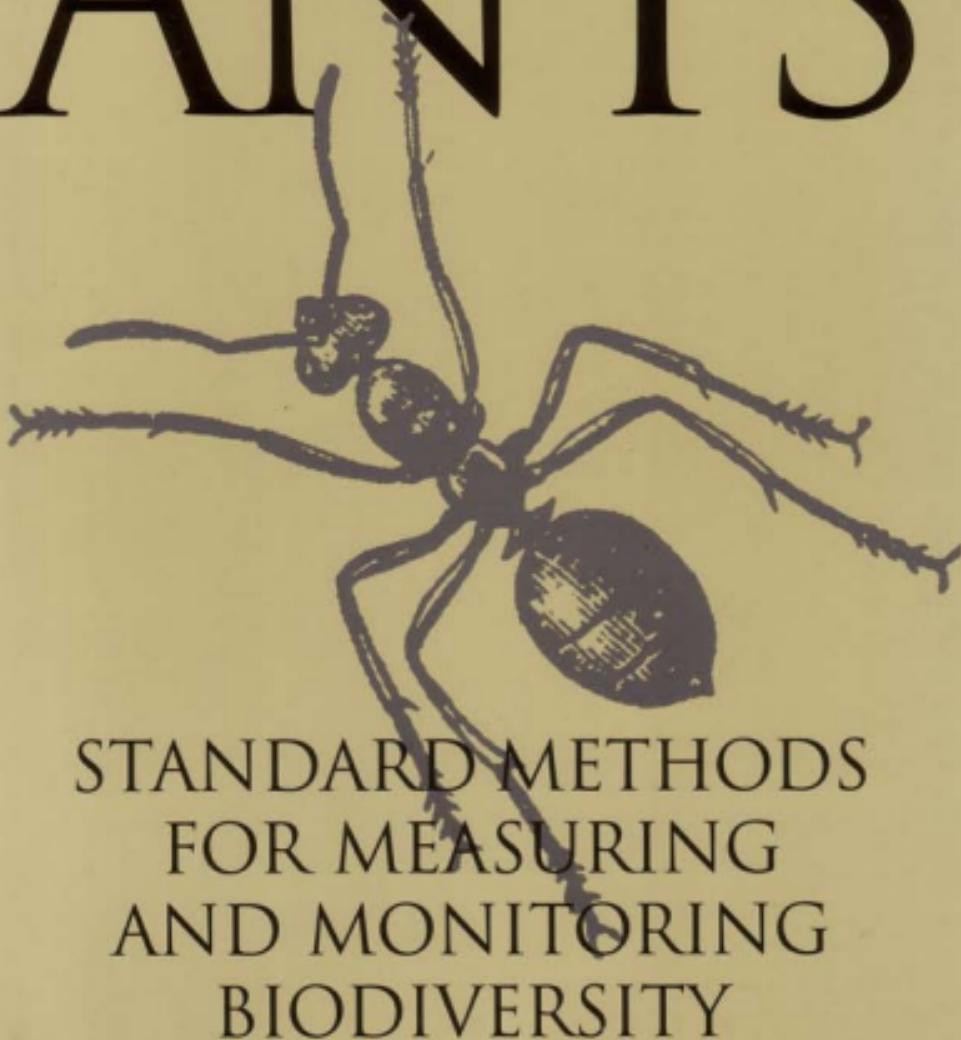


ANTS



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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SMITHSONIAN INSTITUTION PRESS
WASHINGTON AND LONDON

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Copy editor and typesetter:
Princeton Editorial Associates, Inc.
Production editor: Duke Johns
Designer: Amber Frid-Jimenez

Library of Congress Cataloging-in-Publication Data

Ants : standard methods for measuring and monitoring
biodiversity / edited by Donat Agosti . . . [et al.].
p. cm.—(Biological diversity handbook
series)
Includes bibliographical references (p.).
ISBN 1-56098-858-4 (cloth : alk. paper)—
ISBN 1-56098-885-1 (pbk. : alk. paper)
1. Ants—Speciation—Research. 2. Biological
diversity—Measurement. I. Agosti, Donat.
II. Series.
QL568.F7 A575 2000
595.79'6—dc21 00-021953

British Library Cataloguing-in-Publication Data available

Manufactured in the United States of America
07 06 05 04 03 02 01 00 5 4 3 2 1

♾ The paper used in this publication meets the
minimum requirements of the American National
Standard for Information Sciences—Permanence
of Paper for Printed Library Materials
ANSI Z39.48-1984.

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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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A Primer on Ant Ecology



Michael Kaspari



As the first chapter of this book suggests, ants are a taxon that offers much to those interested in long-term monitoring, inventory, and basic ecology. This chapter has two goals. The first is to introduce the reader to key ecological features of ants. Its target audience is those unfamiliar with ants but interested in adding them to monitoring and biodiversity studies. Its coverage will not be exhaustive, and as in any review, this chapter will have a distinct point of view. Other sources of information with different viewpoints are available in this volume and in the form of other reviews (Sudd and Franks 1987; Hölldobler and Wilson 1990; Andersen 1991a). Many topics basic to ant ecology (e.g., functional groups, patterns of species composition, dynamics, and interactions) are scarcely covered here because they are treated elsewhere

in this book (see Chapters 3, 4, and 8). My second goal is to challenge potential myrmecologists by emphasizing that a number of basic puzzles remain to be solved.

This chapter is organized around five topics: Colony Life, The Ant Niche, What Regulates Ant Populations?, What Regulates Ant Communities?, and Open Questions in Ant Ecology. Where appropriate I will make suggestions on how to apply this natural history to the design of a monitoring program. These tips will be greatly expanded upon in Chapter 9.

Colony Life

In an introductory chapter such as this, one inevitably glosses over much of the variation that scientists enjoy studying. Here I describe

the behavior and composition of a generic ant colony, then move on to a few of the interesting variations on this theme.

Ants are eusocial organisms, characterized by cooperative brood care, overlapping generations of workers within the colony, and a highly developed caste system (Wilson 1971). Castes are groups of specialized colony members that perform different functions with corresponding differences in form. For example, if you were to dig into the soil of a large ant colony you would likely see hundreds of *workers* boiling out. The worker caste performs most of the colony's day-to-day tasks. These include collecting food, tending the young, and maintaining and defending the nest. Continued digging would reveal the colony's young—off-white eggs, larvae, and pupae—in small discrete chambers. All ants start as eggs, grow as larvae, and develop into adults as pupae; these immature stages are fed, groomed, and protected by workers. Depending on the time of year, you may encounter larger, winged ants—the male and female *alates* or *sexuals*. Alates are the reproductive phase of the colony and have little to do in the colony while they wait to fly off and mate. Nonetheless, as they represent the colony's reproductive future, they too are often vigorously defended. Eventually you will uncover the *queen* chamber and its occupant, surrounded by still more workers. The queen, once a winged female in another ant colony, is the center of colony life—often the largest ant in the colony, swollen with eggs and fat. The queen's central role is that of the egg-layer, that is, the mother of all the other colony members. No other members of the colony, although there may be thousands, produce eggs.

It has long been apparent that workers within a colony work together gathering food and defending the colony. This apparent cooperation and self-sacrifice was long held out as an example of virtue. How the castes work together and why workers forego reproduction has been a subject of constant fascination, as it seemed to

be a potential exception to Darwin's theory of evolution by natural selection. Individuals were not selfish, but instead appeared to sacrifice themselves for the good of the colony.

One resolution to this paradox came through the study of the peculiar genetic system common to many social insects—*haplodiploidy* (Hamilton 1964, 1972; Alexander 1974; Trivers and Hare 1976). To see how this works, consider that humans differ between the sexes in the genetic makeup of our sex chromosomes. Females inherit two X chromosomes from their parents; males inherit an X chromosome from one parent and a Y chromosome from the other.

Sex in ants is determined in a fundamentally different way—there are no sex chromosomes. Queens, female alates, and workers have two pairs of each chromosome (i.e., are diploid); males have only one set and are haploid. Females and workers receive two sets of chromosomes through the conjoining of egg and sperm. Males are produced from unfertilized eggs.

This simple system has profound consequences for cooperation within the colony. Workers, it turns out, are closely interrelated, sharing 75% of their genetic makeup. Queens, like human mothers, share on average only 50% of their genetic makeup with each of their daughters. They also tend to live longer than their offspring in the insulated environment of the nest. In this situation, workers can advance the cause of their genes most by helping the queen produce more workers and reproductives. The best way to do that is to help keep the queen, and hence the whole colony, alive and functioning. If a worker engages in such "selfless" behavior as a vigorous and fatal defense of the nest or enabling the consumption of its own body by its nestmates, it is actually being selfish, insofar as it improves the chance of the colony surviving and its genes living on. This division of labor and social organization allows a high degree of behavioral sophistication. It

may help account for the amazing proportion of biomass accounted for by social insects in the world's ecosystems (see Chapter 1).

This simple picture of colony life, although somewhat typical, ignores fascinating variation that occurs when workers are fertile (Peeters 1991) or when many queens contribute eggs to the same colony (Hölldobler and Wilson 1977). Both scenarios may enable "selfish" workers to prosper, and both are current, productive avenues of research in ant ecology.

The Ant's World—Life as a Colony of Tiny Organisms

It is often said that ecology and conservation biology suffer from a vertebrate bias (Wilson 1993). Humans choose to study organisms, such as birds and mammals, that experience the world as humans do. But ants live and interact in parts of the environment that are in many ways foreign to humans. An effective monitoring program requires a basic understanding of these differences in order to exploit them in the design of the project.

Most obviously, individual ants are small, with a dry weight typically much less than a gram. Their size allows ants entry into crevices and microenvironments (e.g., between soil particles or in the bark of the trees [Kaspari and Weiser 1999]). It allows ant colonies to exist on limited resources and to exploit the majority of the earth's other organisms, which are also small.

But small size has a cost. Small animals heat up and dry out more quickly (Hood and Tschenkel 1990; Kaspari 1993a). Ants, as ectotherms, are constrained to forage when it is warm enough, but not too warm. This results in a temperature "envelope" in which most ants forage at temperatures greater than 10°C and cease foraging much above 40°C, with an average peak foraging temperature of 30°C (Hölldobler and

Wilson 1990). Low humidity may also constrain foraging; the best time to collect ants in the deserts of North America is after summer rains (Schumacher and Whitford 1976). But even moisture is a two-edged sword, as standing drops of water are sticky and unmanageable to ants, and rain washes away chemical trails.

This interaction with their chemical environment introduces another profound way in which ant societies differ from human societies. Ants are filled with glands that open to the outside world, and these glands have three main functions. First, living in the soil requires a defense against fungal and bacterial pathogens; some glands produce secretions that help to keep the ant clean and disease-free. Second, ants are such a conspicuous part of their environment that they have many enemies. Ants—similar to other members of the insect order Hymenoptera (e.g., bees and wasps)—often defend themselves with their stings. Evolution has modified the ant sting in a variety of ways to produce defensive chemicals that are injected, dabbed, or sprayed on potential enemies and competitors.

Finally, some glands produce pheromones, allowing ants to communicate in sophisticated ways with others in the colony and with other colonies and species (Vander Meer and Alonso 1998). For example, each ant colony has an individual odor; ant queens use pheromones to control workers; ant workers use pheromones to leave scent trails to profitable food resources as well as to mark territories. Still other pheromones are released to alert the colony to dangers. In sum, chemicals are the main currency of communication among ants.

The Colony Life Cycle

The colony life cycle breaks down into three phases: *founding*, *growth*, and *reproduction*. Most ant colonies are founded when a newly mated queen flies off in search of a nest site. Most alates die during this journey, since they

are an attractive source of food for a variety of predators (Whitcomb et al. 1973). Upon finding a nest site, a queen excavates or occupies a cavity in a plant or in the soil, where she lays eggs. The queen then depletes her own reserves and converts them into food for the first clutch of workers, either in the form of trophic eggs or salivary secretions.

Colonies enter the growth phase when the first clutch of workers matures. The queen's duties are reduced to egg production and pheromonal control of the colony. The workers take over the task of caring for young, foraging, nest maintenance, and defense. In this phase, colony growth is often exponential, as all resources are devoted to gathering food and raising more workers (Wilson 1971; Tschinkel 1993).

The length of the growth phase varies among species and is dependent on climate—cold slows brood development. The growth phase ends when colonies grow large enough to produce alates. This colony size threshold varies widely among species—some are sexually mature at 10 workers, others at 10,000 or 100,000. What drives this variation is still unclear, although one pattern that emerges is that the average colony size decreases as one approaches the equator (Kaspari and Vargo 1995) and passes from less productive to more productive environments (Kaspari et al., unpublished data). The determinants of size, growth rate, time to maturity, and other life history traits in ants are still only poorly known (Tschinkel 1991).

The reproductive phase of the colony's life cycle begins when attention is lavished on unfertilized eggs (destined to be male alates) and some fertilized eggs are raised, through extra nutrition, to be female alates (and ultimately queens of their own colonies). As alates are typically larger than workers, resources are diverted from worker production, and colonies may stop growing or even decrease in size.

These alates then fly off to mate with alates from other colonies. The males, after copulating, die. The females fly off in search of another nest site, completing the colony life cycle. Colony cycles are somewhat synchronized in habitats that show seasonal rainfall and temperature. Alate flights often occur at the beginning or end of the “benign season” (the warm season in the temperate zone, the rainy season in the tropics). Colonies may produce alates for as long as the queen lives, often for many decades.

This concludes a sketch of a “typical” ant colony. Most ant species have only one queen per colony, and the colony occupies a single nest. Colonies of some ant species, however, have multiple-queen nests for at least one part of their life cycle. This is a topic of enormous interest since it complicates the genetic-relatedness rules of ant behavior outlined previously. Further, many of these species nest not in one location, but in several nest chambers linked by long tunnels or runways that may stretch tens of meters.

Species with multiple queens and multiple nest sites often dominate habitats, owing to their high potential growth rate and large spatial extent. Such is the case for a handful of introduced ant species (*Linepithema humile*, the Argentine ant; *Pheidole megacephala*, the big-headed ant; *Solenopsis wagneri*, the fire ant). Species introductions are a problem worldwide, and these three ant species have been shown to have an enormous impact (Chapter 4; Williams 1994). They are a nuisance to humans, tending aphids on cultivated plants and invading households; the fire ants have a nasty sting. Introduced ant species are also scourges of their host ecosystems. Although native species perform a variety of ecosystem services (e.g., dispersing seeds) introduced species may not (Bond and Slingsby 1984). Freed of factors that limited their native populations, these species may out-compete and drive to extinction local assemblages of ants and arthropods (Porter and

Savignano 1990) and reduce wildlife populations (e.g., Allen et al. 1995).

The Ant Niche

The ecological niche of a species describes the roles it plays in an ecosystem. Describing a typical ant niche is as vexing as describing a typical ant colony. The variety of diets, nest sites, life spans, and associations of ants in any given habitat makes ants an attractive group for monitoring.

However, some general observations may be offered. Most ant colonies are relatively sessile, at most moving their colonies every two weeks, some not moving at all (Smallwood 1982). Ants derive their energy from other organisms—either plants (nectar, leaves, seeds) or other animals, alive or dead. From a central point, colonies send foragers through the environment, quickly recruit to new food resources, and just as quickly abandon them as the need arises. In this way ants collect and concentrate resources in the environment and are themselves predictable resources for those that exploit them. In many ways, ant colonies are decidedly “plant-like” (Andersen 1991a).

Species in an assemblage may vary along three niche axes of particular concern to those designing a monitoring program. These are the *nest niche*, the *food niche*, and the *temporal niche*.

The Nest Niche

Ant nests take a variety of forms. If you traveled along a gradient, from warm desert to moist tropical rainforest, the variety of nest sites that ants use would increase dramatically. In deserts ants tend to be soil nesters. Some soil-nesting species rarely breach the surface except to release alates (e.g., some *Acropyga* and *Neivamyrmex*). Many of these species are known only from male alates caught in light traps. The diversity and natural history of these

species remain virtually unexplored (Léveillé 1976, 1983).

Other species nest in the ground but emerge from entrances to do at least some of their foraging above ground. This is probably what most people think of when they picture an ant colony, but even this simple idea is expressed in a number of ways. The nest entrance can be a discrete hole in the soil. In cooler deserts, particularly the tundra, soil nests are often found under stones: stones retain warmth longer than soil, and colonies in cool climates take advantage of these environmental hot spots to warm their brood (Brian and Brian 1951). In some upland meadows, almost every large, flat stone appears to have an ant colony underneath. Not surprisingly, then, stone nesting is less common where soil temperatures are warmer (e.g., hot deserts and lowland tropical rainforests; Brown 1973). In other cases ants bring the stones to the nest entrance, often paving a large gravel disk around the entrance.

Ants nest in a variety of soil types, from hard clay to loam to pure sand. Yet whereas a gardener or botanist can speak volumes on how pH, drainage, and other soil properties influence the plant community, ant ecologists can say little about how soil properties influence ant communities. For example, little is known, given the heterogeneity in soil and litter occurring at a given site, about the role that these differences may play in segregating species (but see Johnson 1992).

Moving from deserts into grasslands and savannas, most ants still nest in the soil. However, in dense grasslands, colonies may live in perpetual shade. A solution practiced by some species is to create a disk of bare soil around the nest entrance. Another solution, particularly in the Northern Hemisphere, is to form large thatch mounds that rise a foot or more above the surrounding grass. In woodlands, tree stumps and snags may also be hot spots for ant colonies. In each case, by avoiding or emerging

from the shade, these nests prolong their residents' exposure to the sun.

As we enter forests, the ground becomes covered with a layer of woody debris, leaves, twigs, and fruits (e.g., acorns). In very dry woodlands, soil-nesting species still predominate. As the woods become moister, ants begin to nest in this litter. Litter-nesting ants may nest in cavities in twigs or fruit, between leaves, or in large, decaying logs (Herbers 1989; Kaspari 1993b; Byrne 1994). The fraction of species that nest in the litter is largest in the tropics (Wilson 1959). In the litter a single bit of hollow twig may house a colony of ten to a hundred workers; a scattering of leaves may provide meager shelter for a colony and its pupae, spread over several square meters; a large, rotten log may contain multiple colonies of a variety of species. To find these colonies, one need only crack some twigs, disturb some leaves, or cut into a rotten log. If the environment is seasonally cold or dry, these colonies may periodically move out of the litter and into the soil (Herbers 1985).

In tropical forests, a substantial portion of the local ant fauna will be found living in the plants themselves, from low herbs to the canopies of trees (Jeanne 1979). Some ants build nests out of chewed wood pulp. These "carton nests" are common in the tropics and may be found affixed to trees high in the canopy or in the understory, on the underside of leaves (Black 1987). Species such as the wood ants (*Camponotus*) may excavate a nest chamber in a partially rotting tree (look for regular columns of ants on the trunks of trees). Finally, a host of plants have evolved cavities and food bodies, providing ants food and shelter in exchange for protection from herbivores (Huxley and Cutler 1991, Chapter 4). Only a small subset of plants may have these cavities, but they are often used by species found nowhere else.

The Food Niche

The majority of ants appear to be opportunistic foragers, taking some combination of plant exu-

dates, seeds, and animal matter, alive or dead. Some fraction of an ant assemblage, however, is more specialized in their diets. For example, in the warmer parts of the Americas, the Attini cut vegetation or collect dead insects or insect dung. This material is in turn used as a substrate on which to grow fungus, and this fungus is cultured and harvested for food (Weber 1972a, 1972b).

Other ants specialize to various extents on plant exudates (Tennant and Porter 1991; Tobin 1994). These exudates are obtained either directly from plant organs called nectaries or indirectly through such sucking insects as the Homoptera (Huxley and Cutler 1991). Given the enormous volume of ants in tropical canopies, an increasing body of evidence suggests that canopy ants live in a carbohydrate-rich and protein-poor environment (Tobin 1994; Davidson 1997; Kaspari and Yanoviak, in press).

Many ant genera include specialized predators (e.g., *Cerapachys*, *Neivamyrmex*, *Proceratium*, *Strumigenys*, *Thaumatomymex*) that feed on a restricted set of arthropods. Some "specialists" may have taxonomically narrow diets but feed on insects that are otherwise quite common (e.g., the ant specialists among the army ants *Neivamyrmex*) if not always apparent to the casual observer (e.g., the Collembola specialists in the genus *Strumigenys*).

Finally, ant species that make up a community may specialize to varying degrees on the size and density of a resource. Species with large workers often have access to a broader array of prey sizes (Kaspari 1996c). Likewise, as food comes in packages of different sizes, the larger, richer bits of food are often taken and defended successfully by species with large, aggressive colonies (Kaspari 1993b).

The Temporal Niche

Within an ant community, subsets of species may restrict their activity to some parts of the year or day. For example, *Prenolepis imparis*, which can forage at temperatures approaching

0°C, is a North American forest species commonly active in spring and fall, but rather inactive in summer (Talbot 1943; Fellers 1989).

Over a 24-hour period, the same patch of habitat may reveal very different parts of its ant fauna. Deserts (Whitford and Ettershank 1975; Bernstein 1979; Morton and Davidson 1988) and rainforests (Greenslade 1972; Kaspari 1993a), for example, often have distinctive nocturnal, crepuscular, and diurnal fauna. This segregation likely arises from a combination of physiological tolerances, competitive interactions, and predation risk (Whitford 1978; Orr 1992). However, the paucity of such studies leaves us with no reliable generalizations for an important question in ant monitoring: at what times of day do you sample? As a first approximation, desert (and perhaps rainforest) communities are likely have the most highly developed between-species segregation of daily activity. Desert and temperate communities likely have the most pronounced seasonal segregation. Bait studies in such habitats that fail to sample over the appropriate time intervals may underestimate species richness.

What Regulates Ant Populations?

A population is a collection of individuals of the same species found in a given area (e.g., the *Pogonomyrmex rugosus* population of the Jornada Experimental Range, southern New Mexico). In this section I briefly review what we know about factors that regulate ant populations, that is, factors that cause ant populations to increase, decrease, or stabilize (see also Chapter 3 for more examples).

Factors that regulate populations can be broken down into two groups (see also Chapter 3). *Resource-based* factors regulate populations by controlling the supply of resources as well as a colony's access to those resources. *Mortality-based* factors, in contrast, are those that kill and/or harvest parts of colonies. In short,

resource-based factors determine how fast populations can grow in a habitat; mortality-based factors determine the actual standing crop of a species. How these forces act together is a topic of ongoing research.

Resource-Based Regulation

Resource-based factors set the ability of colonies to grow and reproduce. They are of three types: *resources*, *conditions*, and *population interactions*. Resources are items actually used and depleted by ant colonies (e.g., food, nest sites). *Conditions* are abiotic factors that regulate access to resources (e.g., temperature, humidity). *Population interactions* describe how other populations in the habitat regulate access to available resources.

As habitats become more productive, they often have higher overall numbers of ant colonies. For example, net primary production measures the amount of photosynthesis in a habitat, in units of grams of carbon fixed per square meter per year. In the Americas, the density of ants increases from around 0.03 colonies/m² in the Colorado desert (<10 gC/m²/y) to about 10 colonies/m² in an Ecuadorian rainforest (>1000 gC/m²/y; Kaspari et al., 2000). But the increase is far from uniform. Access to resources is decreased by poor conditions (Andersen's "stressors"; see Chapter 3) and by competing populations of ants and other organisms.

Temperature is a preeminent condition for ant populations (Brown 1973). As a taxon, ants are thermophilic, shutting down in winter and avoiding cold shade (Brian and Brian 1951). Yet even in environments that are mostly cold year round, such as alpine tundra, ants are often common in direct sunshine (Heinze and Hölldobler 1994). Where it is warm year round (e.g., the tropical deserts, savannas, and rainforests) ants are a conspicuous part of the landscape.

Organisms or populations *compete* for resources when an individual or population grows

at the expense of another individual or population. For example, as one colony grows, it may deplete the food supply sufficiently to make food unavailable to other nearby colonies. Likewise, if there are a limited number of hollow twigs or ant plants in a forest, whichever colony or population gets there first may exclude a second colony or population (Davidson et al. 1989; Longino 1991). Competition can be within a species (intraspecific) or between species (interspecific). In the former case, interactions within a species regulate the population; in the latter, interactions between species help regulate the population. Competition may occur indirectly, through the consumption of food or other resources, or quite directly, through the killing of other colonies. The distinction between competition and predation becomes fuzzy in ant-ant interactions (i.e., is a colony that kills a neighboring colony and carries away its pupae and food stores preying upon that colony, or simply getting rid of a competitor?).

Where there is abundant sunshine (or *insolation*), there is growing evidence that ant colonies compete with each other for resources such as nests and food. I can rank this evidence, in order of increasing confidence, as follows.

Many ant species are highly territorial. If colonies deplete resources and kill foundresses near established nests, this should result in a regular distribution of ant colonies in a homogeneous landscape. Many studies have looked for these patterns, mapping out colonies in an area and testing the hypothesis that colonies are more dispersed than would be expected by chance. A summary of the evidence (Levings and Traniello 1981) suggests that territoriality is often, but by no means always, the case. At least one cautionary note for this type of evidence is sounded by Rytí and Case (1992).

Colony density and size can also affect competition between ants. Resources can be subdivided by a population in a number of ways.

All the resources can be dominated by a single large colony, or they can be divided among many, smaller colonies. Put another way, as average colony size in a habitat increases, the density of colonies in that habitat should decrease. This inverse relationship between colony size and density is often observed over the course of a growing season. Early on, habitats are colonized by many foundresses. These foundresses raise broods that find, fight, usurp, and kill other colonies, until that same habitat is left with only a few victors (Rytí and Case 1988b; Tschinkel 1992; Adams and Tschinkel 1995). This is not always the case, however. In one study of tropical litter ants, there was little relationship between colony size and density (Kaspari 1996b); disturbance by rainfall and army ants may be sufficient to prevent colonies from saturating the environment.

If ants compete for resources or good conditions, then removal of one colony should benefit another. Experimental removal of ant colonies often results in the rapid use of the vacated site by foragers and nests of adjacent ant colonies (Davidson 1980; Andersen and Patel 1994).

If resources or conditions limit a colony's growth, then increasing resource availability should enhance that colony's survival or reproduction. This individual success should ultimately result in higher local population densities. This is a simple experiment, but it has rarely been performed by ant ecologists. Food addition studies in warm desert environments have yielded mixed results (Rytí and Case 1988a; Munger 1992). Ants in temperate environments closer to the poles may be more likely to respond to increases in food supply (Deslippe and Savolainen 1994). One reason may be that warm deserts often run on a seed economy, and seeds can be stored for long periods. "Harvester ants" may thus be better buffered against food shortages and more likely to respond only to prolonged periods of shortfall. Shortages of nest

sites may also limit ant populations. In two Neotropical litter ant assemblages, nest densities doubled with the addition of bamboo twigs, but 75% of the nest sites remained unoccupied (Kaspari 1996b).

Clearly resources, climate, and competitors work together to regulate ant populations (Brown 1973). Even in resource-rich environments, cool-damp climates have few ants. A good example is provided by cool, temperate rainforests. In contrast, warm-dry environments appear to have conditions quite well suited to ants. In this case, the number of ants often appears to be set by rainfall—a good predictor of the seed crop on which desert ants feed (Morton and Davidson 1988).

Mortality-Based Regulation

A variety of factors kill and cull ant colonies. The death of a colony's queen generally spells the end for the colony, although it may still produce a final batch of alates from existing eggs (or eggs laid by workers). Colonies of some multiple-queen species may also adopt a new queen (e.g., Tschinkel and Howard 1978).

But as suggested previously, most queen deaths occur early in the colony's life cycle, when roving foundresses are a vulnerable (and nutritious) food to predators ranging from dragonflies to birds. After founding, more queens, newly ensconced in the nest, are killed by roving workers from mature colonies. Mature colonies die less frequently, but the causes of queen death in older colonies are obscure, in part because so many queens are high in the treetops or deep underground, and thus difficult to observe. Weather must play a role. Unable to get up and move quickly (a large colony of *Atta colombica* may take 8 days to execute a nest move; Porter and Bowers 1981), many ant species are probably susceptible to flooding.

Given their densities, biomass, and interactions, ant colonies are a conspicuous part of

the environment (see Chapter 1). It should not be surprising that they have attracted their share of predators and parasites—many of which are other ant species (Kistner 1982). For example, some ant species are social parasites. They have queens that invade the nests of a host species, find the queen, and kill it, “adopting” the colony's workers to raise the intruder queen's eggs (Wilson 1984).

Ant populations are also regulated by harvesting. Just as regular pruning of a garden can keep individual plants in check, predators that drain a colony's resources by killing its workers can help regulate ant populations. In the boreal and temperate zones some ant species conduct “slave raids,” stealing the pupae of other colonies (Topoff 1990). As the term implies, these pupae are carried off and raised by the raiding species to take over many of the colony tasks. Slave-raiding species are replaced (in an intriguing but as yet unexplained pattern) toward the tropics by army ants—nomadic raiding colonies of ants that kill and carry off pupae for immediate consumption. Over 20 army ant species may inhabit a single Neotropical forest. It is possible that their combined effects on the ant community are profound (Rettenmeyer et al. 1983; Kaspari 1996a). But do slave raiders and army ants keep colony densities lower than they would otherwise be? No one has yet performed the simple experiment of removing army ants and slave raiders—or building fences around their prey—to observe the response of the host species.

A host of other animals kill or harvest ant colonies. For example, almost every continent has a series of vertebrates (e.g., anteaters and lizards) that consume ants. It has been shown in rare instances that these predators regulate the distribution of their prey (e.g., where ant lions are common, ants are not; Gotelli 1993). Ant colonies also have live-in associates, including mites, nematodes, spiders, and beetles (Chapter 4; Kistner 1982; Hölldobler and Wilson 1990).

The impact of these associates on the colony's economy is also largely a mystery.

Finally, just the *risk* of parasitism may keep some ant colonies from growing faster. Recent work on the interactions between phorid flies and ants exemplifies this phenomenon. Phorids are tiny parasitic flies, many of which specialize on a single ant species or genus (Brown and Feener 1991a, 1991b; Brown 1993). Phorid flies search for their host ants (often following the odor plume of the ants themselves), hover, then zoom in to lay an egg somewhere on the worker ant's body (Porter et al. 1995a, 1995b; Feener et al. 1996). The worker falls over, stunned, then eventually returns to the colony and dies when the egg hatches and the ant serves as food for the developing maggot.

However, phorid flies first must *catch* worker ants. Therein lies the tale. Host ants often run and hide in the presence of their phorid parasite (Porter et al. 1995c). This reaction is so profound as to interfere with foraging, and perhaps swing the competitive balance away from the host ant to its phorid-free competitor (Feener 1981).

Ant ecologists have compiled a catalogue of parasites and predators, with effects ranging from killing the queens to frightening the workforce. But the effect of these parasites and predators on the number of ant colonies in an area is still largely unknown. Just because horned lizards in a desert bajada consume harvester ants for a living does not mean they play a meaningful role in limiting the number or size of those colonies. Put another way, there is not a single study of an ant population (let alone a community; see later in this chapter) in which all the predators and parasites have been enumerated and their impact on ant colonies has been quantified.

A Word on Patchiness

Density, the number of ant colonies per unit area, is an abstraction—ant colonies are never

evenly distributed over the landscape. In fact, ant colonies can be quite patchy, a phenomenon long recognized (Wilson 1958) and one that continues to fascinate ant ecologists (Levings and Traniello 1981; Levings 1983; Kaspari 1996a, 1996b). For example, a single 1-m² patch of litter in a tropical forest may have 1–17 species nesting in it. The role that top-down and bottom-up forces play in creating this patchiness, and in creating the broader geographical trends of diversity, is a subject of ongoing research.

What Regulates Ant Communities?

An ecological community is a collection of species living in a given environment. Most monitoring programs have as one of their goals the description of an ecological community. Community descriptors can be grouped into those describing *form*, *function*, and *diversity*. *Form* describes the size, shape, and mass of an ant community. *Function* describes what the ants actually do to the ecosystem—what foods they eat, how much soil they turn over, what other populations they regulate. *Diversity* describes the composition, number, and taxonomic relationships of species between and across communities. Community form, function, and diversity vary in time and space in predictable ways.

Form

A community's biomass is the summed weights of all its species. Ants and termites may represent up to one-third of the total animal biomass in some tropical forests (Fittkau and Klinge 1973). This preponderance of ant biomass is especially high in the tropical canopy, where up to half the individuals may be ants (Stork and Blackburn 1993; note that this is not the same as saying that ant population densities are higher

since the majority of these ants are workers from a few colonies).

All the species in a community sum to form a size distribution. What constitutes “size” in ants and other social insects is a bit complicated—ant species have a characteristic distribution of sizes of individual ants and a characteristic number of ants in the colony. Taken together, ant colonies represent some of the largest insects recorded (Kaspari, forthcoming).

Both the average size of ants and the number of ants per colony appear to decrease as one travels from the poles toward the equator (Cushman et al. 1993; Kaspari and Vargo 1995). Tropical ants and ant colonies tend to be smaller. The cause(s) of this pattern, shared with many other organisms, is not yet clear. It may be linked to the increasing use of litter nests in the tropics or to adaptations to living in richer, less seasonal environments (Kaspari and Byrne 1995; Kaspari et al. 2000a). Small size, as discussed earlier, has both costs and benefits. For example, smaller ants may be restricted, on average, to moister environments and cooler, moister times of the day (Hood and Tschinkel 1990; Kaspari 1993a) since they desiccate more quickly.

Even within colonies ants vary in size and shape beyond the obvious differences between workers and reproductives. Sometimes there are discrete worker castes in the colonies (e.g., “minors” and “majors”). In such cases, a persistent question in ant ecology is how and why this occurs, and how caste allocation varies with environment (Wilson 1985; Schmid-Hempel 1992; Kaspari and Byrne 1995). Relatively few species have such distinct forms: species typically show some continuous size variation in the size of the worker caste. Again, the question arises, is this variation a natural outcome of changing food supplies and energy demands within the colony, or is it “fine-tuning” by the colony, allowing larger ants to specialize on larger prey (Rissing 1987; Wetterer 1991)? Ant

ecologists still have not settled this issue, in part due to lack of data on how and when resources limit colony growth (Beschers and Traniello 1994; Kaspari and Byrne 1995).

However, if food is a limiting resource, we might expect the advantages of worker size variation to be greatest when a species has the environment all to itself. In other words, size variation should evolve to exploit the “empty niche space” left in the absence of other species. This appears to be the case with *Messor pergandei*, an ant of the desert southwest in North America. In assemblages with few species, *M. pergandei* workers vary greatly in size (Davidson 1978). In richer environments, with a larger number of ant species, much of that size variation disappears.

Function

Given their diversity and biomass, it is not surprising that ants play such a large role in the functioning of ecosystems. Many of these functions (e.g., seed dispersal) are discussed in more detail in Chapter 3. Here I discuss a few ways in which ants shape ecosystems as soil movers, as “keystone species,” and, pathologically, as introduced species.

First, ants greatly affect the structure of their environments as “ecological engineers”—organisms that rearrange the environment in ways that affect other organisms (Lawton 1994). One way they do this is by moving and enriching soil—large ant colonies may excavate liters of soil in their lifetime, aerating the soil and incorporating litter from the surface in much the same way as do earthworms (Elmes 1991). Lesica and Kannowski (1998) suggest that hummocks in northern peatlands may be abandoned nests of *Formica podzolica*, based on similar elevated levels of soil nutrients.

Since ants bring food in from their entire foraging territory, they may serve to concentrate nutrients in the nest. However, this effect can vary from species to species. For example,

Haines (1978, 1983) has studied two species of leaf cutter ants, *Atta colombica* and *A. cephalotes*. Leaf cutters harvest vegetation and use the cut leaves as a substrate on which to grow fungus. The fungus is then harvested for food. Since leaf cutter colonies can consist of millions of workers, refuse disposal is a big job, handled differently by the two species. These habits, Haines suggests, predispose the two species to have very different effects on the nutrient recycling in the soil. *Atta cephalotes* stores its refuse underground; *A. colombica* dumps its refuse in large conical piles above ground. With *A. cephalotes* the refuse pile's nutrients are leached away deep underground, while with *A. colombica* the nutrients are retained near the surface of the soil and are more easily recycled by the plant community.

Some ants are likely keystone species—organisms that disproportionately impact their community (Paine 1968; Lawton 1994). One potential example is the army ant *Ecton burchelli*. Army ants are nomadic species, with hundreds of thousands of workers. Army ant colonies roam in search of prey, mainly arthropods, especially social insects. *E. burchelli* may be a keystone species for at least two reasons. First, a raid by *E. burchelli* creates a seething crowd of escaping arthropods just ahead of the raid front. These are easy prey for numerous species of birds that form mixed flocks and spend their lives following army ant swarms (Willis and Oniki 1978; Willis 1983), as well as other associates (Rettenmeyer 1962; Kistner 1982). Second, there is some evidence that, by preying on large ant species, *E. burchelli* may open up opportunities for smaller ant species that escape predation (Franks and Bossert 1983).

The role of ants in ecosystems is clearly seen when introduced ants disrupt communities. Ants transported outside their native ecosystems can disrupt the ecosystems of their new homes. Accounts of two introduced species will make this clear. The first is *Linepithema humile*,

the Argentine ant, now common in warm-temperate habitats the world over (Bond and Slingsby 1984). In South Africa, the fynbos plant community is extraordinarily diverse. Many plants of the fynbos depend on native ants to disperse seeds to new habitats away from the parent. As *L. humile* gradually invades, it displaces the native ants but fails to disperse the seeds. As a result, many of the plants appear on their way to local extinction as *L. humile* continues to spread.

In North America, the fire ant, *Solenopsis wagneri* (formerly *S. invicta*), has occupied much of the southeastern United States. A host of studies has begun to assemble a picture of widespread ecosystem disruption. In Texas, *S. wagneri* makes up more than 99% of ants captured at infested sites. In infested sites, the number of common ant species has declined from an average of 13 to 4 species, and the number of other arthropod species has also declined (Camilo and Phillips 1990; Porter and Savignano 1990). In contrast, in *S. wagneri*'s native Brazil, it is found at 0.1–19% of ant baits, and it co-occurs with up to 48 species of ants (Fowler et al. 1990). Population densities of *S. wagneri* are at least four times higher in the United States than in Brazil (Porter et al. 1992).

Such population explosions of pest ants and destruction of native arthropod communities are repeated with *Wasmannia auropunctata* in the Galápagos (Clark et al. 1982; Lubin 1984), *L. humile* in California (Erickson 1971; Ward 1987), and a host of exotic species in Hawaii (Fluker and Beardsley 1970). One goal of this volume is to provide a means for better surveying this damage, and we hope that more scientists will be motivated to study the ecology of introduced species in order to slow or reverse their impact.

Diversity

Studies of diversity document the number and identity of species in a given area. As the

world's habitats disappear, careful quantification of diversity has taken on new import. But diversity is also one of the most difficult things to measure unambiguously (see Chapter 13). Comparing diversities between areas demands a standard protocol, as species richness increases with the size of the area sampled and increased time spent sampling. A chief aim of this book is to summarize those protocols. Here I review a few of the major patterns in species richness and species composition that have been discovered in ants thus far.

The most striking pattern of species richness (the number of species in a given area and time) is its increase from the poles to the tropics. Jeanne (1979) was the first to study this trend in a standardized way. Jeanne investigated the intensity of ant predation along a transect from the New World temperate zone and tropics. The transect consisted of five forest sites, located in the northern and southeastern United States, tropical Mexico, Costa Rica, and Brazil. The same baits (a wasp larva in an open vial) were set out for a specified time in a variety of habitats: old field and intact forest, high and low in trees. A number of trends were apparent. First, species richness in each habitat increased from the temperate zone to the tropics. Richness, however, increased at different rates at different areas within a site. Arboreal ants were all but absent in the north but made up an increasing proportion of the ant fauna toward the tropics. In contrast, old fields made up a decreasing proportion of species richness compared with forests.

The latitudinal gradient has many causes. As we discussed earlier, tropical environments are more productive. Since plants form the bottom of trophic pyramids, more productive environments should be able to support more ants and hence more species. But, as we also discussed earlier, ants are thermophilic. Since ants do better at warm temperatures, temperature may regulate access to productivity (Brown 1973).

Put this way, the other two trends make sense. Arboreal nesting allows ants to be closer to the majority of a forest's productivity—in the canopy. However, the canopy lacks the soil's ability to buffer the colony from hard freezes. As average temperature becomes more amenable, arboreal nesting increases. Likewise, average temperature decreases toward the poles and temperature in the shade is always cooler than temperature in full sun. In cold environments, ant abundance and species richness may be proportionately higher in open areas than in the cool shade of a developed forest.

Species richness shows other patterns. For example, larger islands tend to have more species than smaller islands (Wilson 1961; Goldstein 1975). Species richness also tends to increase, but in an often sporadic way, after an area has been disturbed (see Chapter 7). In contrast, as pointed out earlier, introduced ant species can quickly "simplify" an ant assemblage, driving many native species to extinction.

Major puzzles in the patterns of species richness remain, however. For example, two studies examined the correlation between rainfall and harvester ant diversity in arid environments. Davidson, studying the deserts of North America, found a positive correlation (Davidson 1977a, 1977b). Since productivity in dry environments is largely limited by rainfall, this finding appears to support a productivity explanation for the trend. However, when the same techniques were applied to Australia's desert and shrubland ant faunas, no correlation existed (Morton and Davidson 1988). Species richness is obviously a complex variable shaped by a number of factors, including the unique history of an area (see Chapter 8).

The geographical distribution of species composition is covered by Ward (Chapter 8) and Brown (1973). Here I briefly review how species composition may vary in interesting ways within a habitat.

Much of the work on species composition has centered on the role that interspecific competition plays in arranging species across the landscape. For example, in many temperate communities a regular hierarchy is apparent (Wilson 1971; Savolainen and Vepsäläinen 1988; Savolainen 1990; Andersen 1992b). Hierarchies have been standardized in various ways but boil down to dominants and subordinates. The dominant species often form(s) large colonies. They are aggressively territorial and recruit quickly, in numbers, to food. Ant diversity and density are often low around dominant species. Subordinate species often form smaller colonies, are poor recruiters, and are found on the periphery of territories controlled by dominants. This pattern is exceptionally pronounced in boreal and north temperate habitats, in arid deserts and shrublands in Australia, and in simple communities (Hölldobler and Wilson 1990). A similar phenomenon may occur in tropical canopies, where a few species are dispersed in a mosaic throughout the treetops, making up 95% of the biomass and/or numbers (Majer 1976; Blackburn et al. 1990; Adams 1994; Tobin 1997).

This dominance hierarchy is by no means universal in ant communities (see Chapter 3). In the tropical litter, species show few strong positive or negative correlations in abundance predicted by strong interspecific competition by dominants (Kaspari 1996b). This may be due to a number of factors. Litter colonies may never reach a size that allows them to dominate their neighbors. Litter nests, rotting around their occupants, may prevent them from setting up a large, stable territory. Ants of the tropical canopy, on the other hand, form “islands,” with narrow, defensible trunks leading to the lush canopy above (Hölldobler and Lumsden 1980). A single large colony can thus monopolize whole trees and keep out other species (Hölldobler 1983; Adams 1994). Similar phenomena, on smaller scales, occur in the ant plants of the tropical understory (Davidson et al. 1988, 1989).

Dominance hierarchies may also be muted when predators decrease a dominant's ability to monopolize resources. In a classic study, Feener (1981) studied two species of ants, *Solenopsis texana* and *Pheidole dentata*, with a parasitic phorid fly, *Apocephalus*. *Pheidole* have large-headed soldiers that are recruited to rich food supplies. These soldiers are also the preferred hosts of the flies. As a consequence, when the flies are present, the *Pheidole* soldiers run away in a panic, leaving the *Pheidole* colonies outmatched at food resources compared with *Solenopsis*. A phorid fly may thus tilt the balance in competition among these two common and conspicuous ants of the Texas litter.

In sum, although interspecific competition may play a large role in shaping patterns of species composition, it is by no means common everywhere. Its effects are modified by factors such as the architecture of the environment and the presence of predators.

Open Questions in Ant Ecology

This chapter has presented one view of the status of ant ecology. As has become clear by this point, large gaps remain in our understanding of these important insects. Following are just a few of the unanswered questions.

What kills ant adult colonies? We know that the majority of ant colonies die at the foundress stage. But how do abiotic factors (e.g., floods, drought, cold spells) and biotic factors (e.g., army ants, parasites, slave raiders, viruses, and predators) combine to kill colonies that have reached maturity?

What are the impacts, and possible means of control, of introduced ant species? Wherever they have been studied, introduced ants such as the imported fire ant and the Argentine ant have disrupted ecosystems. What regulates the spread and final distribution of imported ant species? Are their effects ameliorated over time? Can we safely introduce biocontrol?

How does mating system influence interactions? Under what circumstances do large, multiple-queen colonies evolve and occupy landscapes (Davidson 1998; Holway et al. 1998)? Why aren't they more common?

What do canopy ants, litter ants, and subterranean ants do? These forms are all integral parts of ant assemblages, but their inaccessibility has precluded extensive study. Is their biology fundamentally different from that of the soil-nesting ants that have been the subject of most ant research?

What factors regulate ant populations? How do resources and mortality combine to determine long-term population trends in ants? How does this answer differ as we go from boreal to tropical forests, from deserts to grasslands? Does this answer differ fundamentally between regions (e.g., Australia, Asia, North America) with differing histories and taxonomic contributions?

How interchangeable are species? We know surprisingly little natural history about most ants, especially those of the tropics. To what extent, in species-rich communities, do the 30 or so *Pheidole* or *Camponotus* species do much the same thing? What roles do ants play in ecosystems?

How are current environmental changes (climate change, habitat destruction) reflected in changes in ant abundance and diversity? Are ants sensitive indicators of environmental change? Or do their lifestyles buffer them against anthropogenic change?

Tips for Field Work

One never wants to wreak more havoc on populations than is necessary to satisfy the needs of a given scientific study. Thankfully, collecting workers from large colonies is akin to pruning a bush or scraping off some skin cells—you typically leave the colony (the queen and most workers) behind.

Choose a survey period that maximizes ant activity—typically one during which temperatures are high and rainfall is plentiful. Desert and tropical assemblages are often most active during the wet season. Early summer is often a good time to sample most other temperate zone assemblages. Mediterranean climates, where it rains most in the winter and is warm in the summer, often require spring sampling. Avoid collecting when there is standing water or when the vegetation is wet. This can slow ant activity, especially among small ants.

Be careful how you handle baits, pitfall cups, or anything with which an ant will come into contact. Avoid wearing perfumes, colognes, and insect repellent when sampling ants.

If one goal is to monitor colony densities, then species with multiple-nest entrances may be overcounted. There are different ways to compensate for this tendency. One is ignore conspecific nests within a given distance of each other (e.g., 1 m). Another is to perform “transplant experiments” (i.e., if a worker from one nest entrance is vigorously attacked when placed near another nest entrance, it is likely that the two are from different colonies).

If you use bait in your protocol, use small baits that are hard to monopolize by a large, aggressive colony. We have found that shortbread cookies (made with flour, sugar, eggs, and nutmeats) attract the widest variety of ants (compared with peanut butter, tuna, and sugar water). Even Attini (fungus-growing ants) and *Strumigenys* (Collembola specialists) stop to carry off shortbread cookie crumbs. On the dark rainforest floor, the investigator often sees the pale yellow cookie crumb move long before she or he sees the ant!

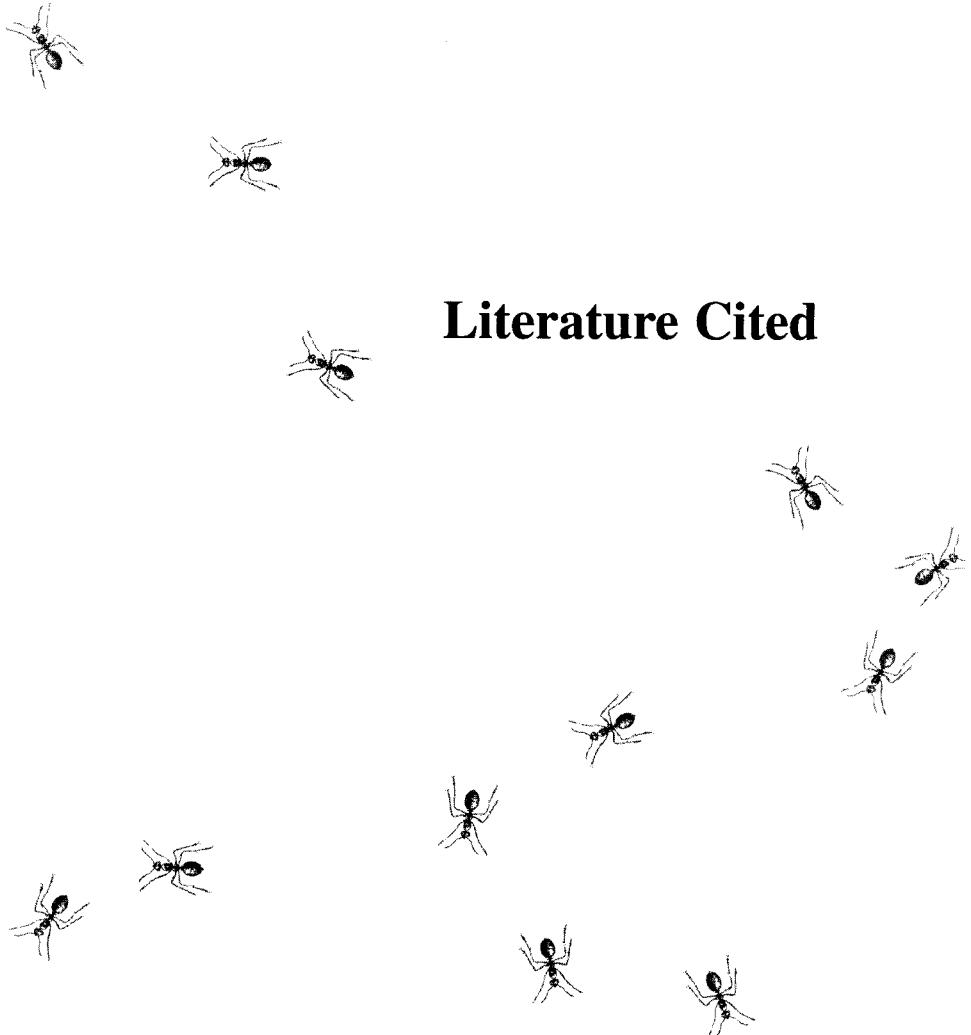
If possible, spread sampling effort out over the hours of the day. One way to do this is to use passive sampling techniques such as pitfall traps.

Patchiness is a problem when putting together a monitoring program. Ant densities can vary so much from 1-m² plot to 1-m² plot, or from

valley to valley, that it is important to locate sample plots randomly and to have enough of them to account for this variability.

In sum, the ecology of ants—small, colonial, sessile, and chemosensory organisms—differs in basic ways from the ecology of vertebrates and hence from our own world. The impact of

ants in today's ecosystems is profound and their presence is ubiquitous. For all these reasons, adding ants to the list of taxa surveyed in a monitoring program is a wise investment. A careful consideration of ant life history during the study's design phase will maximize the returns on that investment.



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