The Ants Study Guide

The Ants by Bert Hölldobler

BOOKRAGS

Contents

Plot Summary

The Ants is a Pulitzer Prize winning nonfiction monograph of natural history and biological information about the Formicidae family of insects. As is typical of scientific monographs, individual personalities are deliberately kept to an absolute minimum.

The text includes a broad overview of information including: taxonomy; colony organization and structure; evolutionary elements; chemical and other communication methods; individual and colony life cycles; population and community ecology; symbiotic and other specializations; a review of the main types of ants; and collecting and observing techniques.

The large-format text contains 732 pages, is divided into twenty chapters, and also includes a glossary and an extensive annotated bibliography. The text is fully indexed, and includes nearly one thousand illustrations, photographs, charts, graphs, and also offers twenty-four, full-color plates. It is generally considered to be the definitive source of introductory scientific knowledge on ants, and is an authoritative encyclopedic reference for all myrmecologists. It has been extensively cited in biological and entomological literature and is frequently used as the text for graduate-level seminars in biology.

Chapter 1 The Importance of Ants

Chapter 1 The Importance of Ants Summary

Ants are a dominant form of animal life on earth. They have complex anatomy, behavior, and social organizations. The importance of ants to global ecosystems is enormous, but poorly understood. Ant population densities are extremely high in nearly all ecosystems. Ants are a very diverse type of insect, having evolved specialization allowing for exploitation of a wide range of resources and colonization of an incredibly wide range of geography and environments. They are able to thrive in disturbed and marginal habitats. They exert a strong influence on local environments and are able to out-compete many other forms of life. Ants offer numerous advantages as a research organism. Their behavioral ecology, sociobiology, complex anatomy, and advanced communication methods all offer areas for further research. Ants have been under-utilized as a research and teaching organism.

Chapter 1 The Importance of Ants Analysis

This brief chapter serves as an introductory statement for the text, and sets a serious but accessible scientific expository tone. The chapter concludes with the explanatory note, "We confess to having written this book mainly to celebrate a personal muse..." (p. 3).

Chapter 2 Classification and Origins

Chapter 2 Classification and Origins Summary

The Ants are composed of a single family, the Formicidae, within the order Hymenoptera. The Formicidae are sub-divided into eleven subfamilies, 297 genera, and about 8,800 species. Probably 100 to 350 genera and 20,000 or more species remain unknown to science. The regional distribution of ant species is summarized in a table, and numerous figures illustrate general ant anatomy used as taxonomic keys.

The subfamilies and genera of fossil and living species are summarized in a table, and references to applicable monographs are noted. Regional studies extant in the literature are summarized in a table, including references. The process of taxonomic classification of ants is described in general review.

A concise overview of the origin of the ants is offered in generally chronological order. Close relatives to ants are briefly described and illustrated. Diagnostic taxonomy of ants, including primitive features, is summarized and a cladogram of aculeate (stinging hymenoptera - ants, bees, and many wasps) families is presented. A phylogeny of subfamilies within Formicidae is presented. The need for revision of ant taxonomy is noted. Several possible scenarios for the evolution of social behavior are put forward, including a comparison of primitive social behavior in selected genera. Comments regarding the probable reasons for the incredible success of ants are offered.

A glossary of terms utilized in ant taxonomy is presented. Ordered taxonomic keys for subfamily determination, including Formicinae, Dorylinae, Ponerinae, Dolichoderinae, Nothomyrmeciinae, Ecitoninae, Aneuretinae, Pseudomyrmecinae, Myrmicinae, Leptanillinae, and Myrmeciinae, are presented in table format. Further ordered taxonomic keys for genus determination, are presented in tables organized by region and selected subfamily. The regions include Palearctic, Ethiopian and Malagasy, Oriental, Australian, Polynesian, Nearctic, and Neotropical.

The chapter ends with fifty-eight pages of illustrations, organized by subfamily, of selected genera and their visible diagnostic traits. The illustrations range from line drawings through completed art, and include side views, top views, face views, and other views of interest. Most illustrations are also identified as to species and region, and many contain source attribution, though many are previously unpublished, including most of the better illustrations.

Chapter 2 Classification and Origins Analysis

The diagnostic taxonomy tables are organized in a linear fashion and early tables direct the reader to later tables for further keys. For example, the first entry in the first table is "Body with a single reduced or isolated segment (the petiole) between alitrunk and gaster ... [continue at bullet] 2" (p. 33), and the second entry is "Body with 2 reduced or

isolated segments (the petiole and postpetiole) between alitrunk and gaster ... [continue at bullet] 10" (p. 33). Following these steps, the subfamily of any common specimen can be determined in a few minutes. Then, the reader is directed to the appropriate region and subfamily table to continue the process and determine a genus. The reader can then use other textual resources to discover extant monographs and other reference materials for further information on the genus in question. In cases where any doubt exists, the reader may refer to the extensive illustrations, which complete the chapter. This taxonomic section is 109 pages in length, and comprises roughly fifteen percent of the book.

Chapter 3 The Colony Life Cycle

Chapter 3 The Colony Life Cycle Summary

Ant colonies are described in general terms as nearly exclusively female social structures dominated by caste (a set of individuals of a particular morphological type or age group that performs specialized labor in a colony - refer to Chapter 8) and communication systems shared by 50 to over one million individual organisms. The stages of colony growth are briefly enumerated and discussed. The Founding Stage begins when the virgin queen leaves the colony where she was raised, and includes mating, location of a suitable nest, construction of a first nest, and the rearing of a first brood of worker-caste offspring. The Ergonomic Stage begins when the first worker-caste ants begin to forage, enlarge and maintain the nest, and perform brood care. The focus of this stage is colony growth, and it persists for one season to several years, depending on the species and the environment. The Reproductive Stage is the final stage of a mature colony, and entails the rearing of new queens and males. Common variations on this basic process are briefly discussed. The remainder of the chapter revisits most of these areas in greater detail.

The mating behavior of virgin queens and males is described. Most potential breeding ants die within hours of leaving the home nest. Various breeding behaviors are described, including the "female-calling" and the "male-aggregation" methods. Several species-specific mating strategies are described in greater detail, accompanied by various illustrations, with particular attention to timing stimuli and sex pheromones. The information discussed is then summarized in a table. Polyandry is briefly described.

The Founding Stage continues when newly fertilized queens remove their own wings. Physiological changes in the new queen are noted and discussed. The new queen produces her first brood of eggs. Some species are claustral (queen seals herself in new nest), some are not (queen may forage). Minims (first worker brood) are produced.

The Ergonomic (Exponential) Stage begins when the minims begin to forage and take over brood care. Various theories regarding energy models and dynamic colony growth are presented. Species-specific information is discussed. Colony growth is at first exponential, but is more properly described by a logistical growth model.

At some point, the colony enters the Reproductive Stage, and begins to produce males and virgin queens. This is dependent upon species and colony maturity. Existing data are summarized in an extensive table. There is no clear cross-species correlation between colony size and reproductive readiness.

Brood care is closely examined. In all studied species, brood care is extensive and lavish. Chemical stimulation of the larvae during development is discussed. In many species, the developing larvae's final physiological plan is strongly influenced by developmental chemical signals provided by the ants performing brood care. Species-

specific examples are discussed in some detail. The caste system is briefly discussed, as it relates to the division of labor.

The demographics of colonies are presented, along with notes on species longevity. Males are noted as generally having particularly short life spans. Although queen longevity varies by species, no obvious correlations with other factors have been identified. The life stages of a typical worker, from egg through larva, adult, and death, are established, with species-specific examples given.

Colony movement of some species is noted; various species of ants have been discovered to move the colony based on external stimuli or apparently according to a schedule (note that detailed examples of this are given in Chapter 16). Colony emigration is typically caused by nest disturbance, flooding, microclimate change, predation, and competition. Other reasons are also elaborated in less detail. Some species-specific examples of alternative colony life cycles are given.

Chapter 3 The Colony Life Cycle Analysis

This chapter summarizes a standard colony life cycle, from the mating of the queen through the development of new mating alates (winged ants). A general strategy is enumerated, with various species-specific examples given to support the text. Exceptions to the standard method are common and many are noted in varying degrees of detail. The chapter is followed by eight full-color, full-page plates, evenly mixed between photographs and illustrations.

Chapter 4 Altruism and the Origin of the Worker Caste

Chapter 4 Altruism and the Origin of the Worker Caste Summary

Altruism (self-destructive behavior performed for the benefit of others) and altruistic behavior are discussed in general terms, and then explored as they apply to the ants. The text does not fully develop theories of altruism, but does provide citations to applicable existing literature.

The function of altruistic behavior in ant colonies is described. An ant colony typically consists of many thousands of individuals (the workers) who forego reproduction in order to assist another individual (the queen) to be enormously reproductively successful. This altruistic behavior is extremely rare outside of the eusocial insects. Haplodiploidy (a mode of sex determination in which males are derived from haploid - unfertilized - eggs, and females from diploid - fertilized - eggs) is thought to exert a strong influence on the altruistic behavior of the ants, as workers are more closely genetically related to their sisters than they would be to their own female offspring.

The biological theory of kin selection is reviewed, including detailed analysis of parental manipulation and offspring consent. Kin selection, in brief, is the selection of genes as a result of individuals favoring the survival and reproduction of relatives who possess the same genes by common descent. The text does not fully develop the theory of kin selection, but does provide citations to existing literature on the theory. The text proposes that kin selection adequately explains altruistic behavior among the ants.

Various methods of testing the theory of kin selection are mentioned and analyzed, and examples specific to ants are given. The degree of genetic relatedness of various species is summarized in a chart, and the reproductive behavior of workers, listed by species, is summarized in a chart. The breakdown of individual and colony reproductive strategies is closely examined, with particular attention focused on relationship to kin selection theories. The eusocial behavior of ants is considered in light of haplodiploidy, and a general review of these topics as they relate to the theory of kin selection is provided.

Chapter 4 Altruism and the Origin of the Worker Caste Analysis

This chapter reviews the fundamental theory of kin selection, and attempts to explain why most individual ants forego reproduction in order to maximally assist the reproductive efforts of the colony's queen ant. The chapter also explains the eusocial

behavior of ants and closely examines ant reproductive strategies. An understanding of the theory of kin selection and altruistic behavior are critical to understanding ant behavior and evolution. Although brief, this chapter explores a critical area in myrmecology. This chapter is also unique in the text in that it is so heavily reliant on external sources of theory and knowledge.

Chapter 5 Colony Odor and Kin Recognition

Chapter 5 Colony Odor and Kin Recognition Summary

Kin recognition is described and considered - the ability to recognize colony members is vital to colony success. Colony members must be able to recognize other colony members, including workers, queens, males, and larvae. They must also be able to distinguish between colony and non-colony members of the same species.

Various responses to individual meetings between ants are categorized and discussed. The ability of ants to recognize each other is summarized, along with information on the various methods utilized for kin recognition. The ability of ants to recognize colony brood is examined. The chemical signature (often referred to as the colony odor) of individual colonies is examined and described in detail, along with the mechanisms of odor production and detection of the colony signature. The chemicals used to produce typical colony signatures are enumerated and discussed. The mechanisms used by individual ants to recognize the colony odor are considered. The ability of individual ants to learn and remember the colony odor is noted.

Chapter 5 Colony Odor and Kin Recognition Analysis

Ants must be able to recognize other colony members and distinguish them from non-members. Each colony produces a distinct odor, or chemical signature, that all colony members learn and remember.

Chapter 6 Queen Numbers and Domination

Chapter 6 Queen Numbers and Domination Summary

The function of the queen ant(s) within a colony is reviewed and briefly summarized. The queen founds the colony and is, generally, the only colony member that is reproductively successful. However, once the colony enters the ergonomic phase, the queen usually has only limited influence on the colony's decision-making processes.

Alternative hypothetical scenarios to eusocial behavior are briefly considered. Some ant colonies are polygynous (include more than one queen). An overview of origin theory of polygyny and monogyny is discussed. Three methods of creating a polygynous colony are considered; pleometrosis, adoption of extra queens; and fusion of colonies. Various field studies of queen numbers are summarized.

Several disparate topics influencing queen numbers are next considered. Marginal populations are considered, and local colony extinctions are simply modeled. Specialized nest sites for certain species are characterized, along with field studies summaries. Some individual species are given further consideration. Variable food supplies are briefly considered.

The colony life cycle described in Chapter 3 is briefly recapitulated; colonies may alternate between the ergonomic and reproductive phases depending on local conditions through time. Several field studies dealing with pleometrosis (the founding of a colony by multiple queens) are synthesized into a generic theory. The demographic consequences of ant polygyny are considered, and several field studies are summarized. A discussion of the role of the queen relative to the worker ants is presented under the title "Who is in charge, queens or workers?" (p. 223). Several field studies resulting in differing points of view are presented.

Chapter 6 Queen Numbers and Domination Analysis

Many ant species form polygynous colonies, where more than a single queen competes for reproductive success. In other species, a single queen is present. Some ant species adopt disparate strategies dependent upon local conditions. This chapter presents extensive information garnered from published field studies.

Chapter 7 Communication

Chapter 7 Communication Summary

Ant communication is categorized into twelve broad functional groups: alarm; attraction; recruitment (a form of assembly where individuals are directed to a place where work is required); grooming; trophallaxis (the exchange of alimentary liquid among colony members); food exchange; group effect; recognition; caste determination; control; territorial signals; and sexual communication.

Chemical ("pheromone") communication is the predominant method utilized by all ant species. Glandular sources of chemicals used for communication are extensively discussed. Numerous photographs, photomicrographs, and illustrations are accompanied by text, which describes the extensive variety of chemical-producing glands found in various ant species.

The molecular design of ant pheromones is considered in general. The efficiency of chemical signaling is reviewed. Various lab assays of ant pheromones are presented, including chemical formulas for some pheromones. Several species are considered in greater detail.

The theory of ritualized communication is presented in general, along with citations to applicable literature, and then applied to ants. Various forms of ritualized communication are described and considered. The methods of sending and receiving ritualized communication are summarized. The theory of modulatory communication (communication intended to alter another organism's behavior) is presented, and the process of synergistic modulatory communication is explained. Different methods of communication by caste are briefly considered.

Acoustic communication is explained, accompanied by anatomic drawings illustrating the stridulatory organ used to produce sound. Tactile communication is described and illustrated with generalized methods; some forms of tactile communication simply enhance the ability to exchange precise chemical messages. Visual communication is reviewed.

In summary, although ants do utilize visual, tactile, and acoustic communication methods, they are in general minor forms of communication in relation to chemical methods. Alarm communication is described in detail. Glands and chemicals used to signal alarm are described and categorized. Propaganda and recruitment methods are described and summarized in a species-specific chart. Trail recruitment pheromone production and use is considered in extensive detail, including summarization of field studies and numerous illustrations. Different species have widely different ways of marking trails and recruiting foraging labor.

Adult transportation (movement from one nest site to another) methods are considered in detail, including the communication methods used to synchronize movement. Various methods of trail and range marking are explained, and numerous illustrations and photographs are provided.

Some ants, such as the weaver ants (refer to Chapter 19) maintain several nest sites simultaneously; other ants, such as the army ants (refer to Chapter 16) move nest sites frequently; other ants may occasionally change nest sites as local conditions dictate. Moving the nest site entails a huge amount of coordinated labor, including preparation of the new site, the movement of all individuals, larvae, eggs, and the queen, and the possibly movement of food items. This must be accomplished within a limited time frame and often under less than optimal conditions.

Several minor forms of communications are listed and briefly described, including attraction pheromones, trophallaxis, group communication, autostimulation, and communication with larvae. A brief consideration of how ants recognize dead ants, and how they dispose of them, is presented in general terms. In some species, dead ants are cannibalized. In other species, dead ants are discarded.

Chapter 7 Communication Analysis

This chapter, the second largest in the book, covers a huge amount of research. As highly social organisms, ants utilize a variety of advanced communication methods. The forms of communication between individuals and groups of ants are summarized, along with extensive illustrations, photographs, and field study citations. Without highly effective methods of mass and individual communication, eusocial organization would not be possible.

Chapter 8 Caste and Division of Labor

Chapter 8 Caste and Division of Labor Summary

Individuals within a colony belong to an identifiable functional group referred to as a caste. Castes allow a colony to function efficiently as a type of transactional system where individual costs are not considered; "[t]he more exact expression is ergonomics, to acknowledge that work and energy are the sole elements of calculation, and also that nothing resembling human transactions with credit and money is involved" (p. 298). Colony ergonomics are based around providing maximum work for minimum energy expenditure, and the loss of individual organisms within the colony is best understood in terms of energy expenditure by the colony. Several field studies of ergonomics are presented and summarized. Ant behavior is codified and presented in charts and graphs, which illustrate how ants belonging to the various castes spend their time and energy.

For example, in *Pheidole dentata*, major workers spend nearly one fourth of their time in trophallaxis with minor workers whereas minor workers spend less than four percent of their time in trophallaxis with major workers. In the same species, major workers spend more than half their time self-grooming, while minor workers spend less than twenty percent of their time self-grooming.

General methods of studying ergonomics are described and clarified. Several approaches to classifying ants in castes are considered. The text selects the following castes as standard: males (all males), queens (reproductive females), workers (sterile females - further subdivided into minors, medias, and majors or soldiers), ergatogyne (females intermediate between queens and workers), gamergates (reproductive females anatomically identical to workers), and dichthadiiform ergatogyne (a specialized form of ergatogyne). The ergatogyne, gamergates, and dichthadiiform ergatogyne castes are confined to individual species or limited circumstances. Other species-specific castes exist which are not enumerated.

In general; minors conduct most of the tasks of a colony (self and other grooming, brood care, trophallaxis, foraging, nest maintenance and construction); medias assist the minors in foraging and construction; majors move trail obstructions and in some species are the primary combatants in colony defense and perform other, species-specific, special tasks; and queens and males are the colony's reproductive members.

Colonies exhibit adaptive demography; that is, the number of individuals of a given caste may change over time, depending on the colony's needs. The evolution of the physical castes is briefly discussed. Individuals perform functions generally belonging to their caste, but the actual functions performed may change over time; for example, a worker may perform nurse duties when young and forage, a particularly dangerous activity, when older. Several examples of such temporal caste behavior are noted.

Numerous studies involving temporal polyethism (division of labor by age) are considered. Existing field studies involving castes and the division of labor are summarized in a species chart, which includes concise results and references, and several interesting case studies are enumerated and discussed in greater detail.

In several species, majors have specialized morphology consistent with specialized roles, including defense, milling, or food storage. "The majors often look like members of an entirely different species" (p. 330). Numerous illustrations of specific examples of each type of specialization are included. Defense-specialized majors have greatly modified head and mandible structures which are geared towards one of four basic fighting techniques: shearing, piercing, blocking (for example, armored heads to block nest entrances), or bouncing (flipping or throwing enemies through the air).

Milling-specialized majors have modified mandible structures, which allow them to rapidly process food, typically grains, through initial stages of processing allowing other castes to subsequently utilize the food. For example, milling might involve stripping off the dense outer husk of large seeds.

Food-storage-specialized majors, termed repletes, grow to enormous sizes and serve the colony by maintaining medium to long-term food storage. "The storage of liquid food in the crop has been carried to great heights by the repletes of certain ant species, individuals whose abdomens are so distended they have difficult moving and are forced to remain permanently in the nests as 'living honey casks'" (p. 333).

Caste optimization is considered, and studies and models dealing with colony ergonomic optimization through caste representation are presented in considerable detail. The propensity of some individual ants, termed elites, to excel in their task, compared to other colony members of the same cast, is noted and discussed. Other peculiar behaviors noted for specific species are presented.

The role of male ants, or males as a caste, is discussed. In general, male ants are produced in limited numbers for the sole purpose of reproduction. They typically do not contribute any physical work or defense to the colony. Male ants develop from haploid (unfertilized) eggs. Several studies and models on the determination of caste are presented. Different species use different mechanisms to determine what caste an individual female larvae will eventually become.

Chapter 8 Caste and Division of Labor Analysis

The caste system of ants is described, and the impact the caste system has on eusocial life is considered. Several methods of study are presented, and numerous mathematical models are presented and considered. This chapter deals with one of the most fundamentally interesting aspects of ant biology.

Chapter 9 Social Homeostasis and Flexibility

Chapter 9 Social Homeostasis and Flexibility Summary

Social homeostatis (the maintenance of a steady social or physiological state by self-regulation) and flexibility are treated in this chapter - how does the colony maintain consistent operation and success over time, given a changing environment? "[T]he organization of ant colonies...permits relatively efficient social regulation with the loosest of command structures" (p. 356).

Approaches to solving complex problems are considered in the abstract; tasks may be accomplished in serial operations or in parallel operations. Depending upon labor available, one method is potentially superior to the other. Strategies for determining which method to use are discussed. From the abstract basis the text moves forward to apply general principles to the specific case of a colony.

An ant colony can be considered to be a single organism in many respects. Regulation of homeostasis, for example, must be exercised by individual organisms but is also critical to whole colony survival. Individuals can display adaptive behaviors, but colony activity is also adaptive and changes through time or circumstances. Individual organisms exhibit variation, and colonies also vary from each other in ways that are more than simply the aggregate of individual variation within each colony.

The role of positive feedback resulting in runaway reactions is briefly discussed. The behavioral flexibility of individuals within a caste is considered. The tempo of colony activity is discussed. Some species are high tempo and perform all tasks in a relatively rapid manner; other species proceed with tasks very slowly. The tempo of the colony is related to both species and colony ergonomics.

Individual ants are capable of learning. Several types of learning are considered. Numerous studies demonstrating the ability to learn are cited and described. Although ants are capable of an astonishing range of learning, they are still fairly limited in types of learning that are categorized as advanced (for example, ants do not appear capable of insight learning). Ants in general are remarkably adept at spatial orientation and geographic learning.

Colonies and individuals exhibit thermoregulation (self-regulation of internal temperature). Ants are strongly thermophilic (attracted to heat). Nest citing, layout, and construction tend to maximize available heat sources. Various field studies of thermoregulation are summarized. Methods of nest construction and insulation are considered.

Humidity regulation is critical to colony health. Nest citing, layout, and construction tend to stabilize humidity. Field studies of several species' methods of controlling nest humidity are summarized.

Chapter 9 Social Homeostasis and Flexibility Analysis

The study of ant colonies is perhaps best performed as if the colony were a single organism. Each colony must maintain homeostasis through environmental changes. Various aspects of homeostasis are described, along with study summaries illustration methods used for control. The chapter includes eight full-color, full-page plates, evenly mixed between photographs and illustrations.

Chapter 10 Foraging Strategies, Territory, and Population Regulation

Chapter 10 Foraging Strategies, Territory, and Population Regulation Summary

Foraging theory is presented in abstract terms. Optimal foraging strategy is constrained by several factors, some external (accidents, predators, competition) and some internal (physiology, limited sensory ability). Foraging must also be considered as an ergonomic activity, as individual worker loss can only be understood in terms of the colony's health.

"Every ant species operates within ranges of temperature and humidity...in other words every species has a temperature-humidity envelope" (p. 379). Field studies on foraging behavior as it relates to temperature and humidity are summarized in a species chart. Temperature-humidity envelope graphs are provided. Daily cycles of activity are also considered. The colony will regulate activity to maximize efficiency.

Different species forage using a variety of distinct methods. Several methods are enumerated and described, including solitary foraging, *ortstreue* (the tendency to repeatedly return to the same foraging site), and central-place foraging. Some species are "energy maximizers" and some are "time minimizers"; most species exhibit a moderate approach to foraging. Many ants exhibit group retrieval, where two or more workers cooperate to retrieve a large food object. Various special stratagems that improve harvesting are considered. Field studies on these approaches are summarized in a chart.

Colony population is regulated and dependent upon numerous factors, including competition with other colonies of the same or different species. Different species display different tendencies towards offensive or defensive responses to threats. Field studies are summarized in a chart with references. Competition models and reactions to differing types of competition are discussed, with a focus on inter-colony competition. Field studies of observed competition and synthesized into a general discussion.

Territorial strategies are considered, and several well-understood strategies are described. African weaver ant, harvesting ant, and honeypot ant territorial strategies are considered in detail. Intercolony communication is described. Various other specialized strategies are enumerated and explained, including ant-ant predation and enslavement.

Many species use the bodies of rival ants killed in combat as a food source. Some species perform territorial raids to kill and harvest large numbers of rival ants as food. Some species, such as *Myrmecocystus mimicus*, raid other colonies of the same species to carry away live workers and brood, which are subsequently utilized as labor in the nest, resulting in true slavery. Other interesting field studies are noted and summarized.

Chapter 10 Foraging Strategies, Territory, and Population Regulation Analysis

This chapter is richly illustrated with photographs, graphs, and drawings. General models of foraging and territorial strategies are synthesized from a broad base of species-specific field studies. Mathematical models are presented and discussed.

Chapter 11 The Organization of Species Communities

Chapter 11 The Organization of Species Communities Summary

Ants coexist with many other species, and frequently these disparate species are organized into species communities. Frequently, species are found to be in direct competition with each other for resources. Ants commonly compete with other closely related ant species for nest sites, food, and foraging grounds. Competition strategies vary widely among species. Several types of competition are discussed.

General biological theory regarding competition, the role of dominant species, and conditions for species coexistence are discussed and applied to ants. Niche and density specialization are considered. Size differentiation and caste polymorphism are considered as factors in competition. Appeasement of competing species is discussed. Species-specific examples are provided for all strategies discussed.

Some interesting field studies on specific enemy identification are enumerated and summarized; "...at least some ant species have evolved defensive maneuvers directed in a precise way to identify and confound their most dangerous adversaries" (p. 429). The biological theory of character displacement is reviewed and applied to ants. The general theories of ecological expansion and equilibrium are reviewed and applied to ants. The role of parasites and predators is briefly considered.

Chapter 11 The Organization of Species Communities Analysis

This chapter considers ants in the context of species communities. This type of field study is always difficult in biology, and the number of ant studies is somewhat limited (excepting symbiotic relationships which are treated in subsequent chapters). This chapter therefore considers several general biological theories and applies them to ants. The chapter concludes with a brief note on "the future of community studies" (p. 435). Note that subsequent chapters (12, 13, 14, and to some extent 17) deal with other interesting aspects of species communities that are more fully studied and understood. This chapter presents numerous general biological theories, which are not fully developed in the text; however, citations to appropriate literature are provided.

Chapter 12 Symbioses Among Ant Species

Chapter 12 Symbioses Among Ant Species Summary

Many species of ants are highly symbiotic. This chapter considers only ant-ant symbiosis, continuing the theme of species communities, which began in Chapter 11. A fascinating case study of the extreme ant parasite *Teleutomyrmex schneideri* is presented in detail; queens (there are no workers in the species) are entirely reliant upon parasitizing *Tetramorium* nests for survival. The life cycles of the two species are discussed.

In brief, *T. schneideri* locates a nest of their host species, invades the queen chamber, and attaches to the back of the host queen. *T. schneideri* anatomy is extensively altered to enable them to securely fasten themselves to their larger host. Once so attached, *T. schneideri* is apparently undetectable to the host species' workers (who feed and groom the parasite), and proceeds to lay eggs, which are cared for and reared by the workers of the host species.

The known types of social parasitism are enumerated and presented as a multi-page chart, complete with citations. The list is extensive. Compound nesting forms are described and considered. Mixed colonies are described. Ants exhibit a wide range of nest types and structures. For example, sometimes two or more species are found cohabitating apparently peacefully and independently within the same nest.

Social parasitism in the ants is described in general terms. The evolutionary mechanisms of social parasitism are discussed at length, and several current theories are enumerated and discussed, including temporary parasitism (a queen of one species enters the nest of another species, kills the resident queen, and utilizes the existing workers to rear her own brood); dulosis (true slavery); xenobiosis (colonies of one species freely live within the nest of another species, utilizing the host species' food, but rearing their own brood); parabiosis (the utilization of the same nest by two species which keep their foraging and brood separate); and inquilinism (permanent parasitism). In particular, the slave-making species are considered in depth with numerous field studies presented and a general theory put forward.

Chapter 12 Symbioses Among Ant Species Analysis

Ants frequently live in close proximity with other ant species, and ant-ant symbiosis is a common phenomenon. Numerous species are specialized parasites on other ant species; perhaps the most studied examples of this are found in the slave-making ants who essentially "take over" another colony's workers for their own reproductive success.

This chapter is exceptionally interesting and provides numerous references to additional fascinating field studies.

Chapter 13 Symbioses With Other Arthropods

Chapter 13 Symbioses With Other Arthropods Summary

This chapter considers symbiosis between ants and non-ant arthropods, continuing the theme of species communities, which began in Chapter 11. "[A]nt guests, commonly known as myrmecophiles, include a great variety of beetles, mites, collembolans, flies, and wasps, as well as less abundant representatives of a wide range of other insect groups" (p. 471). Myrmecophile studies typically divide species into five behavioral categories, including: *synechthrans*, or predators that elicit attacks; *synoeketes*, or predators that do not elicit attacks; *symphiles*, or "true" guests; *ectoparasites* and *endoparasites*; and *trophobionts*, or species that provide their hosts with a benefit such as food in return for a benefit such as protection.

The enormous diversity of myrmecophiles is noted, and the numerous guests of army ants are presented as a detailed case study. For example, among myrmecophilous mites alone, Circocyllibanidae species ride on workers and various species are specialized to live on either mandibles, head, thorax, or gaster; Coxequesomidae species live only on antennae; *Macrocheles rettenmeyeri*, a true ectoparasite, feeds on blood taken from the hind tarsus of its host - in return allowing its entire body to be used by the host as a substitute foot (other mite species parasitize other host species in similar ways). A 14-page chart summarizes species-specific myrmecophiles and provides references. The chart is specific in the types and methods of symbiosis, and makes interesting reading.

The ant colony is considered as an ecosystem. The suitability of ant bodies as hosts for parasites is discussed; in general parasites require modified appendages to remain affixed to their hosts, and require some degree of resistance to the various defensive chemicals produced by their host.

Ant trails and specific areas in nests are discussed, in extensive detail, as suitable habitat for non-ant species. Various areas in the nest provide optimal habitat for a variety of myrmecophiles, and extensive field studies are cited and summarized. Nest areas discussed in detail include the kitchen middens, peripheral nest chambers, and brood chambers. Numerous photographs and illustrations support the text.

Adaptations of brood predators are discussed in detail. Adaptations include chemical disguises, body armor, and specialized feeding procedures. Wasmannian mimicry (where the mimic resembles the host) is described and considered in detail. Symbiosis between ants and lycaenid butterflies is presented in detail, along with numerous field study citations and reviews. Both mutualistic and parasitic relationships are considered, and several photographs and illustrations support the text.

Trophobionts are enumerated and described in some detail. Field studies are summarized and a general theory is presented. "The extreme myrmecophilous homopterans have evolved to the status of domestic 'cattle'" (p. 527); in simpler terms - the ants 'ranch' the aphids. Several specific trophobionts are briefly described.

Chapter 13 Symbioses With Other Arthropods Analysis

Ants commonly live with non-ant species around and even in the nest. There are several categories of ant-arthropod symbioses ranging from benign through predatory. This huge area of research has yielded some surprising items of natural history. This chapter presents numerous fascinating case studies in ant-arthropod symbiosis and provides many references to further resources on the topic.

Chapter 14 Symbioses Between Ants and Plants

Chapter 14 Symbioses Between Ants and Plants Summary

This chapter considers symbiosis between ants and plants, concluding the theme of species communities, which began in chapter 11. The various types of ant-plant symbioses are briefly discussed. Seventeen topic-specific terms are listed and defined in the context of ant-plant symbiosis. The historical understanding of *Acacia* symbiosis is described - the modern interpretation is for a mutualistic symbiosis. Ants commonly protect the plants in which the ants nest; in return the plants offer shelter and food. This particular symbiosis is well studied, well understood, and very widespread in certain geographical areas.

A large chart summarizes known ant-plant symbioses, with a focus on plants-as-shelter, organized by geographic area (including American Tropics; Africa; and Tropical Asia, Oceania, and Australia) and plant family. The chart lists both the plant's adaptations and the ant species typically involved. Several illustrations depict typical plant adaptations. In these cases, the plant offers shelter to the ants, which in turn offer some type of benefit, usually protection, to the plant. A second chart summarizes some known food-based symbioses among five plant genera. In these cases, the plant may not provide shelter, but instead provides food to the ants, which in turn offer some type of benefit to the plant.

Ant gardens, defined as "an aggregate of epiphytes assembled by ants," (p. 546) are discussed; a special case of this topic receives further detailed examination in Chapter 17. These living ant gardens are created when ants bring back seeds and plant matter, and create a typically round ball of growing foliage. The root systems serve as nesting area, and the ants eat some of the plant products.

Food bodies, including extrafloral nectaries, produced by plants are described. Ants often supply key nutrients to their host plant, and they also frequently serve as seed-dispersers. Ants may also pollinate plants under certain circumstances. Ants typically prune and weed around their host plant. Ant pruning behavior is summarized in a chart, which includes citations. A general theory and discussion of ant-plant mutualism is presented. A brief discussion of ant parasites, both microorganisms and fungi, is presented. The text notes that this area is poorly studied.

Chapter 14 Symbioses Between Ants and Plants Analysis

Ants commonly live near or even within plants. There are several categories of ant-plant symbioses varying in degree of dependency. This huge area of research has yielded some surprising natural history. This chapter presents numerous fascinating case studies in ant-plant symbiosis and provides many references for further resources on the topic. The chapter includes eight full-color, full-page plates; most are photographs. Note that the special case of ant-plant-fungi symbiosis found among the so-called leafcutter ants is fully treated in chapter 17.

Chapter 15 The Specialized Predators

Chapter 15 The Specialized Predators Summary

The chapter begins with some exuberant field notes of successful discoveries of peculiar new ant species or radical feeding behaviors. The general biological process of the evolution of prey specialization is described, with a focus on how much of this information originated in ant studies. A chart summarizes prey specialization among ants, organized by subfamily. The chart includes the prey item, and available citations.

The evolution of the Dacetine ants (tribe Dacetini includes 24 genera and 250 species and has nearly worldwide distribution) is described in detail, including field study summaries. The correlation of the evolution of social behavior with species-level adaptations in feeding is considered in particular.

Egg predator strategies are discussed. Termite predator strategies are described, including a description of several physiological adaptations typically found in termite predators. Prey paralysis and storage are considered in general terms. Methods of predator camouflage are briefly described. Several photomicrographs illustrate physiological adaptations enabling prey paralysis and camouflage. Some of the most extreme physiological adaptations found among ants are described in this chapter, and the material is both interesting and surprising. Many of the species described are only known in localized areas, some as small as a single hillside or valley.

Chapter 15 The Specialized Predators Analysis

Numerous unique and interesting physical adaptations enabling specialized predation are considered. This chapter is very accessible and particularly interesting. Numerous ant species have evolved which are niche predators, and have highly modified physiology and behavior to allow them to compete successfully.

Chapter 16 The Army Ants

Chapter 16 The Army Ants Summary

This chapter is the first of four chapters devoted to specific taxa; as such, it contains a large amount of descriptive natural history and is interesting and accessible. The general life history of swarm raider ants is described in detail, accompanied by photographs. Basic trail patterns are described and illustrated. Stages of colony life cycles are considered. Field studies of individual colonies are presented and considered.

Biological characteristics of the army ants are summarized in a chart, which also includes citations. Colony reproduction is discussed. The phylogeny of the army ants is presented, and the diagnostic and other specialized traits are enumerated and discussed. A chart summarizing the species of army ants, with citations, is presented.

The driver ants are described. Other army ant species, besides the doryline and ecitonine ants, are described. Theories on the origin of legionary behavior are presented. This chapter contains a large amount of interesting natural history, and also provides several field anecdotes relating encounters with army ants.

Chapter 16 The Army Ants Analysis

This chapter is particularly interesting and written in an open, accessible style. Illustrations are abundant and interesting.

Chapter 17 The Fungus Growers

Chapter 17 The Fungus Growers Summary

This chapter continues the natural history approach started in Chapter 16, and deals exclusively with fungus-growing ants. "Members of the myrmicine tribe Attini ... [have] ... the sophisticated habit of culturing and eating fungi" (p. 596). Many species within this enormously successful group gather pieces of leaves and flowers to nourish their fungus gardens. The fungus itself subsequently serves as the food for the colony.

An amusing anecdote by V. Wofgang von Hagen, illustrating the amazing leafcutting ability of the fungus-growing ants, is related. In the story, a garden is planted and grows to near maturity only to be stripped bare overnight once discovered by a nest of leafcutter ants. The native populace is greatly amused at the wasted effort expended in the production of the garden, which they correctly predicted would never produce usable crop.

The fungus culturing process used by leafcutter ants is described in detail. The various species of fungus grown are briefly considered. The distribution of leafcutter ants is presented in two charts. The life cycle of leafcutter ants is described, and the structure of the fungus-growing nest is presented. The selection of the plant matter mix used to cultivate fungus gardens is critical, and the methods employed are described.

The origin of leafcutter ants is discussed; several theories are presented. A chart presents several evolutionary trends within the leafcutter ants, organized by genus. Ant-fungus symbiosis involving non-Attini ant species is briefly considered.

Chapter 17 The Fungus Growers Analysis

This chapter is particularly interesting and written in an open, accessible style. The included illustrations are interesting. The fungus-growing ants are also referred to as leafcutter ants. In some parts of the world, they are serious agricultural pests.

Chapter 18 The Harvesting Ants

Chapter 18 The Harvesting Ants Summary

This chapter continues the natural history approach started in Chapter 16, and deals exclusively with harvesting ants; ants "...that regularly use seeds as part of their diet" (p. 609). The history of the study of harvesting ants is briefly recapitulated. These ants, in particular, offer aspects of study, which are easily accessible, and the scientific study of their grain-destroying foraging behavior has gone on for hundreds of years. The earliest work on ants in the modern era, J. Wilde's *De Formica, Liber Unus*, published 1615, deals with these ants. Biblical and earlier references to ants are, most likely, references to harvesting ants. The distribution of harvesting ants is described. A chart summarizes worldwide distribution by species, including citations and comments.

The life history of *Messor pergandei*, an extreme granivore, is presented in some detail, including nest structure. This species is one of the most intensely studied species of ant. Mechanisms used to select seeds are considered. Foraging patterns are described. The effects of foraging on vegetation are summarized.

Many harvesting ants have specialized major workers who serve as millers to the colony; their specialized and massive mandibles are used to crush or process large, hard seeds, which are then passed to minor workers for further processing. Harvesting ants are often in direct competition for food with other non-ant species, such as mice.

Chapter 18 The Harvesting Ants Analysis

This chapter is particularly interesting and written in an open, accessible style. The harvesting ants are serious agricultural pests in many parts of the world, and thus they have been well studied over a very long period of time.

Chapter 19 Weaver Ants

Chapter 19 Weaver Ants Summary

This chapter concludes the natural history approach started in Chapter 16, and deals exclusively with weaver ants. The weaver ants of the genus *Oecophylla* are large-bodied, exclusively arboreal ants. Their remarkable social features have prompted numerous unusually careful and thorough studies. Their nests are composed of large leaves which are pulled over, edge-to-edge, to make a hollow enclosure. The leaf edges are then held together by larval silk, woven together into sheets. In these ants, the larvae surrender their silk on cue and are carried about, by the workers, as living shuttles.

The unique method of nest building employed frees weaver ants from the traditional constraints of colony size and location imposed by more typical nesting sites; "Populations of a half million or more often occur, with nests extending through the crowns of up to three or more good-sized trees" (Chapter 19, p. 619).

Nest structure is described, and the physiology of weaver ants is considered. The process of communal nest weaving is described in step-by-step detail, and field studies are summarized. The process of nest weaving requires the highest grade of cooperation yet found among social insects. Not only does the process require coordinated effort between major and minor workers, it also requires the coordinated effort of larvae.

Intermediate types of nest building among some species are considered. The simplest type of weaving is described. Anatomical changes required for weaving are enumerated and discussed. Several photomicrographs illustrate the text.

Grades of cooperation in nest weaving are presented in a chart, organized by three proposed grades. The limited numbers of ants that utilize nest building are considered, and several areas for further investigation are proposed. The text notes that it is unclear why more species of ants have not evolved to utilize this most useful ability to build arboreal nests. The evolutionary biology of weaver ants is under current study.

Chapter 19 Weaver Ants Analysis

This chapter is particularly interesting and written in an open, accessible style. Illustrations are interesting. The weaver ants embody the highest grade of cooperation yet discovered among the ants, and are fascinating in many ways. Although extensively studied, there are many aspects of their biology that is still poorly understood.

Chapter 20 Collecting, Culturing, Observing

Chapter 20 Collecting, Culturing, Observing Summary

"This chapter provides a primer of simple techniques for studying ants for students and for a wide variety of field researchers..." (p. 630). Methods for collecting ants are enumerated and summarized. Specimen preparation for museum work is considered. Methods used to culture ants are enumerated and summarized. Included is a synthetic diet usable to mass-culture various ant species. Notes on how to transport colonies are given. Methods for breeding new colonies are given.

Chapter 20 Collecting, Culturing, Observing Analysis

This concise chapter condenses decades of first-hand experience into several "big-picture" topics, which are presented as primers. The advice offered is basic, but beyond reproach. The synthetic diet includes contents and preparation methods, and is particularly useful for laboratory studies.

Bibliography

Bibliography Summary

The text includes a briefly annotated bibliography in a 65-page entry. The bibliography lists both works cited and extant literature in a standard author-alphabetized list. As a research tool, the bibliography is indispensable for any serious entomologist and is quite as valuable as the remainder of the text.

Used in conjunction with the numerous topical citation lists presented throughout the text, the bibliography allows easy access to the literature existing at the time of publication. A sample entry reads "Feener, D. H. 1981. Competition between ant species: outcome controlled by parasitic flies. *Science*, 214: 815-817."

Bibliography Analysis

The references included in the bibliography form an invaluable research tool.

Characters

Bert Htzlldobler

Edward O. Wilson

Objects/Places

Army Ants

A group of ant species, which exhibit nomadic behavior and swarming predatory behavior. Army ants will change nest sites frequently, in some species on a nearly daily basis, moving along well-defined and protected migratory pathways. Army ant workers forage in groups and frequently kill much larger organisms. Army ants are also known as driver or legionary ants. *Eciton burcelli* is, perhaps, the best-known species of army ant.

Brood

Ants reproduce by laying eggs, and an individual ant will proceed through several developmental stages from egg, through nymph, larvae, and pupae, to the final, adult stage. Although the egg and pupae stages are not socially active stages, individuals in the nymph and larvae stages interact with other colony members. All immature (non-adult) individuals are referred to, collectively, as the brood. Worker ants spend a great proportion of their time caring for the brood.

Castes

Ant colonies are composed of dozens to millions of individual female ants, nearly all non-reproductive workers. Ants are unique organisms in that the morphology of individual ants is tailored to suit their behavioral role in the colony. For example, some major workers are specialized for combat roles to such an extreme that they are ill suited for any other task. A caste is, therefore, any set of individual organisms of a distinct morphological class that performs specialized labor in the colony.

Colony

Ants are highly social insects and nearly all species live in colonies. A colony is more than a simple aggregation of individuals of the same species - a colony implies cooperation in the rearing of young. Ant physiology and behavior can only be truly understood by realizing that an individual ant has a distinct role in the colony. Ant colonies are generally stable social constructs, but in some species hesmosis, or colony division, will result in a portion of a colony splitting off to found a new colony. A colony will live in one or more nesting sites. A colony may be geographically fixed or, as in the driver ants, move frequently over large distances.

Foraging Trails

Ants typically forage along delineated trails, which lead out from the colony in a branching pattern. As ants move along foraging trails, they periodically drag the tip of the gaster along the substrate and release a chemical signal that marks the foraging trail. As more and more ants move along the same foraging trail, the trail's chemical signature is reinforced thus attracting more ants to the trail. The main foraging trails leading away from a stable colony are thus well-marked and busy routes. As the foraging trails get further from the colony they branch off, much like a tree structure, and lead off to individual foraging areas. Ants will generally retrace the same foraging trail back to the colony.

Harvesting Ants

A group of ant species that exhibit the behavior of collecting and using seeds as part or all of their diet. Harvesting ants often have major workers who are morphologically adapted to perform the initial milling of large seeds, stripping the hull and breaking the seeds into smaller parts that are subsequently processed by minor workers. Harvesting ants are serious agricultural pests in many portions of their range, and have thus been studied both formally and informally for thousands of years. Because seeds are a stable form of food for storage, harvesting ant nests are frequently large and permanent structures. A wide variety of taxonomic groups have developed harvesting behavior independently through evolution.

Leafcutter Ants

A group of ant species, including the genera *Atta* and *Acromyrmex*, that exhibit the behavior of harvesting and collecting leaf matter. The clipped leaf matter is transported into a large, permanent nesting site where it is incorporated into a fungus garden. The fungus that grows upon the leaf matter is the actual food for the ants. Leafcutter ants are serious agricultural pests in many portions of their range. Leafcutter ants are also referred to as fungus growing ants.

Nest

An ant colony will select one or more physical locations to build a nest. A typical nest will include chambers for the queen, the brood, and food storage, though this is not always the case. Nest construction varies widely among different ant species - harvesting ants may dig chambers in the soil, weaver ants may manipulate canopy leaves, and army ants may use fallen trees or rotting logs for temporary shelter. Although nest structure varies widely among ant species, the nest typically provides several benefits, including temperature control, humidity control, and physical protection for the queen, brood, and workers.

Reproductives

Most ants are non-reproductive workers. Within each colony, a handful of individuals are reproductive, including males, queens, and in some species laying females. Queen ants found colonies and thereafter generally do little other than produce eggs in prodigious quantities. Male ants are produced by the colony during breeding seasons and contribute little to the colony other than acting as mates for virgin queens. In some species, some or all of the female workers may from time to time lay small numbers of eggs which, being unfertilized, will develop into male adults. In species with laying workers, many or most male reproductives are not the offspring of the queen. Reproductives are usually alates.

Weaver Ants

A group of ant species, including the genus *Oecophylla*, that utilize larval silk in construction of the nest. Weaver ants frequently use folded leaves as nesting sites, holding the edges together with woven silk. Unlike a traditional soil nest, weaver ants are frequently arboreal and a single colony may consist of dozens of nesting sites spread throughout the tops of several trees. Weaver ants exhibit the most complex social behavior yet observed among the ants.

Themes

Ants Are Social Organisms

All of the known species of ants live in colonies composed of dozens or more individual organisms who chose to forego personal reproduction in order to assist the queen ant in her reproductive goals. Even the rare parasitic ants and the slave-maker ants live in and around highly structured and complex societies, and are dependent upon social structures for their very survival.

Most of an individual ant's behaviors can only be understood by placing them in the context of the social colony. Simply put, ants frequently act in ways that are not particularly logical from the individual ant's point of view - instead; they act in ways that will benefit their colony, including many behaviors that are extremely dangerous.

Many ants physiology is only understood in the context of their caste and role in the colony. Major workers adapted for combat roles, also know as soldiers, often are incapable or barely capable of gathering food for their own use; instead they rely upon the foraging skills of minor workers. Clearly, their physiology is dedicated to social service within the colony over the individual success of the organism.

Many aspects of entomology focus on the study of a colony as the fundamental unit of biology. This allows for the development of ergonomic theory, for example, where the individual organism can be largely ignored except within the context of the larger unit. All aspects of ant biology are, ultimately, strongly related to the fact that ants are social organisms.

Unity in Diversity

The family Formicidae includes at least eleven subfamilies, 297 genera, and 8,800 species. It includes organisms with incredibly diverse physiology, behavior, and sociality, and yet all of these organisms are readily identifiable as ants. Contrast a million or more swarming individuals composing an army ant colony with a solitary parasitic queen *Teleutomyrmex schneideri* - both clearly ants, even to an unskilled observer, yet physically and behaviorally they may have very little in common beyond the most rudimentary basics.

Ants are an enormously successful group of organisms, with a geographic and habitat distribution as wide and diverse as any other animal. The ability of ants to adapt to local environmental conditions, and exploit niche resources, helps them to succeed as a class of organisms. And yet, the strong retention of fundamental primitive traits has kept them all together in the same family, readily identifiable as ants.

Evolution

The single theme in the book that focuses the material into a comprehensible subject is a focus on the process of evolution. No aspect of ant biology can be ultimately understood, except in relation to evolutionary thought. This is particularly true of the social nature and caste systems present in ant colonies.

While it is possible to develop models of, for example, foraging behavior, it is not possible to position those models within the larger scope of myrmecology without understanding the evolutionary history and origins of the species under investigation. The social nature of the ants, their unity as a group, and the individual species diversity observed, only make sense when viewed through the process of evolutionary adaptations.

Style

Point of View

The book is generally presented in the 3rd person point of view prevalent in scientific writing; for example "The life cycle of homopterans, which Zwtzlfer and others have documented thoroughly, crucially affects the success of the trophobiosis" (Chapter 13, p. 524). However, individual sections presenting original research or theory of the authors are often presented in 1st person plural; for example "We have concluded ... that impoverished faunas promote dominant species rather than other way around" (Chapter 11, p. 423).

Language and Meaning

The authors report science in the most straightforward language possible; nevertheless because of the specialized and scientific nature of the book, a large number of specialized terminologies are used. Presented mainly through editorial summarization of existing scientific literature, the book is an interesting and exhaustive work.

The book is written as a traditional biology monograph in a scholarly style, targeted at a college-level reader. The text is very accessible, and thousands of citations and references are provided throughout the text and in the bibliography. The authors assume the reader is familiar with general biology and entomology. The authors also assume the reader is solidly familiar with evolutionary theory, including kin selection, and basic genetics; citations to literature are provided for all topics not developed in detail in the text. An extensive glossary is provided, but most general biology terminology is not included.

Setting

When any setting is implied in the text, it is the setting in which the original scientific work was performed. For most of the book, this would be a research library or laboratory setting. However, much of the fieldwork is put into an implied setting by being identified with a specific geographical place and habitat type; for example "Perhaps the first description of the biology and remarkable nest construction of *Oecophylla* was made by Joseph Banks, who accompanied Captain Cook on the voyage of the H.M.S. *Endeavour* in 1768 to Australia. In his Journal, Banks described his first encounters with the green tree ant in that part of New Holland now called New South Wales ..." (Chapter 19, p. 618).

Structure

The book is structured in a straightforward method, and divided into twenty chapters of uneven lengths, each chapter treating a particular subject area - although a fair amount of self-reference is of course unavoidable in a work of this type, duplication of material is very minimal. Supporting materials, such as a bibliography and index, are also provided.

Quotes

"A 'supercolony' of the ant *Formica yessensis* on the Ishikari coast of Hokkaido was reported to be composed of 306 million workers and 1,080,000 queens living in 45,000 interconnected nests across a territory of 2.7 square kilometers." Chapter 1, p. 1

"All known living ants are eusocial, with strong physical differences separating the queen and worker castes. Thus a large gap in social behavior remains between even the most primitive ants ... and their closest living relatives..." Chapter 2, p. 27

"As expected, mother queens live much longer than workers in all groups of ants. The astounding figures for longevity of *Camponotus*, *Formica*, and *Lasius* queens, ranging from 18 to 29 years, make these ants the most long-lived insects ever recorded." Chapter 3, p. 170

"By almost any conceivable standard, the single most important feature of insect social behavior is the existence of the nonreproductive worker caste." Chapter 4, p. 179

"The ability to distinguish nestmates from strangers is vital to social life among the ants." Chapter 5, p. 197

"The picture that has emerged in contemporary studies is of a moderate amount of struggle within ant colonies. Queens and workers appear to be in general conflict over the management of the ratio of investment in new queens and males." Chapter 6, p. 223

"The sum of current evidence...indicates that pheromones play the central role in the organization of ant societies. In general, it appears that the typical ant colony operates with somewhere between 10 and 20 kinds of signals, and most of these are chemical in nature." Chapter 7, p. 227

"[T]he existence of a subordinate or even completely sterile worker caste ... is ... by far the most significant [eusocial trait] with reference to the further evolutionary potential of social life, for when individuals can be turned into specialized working machines, an intricate division of labor can be achieved and a complicated social organization becomes attainable even with a relatively simple repertory of individual behavior." Chapter 8, p. 298

"What makes social systems most appealing intellectually is the existence of hierarchies. When organization of this kind occurs, there is often more to a whole society than the sum of its parts." Chapter 9, p. 355

"[F]oragers, which are older workers, respond to the nutritional needs of the colony as a whole and not just to their own hunger. How do they monitor this generalized demand? The answer is that they rely on a combined system and individual decisions joined on a massive scale." Chapter 9, p. 355

"Ants do not play ... we know of no behavior in ants or any other social insects that can be construed as play or social practice behavior approaching the mammalian type." (Chapter 9, p. 370)

"When a worker is killed in action, the game is far from over; the colony has merely lost a packet of energy that had been invested earlier through the processes of egg laying, larva rearing, and pupa care. The ultimate payoff in colony-level selection is the summed production of reproductives over a colony generation." (Chapter 10, p. 378-9)

"We have noticed a worldwide tendency in the relation between behavior and species diversity, as follows: *the fewer the ant species in a local community, the more likely the community is to be dominated behaviorally by one or a few species with large, aggressive colonies that maintain absolute territories.*" (Chapter 11, p. 423)

"The ant society is a decidedly more open system than is a lower unit of biological organization such as the organism or cell. In the course of evolution the tenuous lines of communication among members of ant colonies have been repeatedly opened and extended to incorporate alien species." (Chapter 12, p. 436)

"The literature on myrmecophiles is enormous and growing each year, much of it consisting of incidental notes buried in taxonomic and ecological studies of selected genera and higher taxa." (Chapter 13, p. 472)

"Relatively little is known about the pathobiology of ants. The species studied most intensely to date is the red imported fire ant *Solenopsis invicta*, for which entomologists have sought - in vain - a biological control agent. *S. invicta* is evidently typical of ants in that microorganisms and fungal parasites are relatively scare and few in number." (Chapter 14, p. 554)

"Physical adventure and instant scientific rewards await the entomologist who searches for new kinds of ants in unusual food niches or investigates the niches of previously little-known species, the discovery of which in one stroke places these species within the larger context of ant biology. This experience has been especially common in the case of species that hunt unusual prey." (Chapter 15, p. 557)

"To the human eye, and presumably to the eye of many visually orienting predators such as birds and lizards, the ants [of *Basiceros manni*] are difficult to see as they walk over the ground, and virtually invisible when standing still. The effect is achieved in part by the fact that *B. manni* workers are among the slowest-moving ants we have ever encountered during field experience with more than 180 of the approximately 300 ant genera found worldwide. When observed in an undisturbed state, the entire worker force often stands perfectly still for minutes at a time, even holding their antennae in place." (Chapter 15, p. 571)

"The driver and legionary ants are the Huns and Tartars of the insect world. Their vast armies of blind but exquisitely cotzperating and highly polymorphic workers filled with an insatiable carnivorous appetite and a longing for perennial migrations, accompanied by a motley host of weird myrmecophilous camp-followers and concealing the nuptials of

their strange, fertile castes, and the rearing of their young, in the inaccessible penetralia of the soil - all suggest to the observer who first comes upon these insects in some tropical thicket, the existence of a subtle, relentless and uncanny agency, directing and permeating all their activities." (Chapter 16, p. 573 - from Wheeler, W.M., *Ants: Their Structure, Development, and Behavior*, p. 246)

"The leafcutting ants of the genera *Atta* and *Acromyrmex* were pre-adapted for their role as agricultural pests by their ability to use many plant species with the aid of their symbiotic fungi, which serve as a sort of ancillary digestive system." (Chapter 17, p. 596)

"The harvesting of seeds by ants in deserts and grassland is bound to impress human beings who live by the same activity. The storing of seeds by ants in underground granaries has equal appeal. From the Book of Solomon to the writings of the ancient Greeks and Romans, ants were established very early in Western culture as the symbols of industriousness and prudence." (Chapter 18, p. 609)

"[The weaver] ... ants are relatively large, with bodies ranging up to 8 millimeters in length, and exclusively arboreal. The workers create natural enclosures for their nests by first pulling leaves together and then binding them into place with thousands of strands of larval silk woven into sheets. For this unusual procedure to succeed, the larvae must cooperate by surrendering their silk on cue, instead of saving it for the construction of their own cocoons. The workers bring nearly mature larvae to the building sites and employ them as living shuttles, moving them back and forth as they expel threads of silk from their labial glands." (Chapter 19, p. 618)

"Reproductive forms can be easily reared in the laboratory, but those of most species cannot be induced to mate under the culturing conditions ordinarily employed. The reason is that the virgin queens and males must engage in extensive nuptial flights under an exacting regimen of temperature and humidity before they will copulate. The rule is not absolute, however. Few polygynous species mate in or close to the nest, so that laboratory colonies can be maintained and multiplied indefinitely." (Chapter 20, p. 633)

Topics for Discussion

What unique evolutionary problems are presented by the existence of the non-reproductive worker castes?

Is the condition of haplodiploidy, coupled with the theory of kin selection, sufficient to explain the altruistic behavior of the worker castes?

What evolutionary mechanisms could account for the existence of polygyny?

Is the behavior of non-reproductive worker ants truly altruistic?

What methods are typically used to maintain colony homeostasis?

What foraging strategies do ants use to gather resources?

What caste systems are found among the ants?

How do ants communicate with one another?

What are the possible benefits and drawbacks for a plant maintaining a symbiotic relationship with an ant colony?

Why do army ants move their nests so frequently?

What do leafcutter ants do with all of the leaf clippings they take into the nest?

How many colonies of harvesting ants would it take to put a wheat farmer out of business?

What process do weaver ants use to build their nests?