EXCELLENCE IN ECOLOGY

2

O. Kinne, Editor

Edward O. Wilson

Success and Dominance in Ecosystems: The Case of the Social Insects

Published September 1990 by
Ecology Institute, D-2124 Oldendorf/Luhe
Federal Republic of Germany

EXCELLENCE IN ECOLOGY

OTTO KINNE
Editor

2

Edward O. Wilson

SUCCESS AND DOMINANCE IN ECOSYSTEMS: THE CASE OF THE SOCIAL INSECTS

Introduction (Otto Kinne)
Edward O. Wilson: A Laudatio (Sir Richard Southwood)

2

Publisher: Ecology Institute
Nordbünte 23, D-2124 Oldendorf/Luhe,
Federal Republic of Germany

Edward O. Wilson

Museum of Comparative Zoology
Harvard University
Cambridge, MA 02138
USA

ISSN 0932-2205

Printed in F. R. Germany
Typesetting, printing and bookbinding by Konrad Triltsch, Graphischer Betrieb, Würzburg

The god of the bees is the future.
Maeterlinck

Contents

Introduction

O. Kinne

Ecology Institute, Nordbünte 23, D-2124 Oldendorf/Luhe,
Federal Republic of Germany

"Excellence in Ecology" (EE) presents books authored by noted ecologists of our time: the recipients of the Ecology Institute Prize. EE is published by the international Ecology Institute (ECI) which presently has a staff of 41 marine, terrestrial and limnetic research ecologists – all of high professional reputation. Every year a jury composed of ECI members selects – in a rotating pattern – prize winners among marine, terrestrial or limnetic ecologists. Director and scientific staff members receive no remuneration. EE books are made available world-wide at cost price; a large number of books is donated to libraries in Third-World Countries.

The Ecology Institute

The Ecology Institute strives to (1) further the exchange of information between marine, terrestrial and limnetic ecologists; (2) compensate for the lack of balance between analyzing and synthesizing research efforts and thus help to provide more feedback and critical overview for ecological sciences; (3) draw the attention of scientists, administrators, politicians and the general public to important issues resulting from ecological research; (4) assist in finding a long-term compromise between the increasingly destructive potential of modern industrial societies and the need for defining and applying measures to protect nature, commensurate with achieving and sustaining the highest possible living standard for human societies.

ECI's aims and activities have been described more fully in the foreword to Book 1 as have been the procedures for selecting and awarding ECI Prizes. ECI is funded by Inter-Research*, the publisher of the international scientific journals 'Marine Ecology Progress Series', 'Diseases of Aquatic Organisms' and 'Climate Research'.

The books authored by Ecology Institute Prize winners take into account the institute's aims. They offer the authors a chance to express their personal views on important ecological issues and to interpret current scientific knowledge on the basis of their own experience and insight. Thus, EE books differ from textbooks or handbooks which must review objectively defined areas of scientific information.

Ecology Institute Staff 1990 (in brackets: year of appointment)

Director: Professor O. Kinne, D-2124 Oldendorf/Luhe, F.R. Germany

Marine Ecology

Dr. F. Azam, La Jolla, USA (1985)
Prof. H.-B. Bulnheim, Hamburg, FRG (1984)
Prof. J. D. Costlow, Jr, Beaufort, USA (1984)
Prof. T. Fenchel, Helsingør, Denmark (1985)
Dr. N. S. Fisher, Upton, USA (1985)
Prof. J. Gray, Oslo, Norway (1984)
Prof. B.-O. Jansson, Stockholm, Sweden (1989)
Dr. G. I. Müller, Constanta, Romania (1988)
Prof. E. Naylor, Bangor, UK (1984)
Prof. S. W. Nixon, Narragansett, USA (1989)
Dr. T. Platt, Dartmouth, Canada (1984)
Prof. G. G. Polikarpov, Sevastopol, USSR (1985)
Dr. T. S. S. Rao, Bambolim, India (1985)
Acad. Prof. A. Zhirmunsky, Vladivostok, USSR (1988)

---

* D-2124 Amelinghausen, F.R. Germany, PO Box 1120

Terrestrial Ecology

Prof. T. N. Ananthakrishnan, Madras, India (1984)
Prof. F. S. Chapin, III, Fairbanks, USA (1986)
Prof. J. Ehleringer, Salt Lake City, USA (1986)
Prof. M. Gadgil, Bangalore, India (1985)
Prof. J. L. Harper, Bangor, UK (1986)
Prof. E. Kuno, Kyoto, Japan (1986)
Prof. A. Macfayden, Coleraine, UK (1986)
Prof. H. Remmert, Marburg, FRG (1985)
Dr. M. Shachak, Sede Boker Campus, Israel (1989)
Acad. Prof. V. E. Sokolov, Moscow, USSR (1986)
Prof. Sir R. Southwood, Oxford, UK (1986)
Prof. S. Ulfstrand, Uppsala, Sweden (1986)
Prof. E. O. Wilson, Cambridge, USA (1988)

Limnetic Ecology

Prof. J. I. Furtado, London, UK (1985)
Prof. S. D. Gerking, Tempe, USA (1986)
Prof. J. E. Hobbie, Woods Hole, USA (1986)
Prof. G. E. Likens, Millbrook, USA (1989)
Prof. K. Lillelund, Hamburg, FRG (1985)
Prof. R. Margalef, Barcelona, Spain (1986)
Prof. J. Oberbeck, Plön, FRG (1984)
Prof. T. J. Pandian, Madurai, India (1985)
Prof. E. Pattée, Villeurbanne, France (1987)
Prof. T. B. Reynoldson, Bangor, UK (1985)
Prof. J. G. Tundisi, Sao Paulo, Brazil (1990)
Prof. D. Uhlmann, Dresden, GDR (1989)
Prof. W. Wieser, Innsbruck, Austria (1987)
Prof. W. D. Williams, Adelaide, Australia (1986)

Technical Staff
(all Oldendorf/Luhe, FRG)

J. Austin
G. Bendler
M. Bruns
A. Eggers
B. Eggers
R. Friedrich
H. Kinne
S. Matthews
H. Witt

ECI staff members are recruited among leading ecologists. Nominations, to be addressed to ECI's director, are welcome. It now has become a tradition that prize winners are invited to join the institute's staff. This provides for 'fresh blood', assures a high level of expertise and strengthens impartiality (prize winners are excluded from future nominations). Nominations for ECI Prize Winners should be sent to the appropriate jury chairperson, alternatively to ECI's director who will then forward them to the chairperson.

Ecology Institute Jury 1987 for the Field of Terrestrial Ecology

Jury members are appointed by the director. They elect mong themselves the chair-person. The jury is responsible for selecting the prize winners using the nominations received (all research ecologists wordwide are eligible to make nominations) as well as their own professional judgement.

Professor Sir Richard Southwood (Chairman), Department of Zoology, Oxford University, South Parks Road, Oxford OX1 3PS, England
Professor T. N. Ananthakrishnan, Entomology Research Institute, Loyola College, Madras 600 034, India
Professor J. L. Harper, Cae Groes, Glan-y-coed Park, Dwygyfylchi, Penmaenmawr, Gwynedd, LL34 6TL, United Kingdom
Professor E. Kuno, Entomological Laboratory, College of Agriculture, Sakyoku Kyoto 606, Japan
Professor A. Macfayden, 23 Mountsandel Road, Coleraine, Northern Ireland BT52 1JE
Professor H. Remmert, Fachbereich Biologie, Zoologie, Philipps-Universität Marburg, Postfach 19 29, D-3550 Marburg, F.R. Germany
Professor S. Ulfstrand, Department of Zoology, Uppsala University, Section of Animal Ecology, S-75 122 Uppsala, Sweden

Ecology Institute Prize Winners and Their Books

Book 1: Tom Fenchel (Helsingør, Denmark), ECI Prize Recipient 1986 (marine ecology)
Ecology – Potentials and Limitations

Book 2: Edward O. Wilson (Cambridge, USA), ECI Prize Recipient 1987 (terrestrial ecology)
Success and Dominance in Ecosystems: The Case of the Social Insects

Book 3: Gene E. Likens (Millbrook, USA), ECI Prize Recipient 1988 (limnetic ecology)
Insights from Sustained Ecological Research: An Ecosystem Perspective

Book 4: Robert T. Paine (Washington, USA), ECI Prize Recipient 1989 (marine ecology)
Ecological Pattern and Process on Rocky Shores (tentative title)

Please address book orders to: Ecology Institute, Nordbünte 23, D-2124 Oldendorf/Luhe, F.R. Germany (Fax 0 41 32/88 83).

Book 2: Success and Dominance in Ecosystems: The Case of the Social Insects

Book 2 is authored by Professor Edward Osborne Wilson (Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138, USA), the recipient of the ECI Prize 1987 in terrestrial ecology. Ed Wilson has demonstrated excellence in numerous publications centering on the fields of population biology, biogeography, sociobiology, biodiversity, and evolutionary biology. His outstanding achievements and his unique career as research ecologist are highlighted in a laudatio (p. XVII) by Professor Sir Richard Southwood, who chaired the 1987 ECI Jury. The achievements which won Ed Wilson the ECI Prize, as formulated by the jury, have been printed in a document which is reproduced on p. XIV.

Ed Wilson's book addresses success and dominance in ecosystems with professional mastery – matured over decades of devoted, critical research. Defining 'success' as evolutionary longevity of a clade (a species and its descendents), and 'dominance' as abundance of a clade controlling the appropriation of biomass and energy and thus affecting coexisting organisms, Wilson exemplifies his subject by referring to eusocial insects, especially termites and ants but also bees and wasps. Eusocial insects are characterized by care of young, overlap of

ECOLOGY INSTITUTE PRIZE 1987

In Terrestrial Ecology

Professor Edward O. Wilson

has been elected by the Terrestrial Ecology Jury of the Ecology Institute (ECI) as the winner of the 1987

ECOLOGY INSTITUTE PRIZE

Professor E. O. Wilson is distinguished for his many contributions to different aspects of ecology and evolutionary biology. His life-time love of Nature, a theme explored in his book 'Biophilia', has been particularized in his study of ants leading to major new insights on the evolution of castes and the operation of social systems. His seminal 'Sociobiology', derived from this work, has founded a new branch of science, between ecology and the social sciences. With the late Robert MacArthur he was the originator of the modern theories of island biogeography that have contributed not only to the understanding of island biota, but to community and population ecology.

Terrestrial Ecology Jury ECI:

Professor Sir Richard Southwood, Oxford, UK (Chairman)
Professor T. N. Ananthakrishnan, Madras, India
Professor J. L. Harper, Bangor, UK
Professor E. Kuno, Koyto, Japan
Professor A. Macfayden, Coleraine, UK
Professor H. Remmert, Marburg, FRG
Professor S. Ulfstrand, Uppsala, Sweden

ECOLOGY INSTITUTE

The Director

Kinne

Professor Dr. Otto Kinne

Oldendorf/Luhe, Federal Republic of Germany, December 1, 1987 adult generations and division of labor among reproductive and nonreproductive castes. They have achieved an overwhelming dominance and exert a great impact on many other organisms. Their dominance results from competitive superiority based on a sophisticated social organization. Eusocial insects cover a large trophophoric area with near-continuous exploration and defense. Functionally, their colonies are so tightly integrated as to act as superorganisms. Success and dominance of colonial life derive from parallel operations of multiple workers maximizing achievements in the completion of tasks; aggressive, even suicidal behavior; superior protection and exploitation of resources; and enhanced control of a population's microenvironment.

Why then have social insects not entirely outcompeted their solitary counterparts? The essence of Wilson's answer to this question: while social insects prevail in terms of biomass in most terrestrial habitats, solitary insects appear to 'fill the cracks' left by social insects, and they breed faster on smaller amounts of resources.

Hawaii was not colonized by social insects before the establishment of human societies. This remote archipelago thus provides a chance to study the evolution of the endemic fauna and flora in the absence of social insects. Wilson considers that freedom from social insects – especially ants and termites – may have contributed significantly to some of the characterizing traits of the Hawaiian biota, such as flightlessness, lack of evasive behavior, increased abundance and diversity of beetles and spiders, adaptive predation in some insect groups, and loss of extrafloral nectaries in flowering plants.

Ed Wilson's small book is packed with facts, ideas and visions. It floats on a sea of admiration and love for nature. I am sure the book will stimulate further research, as well as interchange among terrestrial, marine and limnetic ecologists, and it will carry the word of a leading scholar devoted to analyzing, comprehending and protecting nature far beyond professional borderlines.

◄———

Ecology Institute Prize 1987 in the field of terrestrial ecology. Reproduction of the Prize Awarding Document.

Edward O. Wilson – Recipient of the Ecology Institute Prize 1987 in Terrestrial Ecology: A Laudatio

T. R. E. Southwood

**Department of Zoology, University of Oxford, South Parks Road,
Oxford OX1 3PS, England**

Whether we seek a good primer in population biology, the seminal work on biogeography, the definitive treatise on sociobiology, the key work on ants or the overview on biodiversity, we turn to the writings of Ed Wilson. At a time when evolutionary biology and ecology are increasingly illuminating the other field and when these subjects are impinging and interacting with public policy, through conservation and environmental concern, we find one person who more than any other spans the whole area with his research and writings. That person is our ECI Prize winner – Edward Osborne Wilson.

Born in Birmingham, Alabama, on 10 June 1929, Ed Wilson was soon to show his fascination with natural history. His father, a federal employee, moved frequently as the agencies he worked for were created and disbanded in the days of the deep depression, so that the young Ed attended sixteen different schools in eleven years. The woods, the fields and their organisms that he came to know so well, were a constant feature in this peripatetic life: whilst school mates were hardly known before they were left behind. Although his own parents moved so frequently, the family had deep roots in Alabama, as farmers (on his mother's side) or as shipowners, pilots or railroad engineers (on his father's) and these relations admired, in a somewhat puzzled way, the unusual interests of 'Sonny' Wilson. From butterfly collecting at the age of nine and ten, this main interest soon switched to ants, having discovered a large colony of *Acanthomyops* in Rock Creek Park, near the National Zoo, Washington, DC. In spite of a first publishable observation made on ants (the distribution of *Solenopsis*) at the age of thirteen, there followed a brief seduction by snakes, frogs and salamanders; but by the age of sixteen, ants had again become the main focus of attention and so they have remained for more than forty years.

At the age of nineteen, when a student at the University of Alabama, Ed Wilson made contact with William L. Brown, than a graduate student at Harvard. As Wilson has so aptly written, "one of the warmest and most generous human beings I have ever known", continuing "the single greatest influence on my scientific life". Brown encouraged Wilson to broaden the scope of his studies, to change his objective from a local survey to a monograph of an important group. At the age of twenty-four (in 1953) Wilson moved to Harvard, his horizons ever widening as he listened to Lorenz lecture, as he pondered the implications of modern biology for the study of ants and travelled (on a grant from the Society of Fellows) through the Pacific and Indian Oceans, from Fiji and other islands, through New Guinea and Australia to Sri Lanka.

Just as the voyage of the Beagle, superimposed on a deep knowledge of natural history (especially entomology), laid the foundations for Charles Darwin's contributions, so did this *Wanderjahr* inspire Ed Wilson. Like Darwin he is a man of enlarged curiosity.

From junior Fellow, Wilson has progressed at Harvard to the Frank B. Baird Professorship of Science, also holding the Curatorship of Entomology in the University's Museum of Comparative Zoology. His current titles are a happy reflection of his activities: well rooted in entomology he ranges widely through the whole of science.

Based on his detailed knowledge of ants, Wilson formulated two broad concepts at the interface of ecology and evolution: character displacement (with William Brown) and the taxon cycle. Then his work proceeded in several directions at once: chemical communication and behaviour, distribution and zoogeography, speciation and diversity, but always continuing his profound taxonomic work on ants. Wilson has written that around 1960 he felt himself squeezed between the older generation of evolutionary biologists, completing their great 'synthesis', and the young triumphalist molecular biologists who denied the value of much biology at the organismic and population level. Yet from the perspective of today one can see how Wilson himself was staking out new territory, laying the groundwork for so many important advances that constitute modern biology. For example he demonstrated the role of chemical communication in ants and postulated its overwhelming importance, even before the term 'pheromone' had been coined. There are three other areas where his past and present work are even more dominant: island biogeography, sociobiology and the significance and conservation of biodiversity.

With the late Robert MacArthur, Ed Wilson revolutionised our approach to biogeography: the fauna of an area at any one time was to be viewed as a consequence of the opposing dynamic processes of colonisation and extinction, and with Daniel S. Simberloff he participated in large-scale field experiments on island colonisation: the first of their type. In the classic monograph *The Theory of Island Biogeography* (1967) the concept of r and K selection was briefly introduced: but in such a clear and insightful way that it caught the interest of evolutionary ecologists and has burgeoned into that active field of research (and dispute), the study of life history strategies.

Expanding from his deep knowledge of the social behaviour and organisation of ants, Ed Wilson reviewed comparable work on vertebrates and colonial invertebrates and this led to the publication of his *magnum opus* (to date!) *Sociobiology: The New Synthesis* (1975). Carefully and meticulously in this great work the evolution of social behaviour is traced, the behavioural and reproductive trade-offs, the costs and benefits of altruism, the genetic basis of much that we observed laid bare. The work established a new area of biological work doing much to bring together population genetics, ethology and ecology within an evolutionary framework. But Wilson's final chapter, in which he applied some of these concepts to human society, has proved highly controversial. Although he stressed that most human behaviour was undoubtedly learnt (i.e. due to environment), he claimed that some small component (say 10%) was inherited. This clearly took the insights of evolutionary biology into other fields: anthropology, ethnology, psychology, sociology and, most explosively, political science. For some, in my view perceptive, students of these subjects, sociobiology has provided a valuable new dimension. Others have rejected it with a fervour more reminiscent of religious than scientific discussion. Wilson continued participating in the debate writing *On Human Nature* (1978), which was awarded the Pulitzer Prize for non-fiction, *Genes, Mind and Culture* (1981) and *Promethean Fire* (1983) – the two last named with Charles Lumsden –

which set out a picture of gene-culture co-evolution. As Wilson himself has written "Whether or not the theory . . . proposed constitute(s) the dreamed of breakthrough remains to be seen", but whatever the outcome, human ecology, psychology and sociology will have been profoundly influenced.

Ed Wilson has a deep love of Nature, a trait for which he has coined the term 'biophilia', explored in a book with that title (1984). In the last decade he has been increasingly worried by man's destruction of the environment, more particularly the loss of diversity. Characteristically he took up the challenge of awakening the politicians and the populace: the opening shot in this campaign was a paper in 1985 'The Biological Diversity Crisis'. A year later he was the moving spirit for a conference (a National Forum) on BioDiversity held under the sponsorship of the US National Academy of Sciences and the Smithsonian Institution. The resulting volume (*BioDiversity*) (1988) which Wilson edited, has been described as "The most comprehensive book ever published on one of the most important subjects of our (and all) times" (Stephen J. Gould). That there is now such widespread public understanding of this subject is in no small measure due to Wilson, his authority being especially great because of his own first-hand knowledge of the issues involved – knowledge derived from the study of ants. Indeed throughout all this period, whilst fathering new fields such as island biogeography, sociobiology and biodiversity, Ed Wilson has maintained an active research and publishing programme on ants. Undoubtedly the work that he has prepared for the ECI Prize will prove to be another milestone in the progress of our subject.

Preface

Since scientists are social mammals above all else, peer approval is a priceless reward for a lifetime devoted to research. I am grateful to Professor Otto Kinne for conceiving the Ecology Institute (ECI), and to Sir Richard Southwood and the ECI Terrestrial Ecology Jury he chaired for awarding me the 1987 prize. The requirement of a book from each laureate is an excellent idea. I took the occasion to return to two subjects that have fascinated me throughout my career: the rise and fall of world-dominant groups of organisms, and the role of social organization in adaptation. In so doing I thought through topics and committed ideas to paper in a way that would not have occurred otherwise. One concrete result, for example, was the realization that there are no native social insects on Hawaii, making the extraordinary fauna on the islands even more important for ecological research than had been previously understood.

I thank the following colleagues for help and advice during the preparation of the manuscript: Kenneth J. Boss, Bert Hölldobler, Scott Miller, Daniel Otte, Stuart Pimm, Charles L. Remington, and John E. Tobin. Kathleen Horton deserves special recognition, as in most of my previous published work, for her careful and expert attention to the preparation of the final manuscript and bibliography. Finally, I am grateful to Otto Kinne for the conception of the award, his novel idea for lashing ecologists into general communication, and his warm support and encouragement throughout my own effort.

Cambridge, Massachusetts, USA, December 1989 Edward O. Wilson

I The Dominance of the Social Insects

Social insects saturate most of the terrestrial environment. In ways that become fully apparent only when we bring our line of sight down to a millimeter of the ground surface, they lay heavily on the rest of the fauna and flora, constraining their evolution.

That fact has struck home to me countless times during my life as a biologist. Recently it came again as I walked through the mixed coniferous and hardwood forests on Finland's Tvärminne Archipelago. My guides were Kari Vepsäläinen and Riitta Savolainen of the University of Helsinki, whose research has meticulously detailed the distribution of ants in the archipelago and the histories of individual colonies belonging to dominant species. We were in a cold climate, less than 800 kilometers from the arctic circle, close to the northern limit of ant distribution. Although it was mid-May, the leaves of most of the deciduous trees were still only partly out. The sky was overcast, a light rain fell, and the temperature at midday was an unpleasant (for me) 12°C. Yet ants were everywhere. Within a few hours, as we walked along trails, climbed huge moss-covered boulders, and pulled open tussocks in bogs, we counted nine species of *Formica* and an additional eight species belonging to other genera, altogether about one-third the known fauna of Finland. Mound-building Formicas dominated the ground surface. The nests of several species, especially *F. aquilonia* and *F. polyctena*, were a meter or more high and contained hundreds of thousands of workers. Ants seethed over the mound surfaces. Columns traveled several tens of meters between adjacent mounds belonging to the same colony. Other columns moved up the trunks of nearby pine trees, where the ants attended groups of aphids and collected their sugary excrement. Swarms of solitary foragers deployed from the columns in search of prey. Some could be seen returning with geometrid caterpillars and other insects. We encountered a group of *F. polyctena* workers digging into the edge of a low mound of *Lasius flavus*. They had already killed several of the smaller ants and were transporting them homeward for food. As we scanned the soil surface, peered under rocks, and broke apart small rotting tree branches, we were hard put to find more than a few square meters anywhere free of ants. In southern Finland they are in fact the premier predators, scavengers, and turners of soil. Exact censuses remain to be made, but it seems likely that ants make up 10% or more of the entire animal biomass of the Tvärminne Archipelago.

Two months earlier, in the company of Bert Hölldobler of the University of Würzburg, F. R. Germany (then at Harvard University, USA), I had walked and crawled on all fours over the floor of tropical forest at La Selva, Costa Rica. The ant fauna was radically different and much more diverse than in Finland. The dominant genus was *Pheidole*, as it is in most tropical localities. Within a 1.5 km^2 area along the Rio Sarapiquí, my students and I have collected 34 species of *Pheidole*, of which 16 are new to science. The total ant fauna in the sample area probably exceeds 150 species. That is a conservative estimate, because Neotropical forests have some of the richest faunas in the world. Manfred Verhaagh (personal communication) collected about 350 species belonging to 71 genera at the Rio Pachitea, Peru. That is the world record at the time of this writing. I identified 43 species belonging to 26 genera from a single leguminous tree at the Tambopata Reserve, Peru (Wilson, 1987a). From my experience in ground collecting in many Neotropical localities, I am sure that an equal number of still different species could have been found on the ground within a radius of a few tens of meters around the base of the tree. In other words, the fauna of the Tambopata Reserve is probably equivalent to that at the Rio Pachitea.

The abundance of ants at Neotropical localities, as opposed to species diversity, is comparable to that on the Tvärminne archipelago, and they occupy a great many more specialized niches as well. In addition to a large arboreal fauna, lacking in Finland*, leaf-cutter ants raise fungi on newly harvested vegetation, *Acanthognathus snare* tiny

---

* In an interview with the vice-rector of the University of Helsinki, I mentioned the 43 ant species found on one tree in Peru. He asked how many kinds occur on one tree in Finland, whereupon Kari Vepsäläinen answered for me: "If you cut down all the forests of Finland, you will find two species."

collembolans with their long traplike mandibles, *Prionopelta* species hunt campodeid diplurans deep within decaying logs, and so on in seemingly endless detail. Roughly one out of five pieces of rotting wood contains a colony of ants, and others harbor colonies of termites. Ants absolutely dominate in the canopies of the tropical forests. In samples collected by Terry Erwin by insecticidal fogging in Peru, they make up about 70% of all of the insects (personal communication). In Brazilian Terra Firme forest near Manaus, Fittkau and Klinge (1973) found that ants and termites together compose a little less than 30% of the entire animal biomass. These organisms, along with the highly social stingless bees and polybiine wasps, make up an astonishing 80% of the entire insect biomass.

While few quantitative biomass measurements have been made elsewhere, my own strong impression is that social insects dominate the environment to a comparable degree in the great majority of land environments around the world. Very conservatively, they compose more than half the insect biomass. It is clear that social life has been enormously successful in the evolution of insects. When reef organisms and human beings are added, social life is ecologically preeminent among animals in general. This disproportion seems even greater when it is considered that only 13,000 species of highly social insects are known, out of the 750,000 species of the described insect fauna of the world.

In short, 2% of the known insect species of the world compose more than half the insect biomass. It is my impression that in another, still unquantified sense these organisms, and particularly the ants and termites, also occupy center stage in the terrestrial environment. They have pushed out solitary insects from the generally most favorable nest sites. The solitary forms occupy the more distant twigs, the very moist or dry or excessively crumbling pieces of wood, the surface of leaves – in short, the more remote and transient resting places. They are also typically either very small, or fast moving, or cleverly camouflaged, or heavily armored. At the risk of oversimplification, the picture I see is the following: *social insects are at the ecological center, solitary insects at the periphery.*

This then is the circumstance with which the social insects challenge our ingenuity: their attainment of a highly organized mode of colonial existence was rewarded by ecological dominance, leaving what must have been a deep imprint upon the evolution of the remainder of

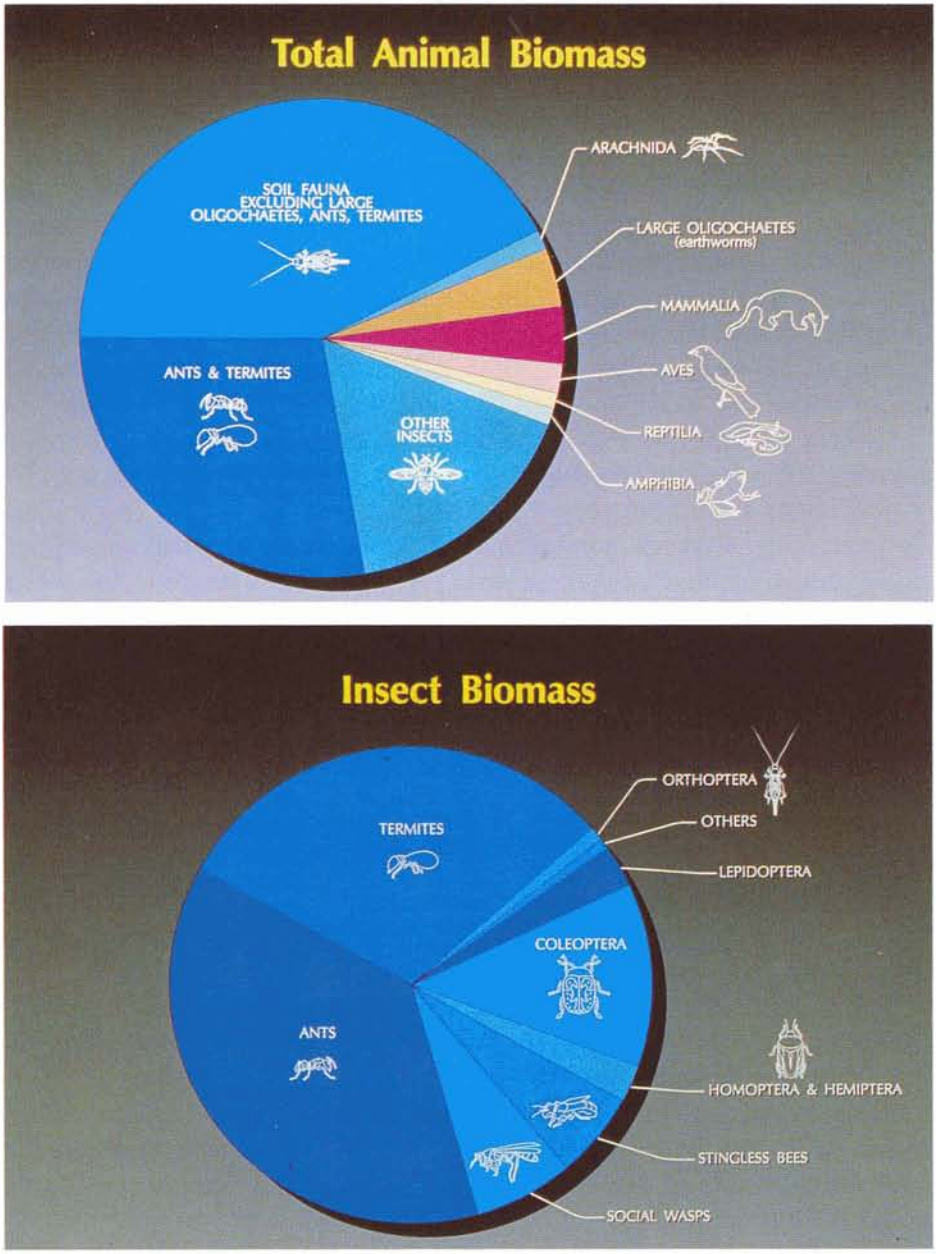

Fig. 1. The apportionment of biomass among groups of animals and insects respectively, in rain forest near Manaus, Brazil. (From Wilson, 1988; based on data from Fittkau and Klinge, 1973, and reproduced with the permission of the National Geographic Society.)

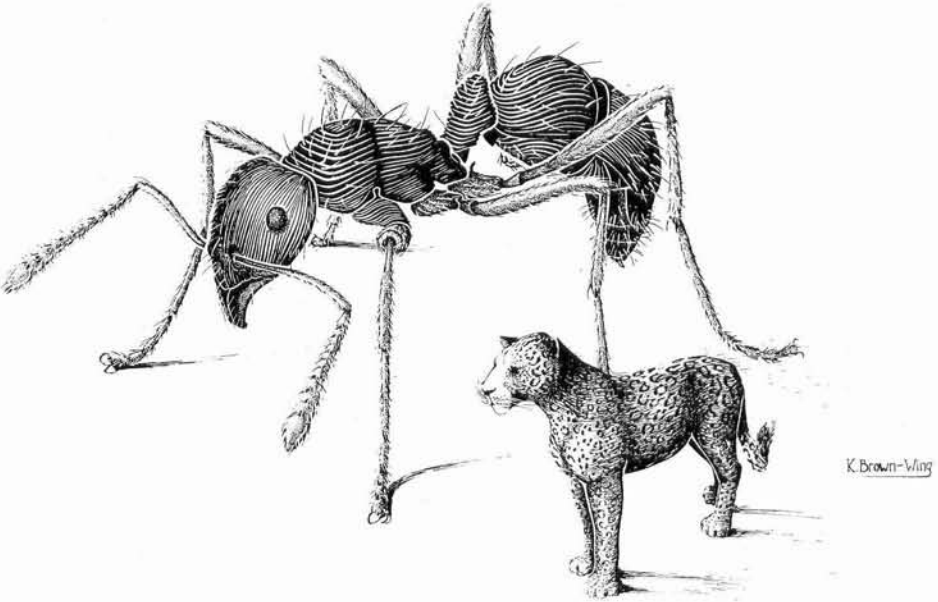

Fig. 2. In Brazilian tropical forest, the biomass of ants is approximately four times greater than the biomass of all of the vertebrates (mammals, birds, reptiles, and amphibians) combined. The difference is represented here by the relative sizes of an ant, *Gnamptogenys pleurodon*, and a jaguar. The measures are provided in Fig. 1. (Original drawing by Katherine Brown-Wing.)

terrestrial life. In this book I will explore the themes in ecological research suggested by this achievement. They include:

- In a more explicitly heuristic framework, the general meaning of success and dominance in organisms other than man.
- The general characteristics of social insects and the manner in which they might have contributed to success.
- The nature of social solutions to particular environmental challenges.
- The impact of the social insects on the terrestrial fauna, in other words the actual workings of their dominance.

To a degree unappreciated even by most field biologists, social insects, especially ants and termites, dominate the terrestrial environment. It is tempting to think that colonial life has contributed to this preeminence, and that the social insects might serve as a paradigm for the study of dominance in ecosystems generally.

II The Social Insects: A Primer

Despite the accessibility and ease of study of social insects, they have received relatively little attention in general textbooks of biology, ecology, and behavior, perhaps because their life cycles and anatomy initially seem more complex, their diversity greater, and the literature consequently more "technical." All of this remoteness is due to the accident of our mammalian origins. If the first highly intelligent, linguistic species had been a termite instead of an Old World primate, the reverse perspective would exist. Vertebrates would be noted chiefly for their gigantism, scarcity, and unfamiliar anatomy. To lessen this phylogenetic handicap and aid the general reader, I now offer a brief synopsis of social insect biology.

Let us descend to the millimeter level.

The most advanced social insects are referred to as eusocial, an evolutionary grade combining three traits: some form of care of the young, an overlap of two or more generations in the same nest site or bivouac, and the existence of a reproductive caste and a nonreproductive or "worker" caste. The eusocial grade has been attained by 4 principal groups of insects: the ants (order Hymenoptera, family Formicidae, 8800 described species), the eusocial bees (order Hymenoptera, about 10 independent evolutionary lines within the families Apidae and Halictidae, perhaps 1000 described species overall), the eusocial wasps (order Hymenoptera, mostly in the family Vespidae and a few in the family Sphecidae, 800 described species), and the termites (order Isoptera, 2200 described species). The presence of a worker caste is by far the most important feature, because it enhances division of labor and a more complex society overall. The most familiar social insects, those with the striking social adaptations such as honeybees, mound-building termites, and army ants, all have strongly differentiated worker castes.

Evolutionary grades below the eusocial state abound in the insects. They are lumped together in the category "presocial," in which one or two but not all three of the aforementioned eusocial traits are displayed. One of the most frequently remarked forms of presocial behavior is subsocial behavior, which simply means that the parents care for their own nymphs or larvae. For example, the females of many true bugs (order Hemiptera) remain with their young to protect them from predators and sometimes even to guide them from one feeding site to another. Some scolytid bark beetles not only guard their young but feed them fungi in specially constructed nursery chambers. In neither case, however, do the offspring later function as nonreproductive workers. Hence neither hemipterans nor scolytid beetles, remarkable as they are, qualify as social insects.

Ants, bees, and wasps, being members of the order Hymenoptera, have a life cycle marked by complete metamorphosis. To use the appropriate adjective, they are holometabolous. As illustrated in Figure 3, the individual passes through four major developmental stages radically different from one another: egg, larva, pupa, and adult.

The significance of this tortuous sequence is the difference it allows between the larva and the adult. The larva is a feeding machine, specialized for consumption and growth. It typically travels less, remaining sequestered in a nest site or other protected microenvironment. The adult, in contrast, is specialized for reproduction and in many cases dispersal as well. It often feeds on different food from that of the larva or no food at all, living on energy stores built up during the larval phase. Finally, the pupa is simply a quiescent stage during which tissues are reorganized from the larval to the adult form. The effect of complete metamorphosis on social evolution is profound. The larva can do little work and must be nurtured. Its dependence on the adults is increased by its limited mobility, since even if it were capable of independent feeding it could not travel to distant food sources. Consequently a large part of adult worker life is devoted to larval care, during which individuals search for food to give to the larvae, then feed, clean, and protect them.

Termites, in contrast, have incomplete metamorphosis; in adjectival expression they are said to be hemimetabolous. Eggs yield nymphs rather than larvae. These immature forms basically resemble the adults in form, insofar as they possess antennae and locomotory appendages and are fully mobile (see Figure 4). The smallest nymphs, or "larvae"

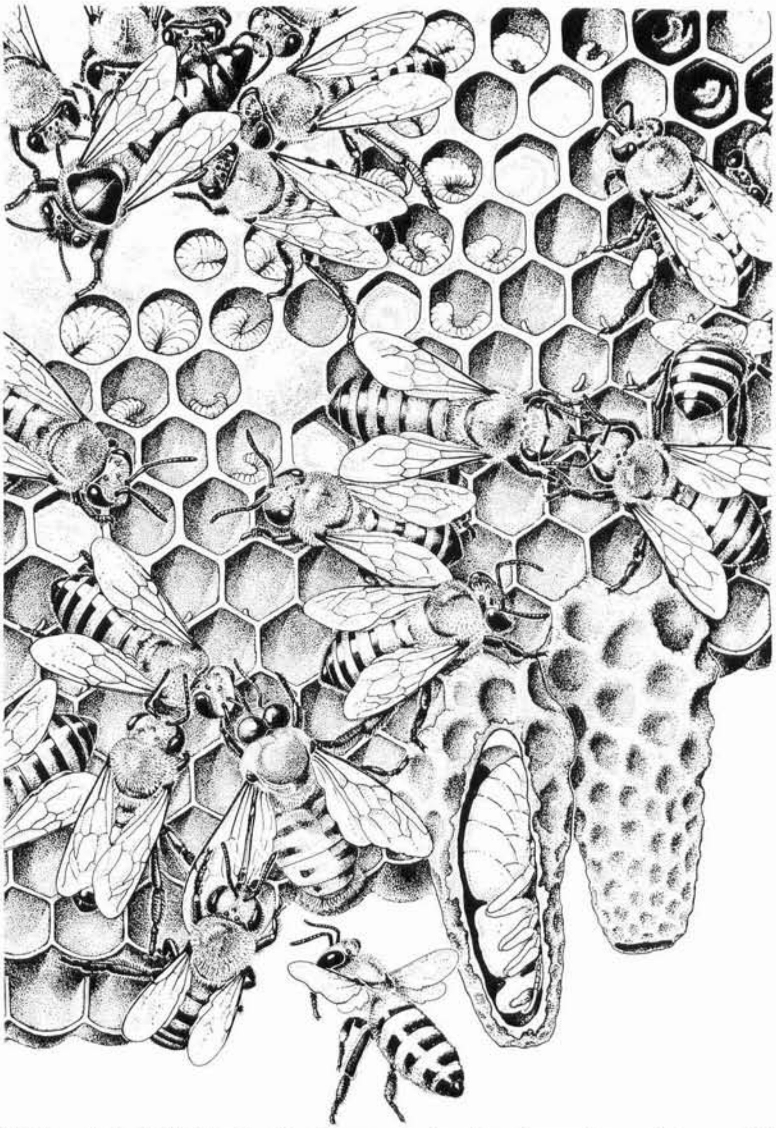

Fig. 3. Caste and individual development in the honeybee *Apis mellifera*, a holometabolous eusocial species. The queen, the sole reproductive individual, rests on a portion of the brood comb in the upper left hand corner of this figure. A large-eyed male (drone) sits at the lower left. The other winged, adult individuals, who are all the queen's daughters, serve as nonreproductive workers. In the brood cells are seen small elongate eggs laid by the queen, as well as larvae that have hatched from them and are now in various stages of development. In the lowermost "royal" cell hanging from the edge of the comb is the pupa of a new queen. All honeybees pass through the four stages of complete metamorphosis: egg, larva, pupa, and adult. (From Wilson, 1971.)

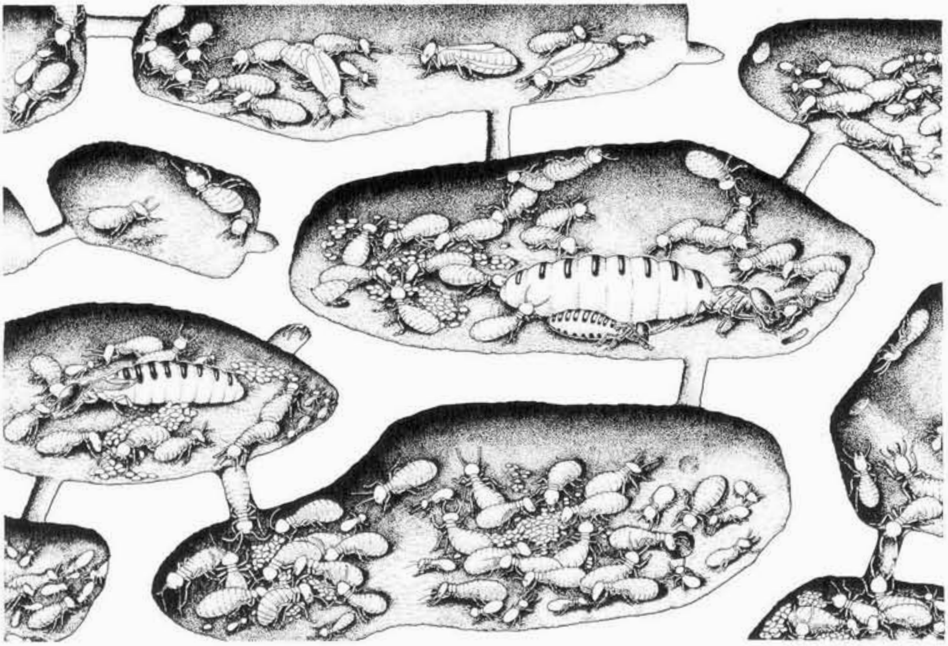

Fig. 4. Caste and development in the South African termite *Amitermes hastatus*, a hemimetabolous insect species. The figure depicts a small section of an earthen mound nest. The central cell is occupied by the primary queen, possessing an abdomen swollen with ovarioles, and the much smaller king at her side. On the lower left can be seen a secondary queen. A single long-mandibled soldier, one of the adult nonreproductive castes, is at the lower right. Many adult workers occur elsewhere, busily attending the scattered eggs and offering regurgitated food to nestmates. Also present are nymphs in various stages of growth, including three individuals in the cell at top center destined to become reproductives. (From Wilson, 1971.)

as they are sometimes perversely called by termite researchers, are helpless and must be cared for by older nestmates. In the case of the most primitive termite species, after the nymphs have molted their skins as part of the growth process (and are thus said to have passed from the first to the second instar), they begin to contribute to the labor of the colony. The incomplete metamorphosis of the termites means that their caste differentiation is not a final product of metamorphosis solely manifested in adults, as in the hymenopterans, but is intimately tied to the successive molts of the immature stages. Labor specialization often varies within the same individual from one molt to the next. In the higher termites, the immature forms are helpless and dependent on the adults, the same pattern as in the social Hymenoptera.

It will be useful at this point to review the broad features of classification of the several groups of eusocial insects, with some of the terminology most often encountered in the literature.

Ants. These insects, composing the single taxonomic family Formicidae, have enjoyed the most impressive adaptive radiation of any of the eusocial insect groups. Most species are scavengers or prey on other arthropods. Some of the predators are extremely specialized. For example, species of *Proceratium* and *Discothyrea* collect arthropod eggs; *Belonopelta* and *Prionopelta* hunt campodeid diplurans; *Thaumatomyrmex* feeds on polyxenid millipedes; and so on. Other ants raise fungus for food, and the two leafcutter genera *Acromyrmex* and *Atta*, among the most abundant ants of tropical America, collect fresh vegetation to serve as a substrate. Army ants hunt large or otherwise formidable prey, such as wasp colonies, in tightly organized foraging parties. Still other ants live primarily or exclusively on "honeydew," the sugary excrement of homopterous insects such as aphids and mealybugs.

The living Formicidae are divided by taxonomists into 11 subfamilies, of which 7 are prominent enough in the environment to deserve special mention. The Ponerinae are relatively primitive in body form, relying on their stings for combat in the manner of wasps. Heavily concentrated in the tropics, they are also mostly predators. The Dorylinae include the African and Asian driver ants (*Dorylus*) and smaller army ants of possibly independent origin (*Aenictus*). The Ecitoninae are the New World army ants, among which the spectacular tropical species of *Eciton* are the best known. The Myrmicinae are the most diverse and abundant of all the ant subfamilies. Among their species are specialists of virtually every conceivable kind, from exclusive predators to army ants, seed harvesters, and aphid pastoralists. One group, the Neotropical tribe Attini, raise fungi on insect excrement or decomposing vegetation. Leafcutters in the genera *Atta* and *Acromyrmex* are so successful in this endeavour as to constitute the dominant herbivores in most habitats. The Pseudomyrmecinae, comprising the two genera *Pseudomyrmex* and *Tetraponera*, are important arboreal ants of the tropics and subtropics worldwide. They are most often noted for the tight mutualistic symbioses a few of the species have formed with ant-plants, that is, with trees or shrubs specialized to house and feed ants while receiving their protection from herbivores. The Dolichoderinae are predators, scavengers, and pastoralists characterized by formidable chemical defenses. Finally, the Formicinae rival the Myrmicinae in abundance and ubiquity but not in diversity. Phylogenetically more distant from the other ant families than these families are to each other, they are variously predators, scavengers, and pastoralists, and overall the only ants to use formic acid as a weapon. The best known formicines, and among the best studied ants in the world, are species of the abundant north temperate genus *Formica*.

Bees. The many species of sweat bees of the family Halictidae show among themselves virtually every conceivable grade in behavioral evolution from a purely solitary existence to eusociality. Their close study has therefore illuminated the origins of social behavior in insects (Michener, 1974). The phylogenetic tracings are all the more useful because eusociality has originated at least five times within the family.

The pinnacles of social evolution within the bees, however, have not been attained by halictids but by three lines within the family Apidae. Of interest to biologists generally are the bumblebees (subfamily Bombinae), whose burly, hirsute bodies and annual life cycles adapt them especially well to cold climates. Two species reach the northern limits for all social insects, on Ellesmere Island.

The honeybee genus *Apis* contains six or seven species native to the Old World. One, the domestic honeybee *Apis mellifera*, is by far the most celebrated social insect and among the best studied of all organisms. The genus *Apis* represents one of two principal branches of the subfamily Apinae. The second comprises the stingless bees, or meliponine bees, whose five living genera include *Melipona* and *Trigona*. Being strictly limited to the tropics and subtropics, these insects are less well known than the honeybees but match them in the complexity of their communication systems and social organization.

Wasps. Almost all of the eusocial wasps belong to the family Vespidae. The single exception is the New World tropical genus *Microstigmus*, a rare and little known member of the family Sphecidae. The most frequently studied vespid wasps are the members of the genera *Vespa*, known as hornets in the American vernacular; *Vespula*, hornets and yellowjackets; and *Polistes*, the paper wasps. These insects typically build large colonies that generate queens and males in the late summer and then die out in the fall, leaving the new royal reproductives to overwinter and start new colonies in the spring. They are also characterized by the presence of a single queen, which in the case of *Vespa* and *Vespula* is conspicuously larger than the workers. This is not the case, however, for the great majority of social wasps, which live in the tropics. These vespids, constituting the tribe Polybiini, are perennial. The queen caste in each colony is represented by multiple females that are only weakly differentiated, if at all, from the workers. Over 20 genera of polybiines are recognized. Social wasps have much less complex castes and communication systems than is the rule in the ants and termites, but their nests are typically as elaborate in structure. Like the bees, the vespid wasps possess among their species graded series of advance in social organization, from simple brood care without castes to well established eusociality and strongly differentiated queens.

Termites. Three features of termite biology stand out. First, these insects harbor symbiotic microorganisms in their guts to digest cellulose, and as a consequence have become dominant decomposers over the warmer parts of the earth. Second, they are essentially social cockroaches. The anatomical and fossil evidence suggests that termites originated from very primitive cockroaches (order Blattaria) or a common cockroach-termite ancestor sometime during the early Mesozoic. Finally, despite the fact that they differ so profoundly from the Hymenoptera in origin, anatomy, and form of metamorphosis, the termites have converged in remarkable degree to the ants in social organization. To wit, they possess complex caste systems with wingless workers. They rely primarily on chemical communication, employing recruitment pheromones, alarm pheromones, and colony-specific odors in a manner basically identical to that of ants. Trophallaxis, the exchange of liquid food, is prominent in the sharing of food and transmission of chemicals used for communication. The two groups, true ants and "white ants" (termites), are also deadly enemies to each other. They compete for nesting space, and many species of ants are more or less specialized for preying on termites. For their part, various termite phyletic lines have evolved an astonishing array of combative mandibles and chemical discharges that are effective in defending the colonies against ants. A substantial part of the biology of both groups can be interpreted in terms of this global hundred-million-year war.

The 2200 species of termites, making up the order Isoptera, are roughly divided into two major divisions. The "lower termites," which are generally more primitive in anatomy and caste structure, comprise the families Mastotermitidae (including the single Australian *Mastotermes*, thought to be primitive), Hodotermitidae (including *Zootermopsis*, also primitive and a favorite laboratory subject), Kalotermitidae, and Rhinotermitidae. These termites, which are concentrated in the north temperate zone, digest cellulose with the aid of flagellate protozoans. Most are specialists on logs and other large pieces of dead wood. The "higher termites" consist of one huge family, the Termitidae (along with a small, obscure South American family, the Serritermitidae), which are primarily tropical in distribution. Termitids have replaced the flagellates with symbiotic, cellulose-digesting bacteria. Extremely abundant in both moist forested and xeric environments, they are among the chief decomposers and soil movers of the environment. The colonies of some species, especially the nasute termites in the subfamily Nasutitermitinae and *Macrotermes* and other mound-building termites in the subfamily Macrotermitinae, are among the most populous found in the social insects, containing into the millions of workers. Macrotermitines also raise fungi to assist in the digestion of cellulose and to supplement their diet.

In the broadest sense, the fundamental caste division in the social insects is between the reproductives, or queens and males, on one side and the nonreproductives, or workers, on the other. In the social Hymenoptera, however, the males are exclusively reproductive and transient. They contribute virtually no labor and typically remain in the home nest only to the time of their mating flight, after which they die without returning home. Termite males, in contrast, are full members of the colony. The reproductive males, sometimes called kings, remain close to the queens and inseminate them periodically. In addition, the worker caste consists of both males and females. In some species the two sexes become different worker subcastes.

Well differentiated worker subcastes occur only in the ants and termites. The simplest differentiation is based on size and allometric growth, so that it is possible to distinguish large major workers from small minor workers. In most species the major workers are specialized for defense, in which case they are called soldiers. Such is exclusively the case in termites and in most species of ants that possess subcastes. The majors of some ant species, however, function primarily or exclusively as millers of seeds or living "honey casks" for the storage of liquid food. The minor workers are generally much less specialized in anatomy and behavior, and they take responsibility for brood care, nest construction, foraging, and other quotidian tasks of the colony.

With the exception of termites of certain species whose castes are fixed according to sex, the castes of individual colony members are determined by environmental rather than genetic factors. Each species has its own particular combination of factors, but in general three factors are paramount. In wasps and primitively social bees, dominant females possess the best developed ovaries and serve as the queens. In other social insects, including the lower termites, caste pheromones play the key role. Queens produce substances that inhibit the development of immature females into new queens, or else they induce the attending workers to prevent the development by the control of larval feeding or some other action. The third caste-controlling factor is nutrition: queens and major workers receive larger quantities of food or special stimulatory materials in their diet during development. The critical stage at which caste determination occurs can be anywhere from the egg to the adult – again according to species.

Division of labor is generated not only by physical castes but also by programmed changes in the behavior of workers as they age. This "age polyethism" almost always follows the same general pattern: care of the queen and brood at first, followed by nest construction and patrolling, and finally nest guarding and foraging. In topographic terms, the worker starts deep within the nest near the queen and immature forms and moves outward as it grows older. Workers are nevertheless very flexible in their individual schedules. They are able to skip stages or even revert to earlier roles if the needs of the colony require it. For example, a young nurse worker can begin foraging very early if the colony is hungry, and a forager can return to brood care if nurses are in short supply.

Communication in the social insects is more than 90% chemical. That is, for the vast majority and perhaps all of the species, at least 90% of the kinds of communication, such as alarm, assembly recruitment, and caste identification, are mediated principally by pheromones. Similarly, at least the same proportion and perhaps many more of the individual signals transmitted by colony members are pheromonal in nature.

The most complex social organizations are possessed by species that attain large colony size, which favors an intricate division of labor and a rich repertory of chemical communication. They arise by sociogenesis, the process by which colony members undergo changes in caste, behavior, and physical location incident to colonial develop-

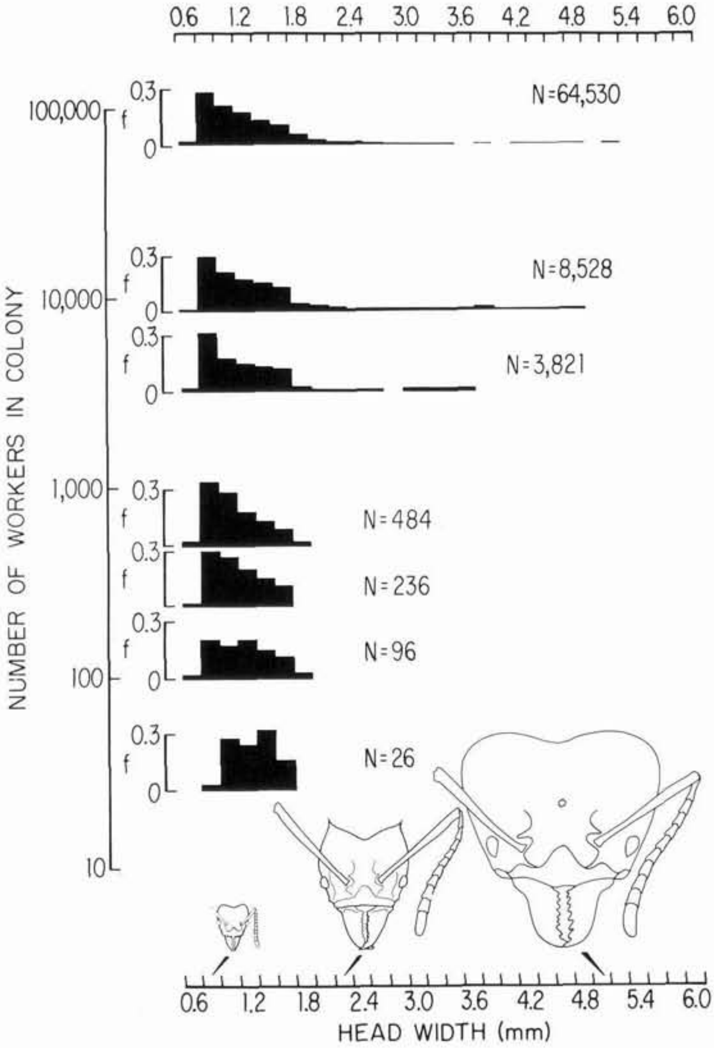

Fig. 5. The ontogeny of the caste system of the leafcutter ant *Atta cephalotes*, illustrated by seven representative colonies collected in the field or reared in the laboratory. The worker caste is differentiated into subcastes by continuous size variation associated with disproportionate growth in various body parts. The number of workers in each colony (*n*) is based on complete censuses; *f* is the frequency of individuals according to size class. The heads of the three sizes of workers are shown in order to illustrate the disproportionate growth of the *Atta* body. (From Wilson, 1985b.)

ment. As the colony grows, its workers maintain a changing age-size frequency distribution of the worker population that enhances survival and reproduction of the colony as a whole, typically at the expense of the individual. This "adaptive demography," which will be treated in more detail in Chapter V, varies in a predictable manner according to the species and size of the colony. An example from the leafcutting ants is shown in Figure 5. The species depicted, *Atta cephalotes*, has one of the most advanced physical caste systems found in ants. The largest workers are soldiers, devoted almost exclusively to the defense of the colony. The middle-sized workers are principally responsible for finding and harvesting fresh leaves and other vegetation on which the symbiotic fungus can be grown. Successively smaller workers, the minor class, process the vegetation, cultivate the fungus, and care for the queen and brood.

This brief review of the social insects focuses on eusociality, which is the highest evolutionary grade and is defined by the combination of three traits: care of young, overlap of generations, and division of the colony members into a reproductive caste (queens, males) and nonreproductive caste (workers). Eusociality occurs in the ants, bees, and wasps, which belong to the order Hymenoptera, and in the termites, which constitute the order Isoptera. These two orders are notable for the degree to which they have converged in the basic features of their caste and communication systems.

III The Meaning of Success and Dominance

"Success" and "dominance," laden with the history of Western culture, are risky words to use in biology. But they are nonetheless used all the time and sometimes interchangeably. We intuitively feel them to be necessary words in the biological vocabulary. Indeed, some kinds of organisms *are* successful and dominant. There is real biology in the distinction, and neologisms that we might invent would not be welcomed. So it is important for more than lexicographic reasons to try to render more precise the usage of success and dominance.

Upon reflection success and dominance can be seen to apply to radically different properties of organisms. If we stay within the framework of biology, success is most effectively employed as an evolutionary term, and dominance as an ecological term. Success is best measured by the Darwinian criterion of the longevity of clades. A clade is a species and all of its descendents, which collectively may be recognized as a genus, family, or even higher ranked taxon, or simply as a species group within a previously existing genus. The longevity of a clade is the interval from the time the ancestral species splits away from its sister species to the time the last of its descendents become extinct. Success is Darwinian in the sense that it measures fitness, and the fitness of a species or clade is equated with its survival through time. Dominance, in contrast, is best measured at two levels: at any given time, by the relative abundance of the clade in comparison with related clades, and over its entire history, by the ecological and evolutionary impact it has on the coexisting fauna and flora.

Other properties of clades often raised in connection with success and dominance are the numbers of species in the clade (speciosity), the breadth of adaptive radiation among the species, the extent of geographical range, and innovation, or the penetration of a new adaptive zone. An examination of each of these traits shows them to be uncoupled from success and dominance. They are loosely correlated with success and dominance yet independently evolving in particular cases. A tardigrade genus, for example, can be worldwide and ancient yet monotypic and rare; a species swarm of cichlid fishes can be middle-aged and extremely diverse, yet limited to a single African lake; a terrestrial and hence ecologically unique species of damselfly can be very young and limited to several localities in Hawaii; and so on through all of the permutations of the population-level traits.

In particular, success (longevity) and dominance (abundance and impact) are correlated with each other yet qualitatively different phenomena. A clade can enjoy enormous success by virtue of chronological persistence, but also be so rare as to have negligible impact on the ecosystem in which it lives. At the opposite extreme, a clade can be so abundant and diverse for a while as to exert a profound and lasting impact on the rest of life, yet be extremely short-lived. One need only look inward: if humanity were to extinguish itself right now, future sentient beings would classify it as ecologically dominant, its clade having stamped a permanent imprint on the remainder of the world biota, but only two million years in duration and hence relatively unsuccessful in a strict Darwinian sense. Dominance and success arise fortuitously from the acquisition by individual species of certain character states in response to local environmental conditions.

A long-lived clade can remain either ecologically insignificant or dominant continuously throughout most of its existence, or it can alternate periods of dominance with periods of ecological insignificance. In other words, success and dominance are not just very different phenomena. They can be fully uncoupled for separate analysis.

The uncoupling of success and dominance is strikingly illustrated by two of the oldest known fully terrestrial arthropods. Bristletails (order Thysanura, suborder Archaeognatha) and oribatid mites (order Acariformes, suborder Oribatida) have persisted on the land since Devonian times, some 375 million years before the present, and as such they must rank as among the evolutionarily most successful of all organisms. More precisely, since all living species date from the origin of life, it is the constellation of traits by which archeognaths and oribatids are defined that can be said to be successful. Organisms with the diagnostic qualities of these modern groups have persisted since Devonian times. In terms of dominance, however, the two groups (i.e., living species both with the diagnostic traits and descended from the Devonian ancestors) are totally different. Today archeognaths are relatively scarce and represented by only a single taxonomic family worldwide, the Machilidae. Oribatid mites are among the three most abundant groups of soil and litter animals in the 1 to 10 millimeter range worldwide (the other two are collembolans and ants). Composed of 145 or more taxonomic families, they are among the principal consumers of fungi and decomposing vegetable matter. If bristletails were to disappear, the effect on the terrestrial environment would probably be negligible. If oribatids were to disappear the effects would be profound and possibly catastrophic.

To summarize to this point, let me suggest the following brief definitions:

Success. Longevity of the entire clade through geological time. It arises fortuitously from the evolution of particular character states in individual species in response to local environmental conditions, and is not a "goal" of natural selection.

Dominance. Relative abundance, especially as it affects the appropriation of biomass and energy and impacts the life and evolution of the remainder of the biota. Dominance, like success, is an accidental result of natural selection in individual species and not the result of a particular drive or goal in evolution.

Speciosity. The number of species, which in turn can be usefully separated into the geographically expanding components of diversity (Magurran, 1988): alpha (the number of species occurring together within a particular habitat), beta (the rate of turnover in species along a transect in a heterogeneous habitat or in passing from one habitat to another), and gamma (the number added when all the occupied localities are sampled). The greater the alpha and beta diversity, the greater the adaptive radiation, as noted below.

Geographic range. The entire area occupied by a clade at a particular time.

Adaptive radiation. The spectrum of niches occupied by the various species of a clade, with an appropriate distinction being made between sets of species that live in the same localities (sympatric; hence alpha and beta diversity) and those that live in different localities (allopatric).

Innovation. The acquisition of a character trait or set of traits that allows the clade to penetrate a major new adaptive zone. The innovation may be new merely with reference to the larger group of species to which the clade belongs, such as the praying-mantis-like action used by caterpillars of some Hawaiian geometrid moths (*Eupithecia*) to capture prey, or it can be new for all life, such as the use of flagellate protozoans by primitive cockroaches and their relatives the cryptocercid cockroaches to digest wood. Extremely few innovations are genuinely unique breakthroughs. Innovations often but not always lead to an adaptive radiation, and this is especially likely to be the case when there are no previous competitors in the vicinity. In other words, having broken into an important new and empty adaptive zone, the clade often proceeds to fill it by speciating into its many available spaces.

Finally, the concept of *progress* often enters into discussions of evolution and biodiversity, spawning a good deal of ambiguity and dispute (see the excellent analyses by Francisco Ayala, Michael Ruse, and others in Nitecki, 1988). The difficulty with the word is that in the strictest sense it implies a goal, and evolution has no goal. Goals are not inherent in macromolecules, the foundation of hereditary variation on which natural selection impersonally acts. Instead, goals are organismic and represent a specialized form of behavior. Once assembled by natural selection, human beings and other sentient organisms formulate goals as part of their life history strategies. Goals are the ex post facto responses of organisms to the exigencies imposed by the goalless environment. Neither the environment nor the evolutionary process look to the future.

And yet . . . there is another meaning of progress that does have considerable relevancy to evolution. Biological diversity is structured by many transformational series that pass from simple to complex, wherein the simple states appeared first and the more complex later. Many reversals may have occurred along the way, but the overall average has moved from simpler to more complex rather than in the reverse direction. Thus, as Vermeij (1987) and Bonner (1988) have argued, animals as a whole moved upward in size, feeding and defensive techniques, brain and behavioral complexity, social complexity, and precision of environmental control – in each case farther from the nonliving state than from the simpler antecedents. More precisely, the overall average and the upper extremes shifted higher. Progress, in short, is a property of the evolution of life as a whole by almost any conceivable intuitive standard. It seems nonsensical to declare it to be merely an arbitrarily measured concept. To borrow a phrase from C. S. Peirce, let us not pretend to deny in our philosophy what we know in our hearts to be true. An undeniable major event of progressive evolution was the origin of the social insects from nonsocial ancestors.

Are Social Insects Evolutionarily Successful?

On the basis of phyletic longevity alone, in other words on the basis of the Darwinian criterion, social insects can be judged as at least moderately successful. Since we are confined to the evaluation of living groups without knowledge of their future geologic life span, the most that can be said in this case is that they are *at least* moderately successful. Clades (species from their points of origin in the speciation process plus all the species to which they give rise) last on an average of 1 to 10 million years according to taxon. Such is the case at least for the best preserved invertebrate and fish clades of the Paleozoic and Mesozoic Eras and the flowering plants of the Cenozoic Era (Raup, 1984). These estimates are of true longevity, that is, the duration of a discrete set of populations from the time they attain reproductive isolation to the time of their complete demise. But there is another way a taxon can go "extinct": by giving rise to a new constellation of character states so different that the phyletic line is classified as a new taxon. This is chronotaxon extinction. The way we treat the transition is subjective, since both chronospecies (succession of species in a single line partitioned by time), chronofamilies, and so forth are arbitrarily demarcated. The distinctions made, however, are not trivial. At some point in the Mesozoic Era a clade of aculeate wasps evolved the metapleural gland, worker caste, and other traits by which we define ants. In the first sense of absolute clade survivorship those aculeate wasps are still with us, but in the second, chronotaxon sense they are not, because some of the major character states that defined them gave way to the major character states that define ants.

The question of interest concerning evolutionary success can now be put as follows: how long did the *traits* characterizing particular taxa (such as those diagnosing pre-ant wasps as opposed to ants) persist before either the taxa were extinguished or the traits gave way to such distinctive new diagnostic traits that the taxonomist is compelled to give the clade a new name?

There follows a summary of how long the several groups of social insects have persisted to date, according to current fossil data.

Ants. The earliest primitive known ants, the archaic subfamily Sphecomyrminae, originated at least as far back as the earliest part of the late Cretaceous, about 100 million years ago. They were widespread in Laurasia, the northern supercontinent embracing modern

North America and Eurasia, but relatively rare in all of the fossil deposits where they have been encountered (Wilson, 1987b; see Figure 6). A fossil ant, probably belonging to the extant subfamily Myrmeciinae has recently been discovered in mid-Cretaceous deposits in Brazil, revealing the early presence of at least one phyletic line in Gondwana contemporaneous with Sphecomyrminae (Brandão et al., 1989). By early Eocene times, about 60 million years ago, the primitive Mesozoic ants had given rise to many of the subfamilies living today. By the end of the Eocene at the latest, ants were among the most abundant insects, and they remain so today.

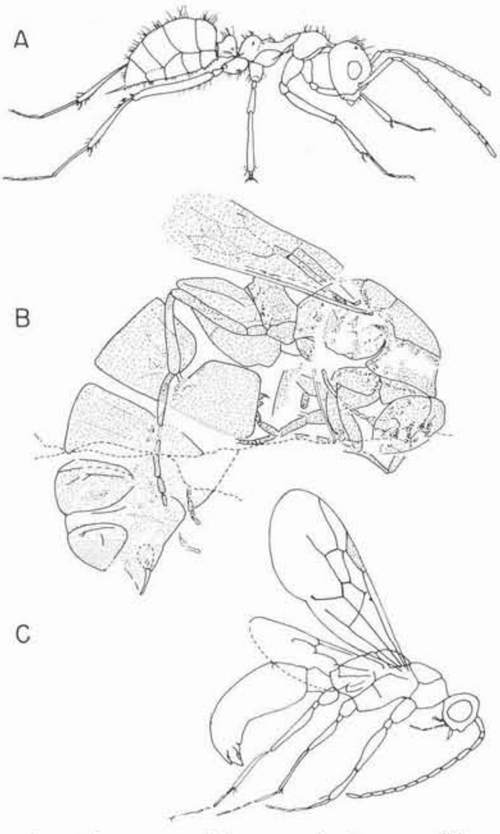

Fig. 6. Ants are a moderately successful group in terms of longevity. The earliest known ants comprise the family Sphecomyrminae and date back to the lower part of the Upper Cretaceous 80 to 100 million years before the present. Fossils found in North America and the Soviet Union are considered by the author to represent respectively (A to C) the worker, queen, and male. (From Wilson, 1987b; B and C from Dlussky, 1983.)

Wasps. Solitary vespid wasps date back to the late Cretaceous, but the earliest social vespoids, belonging to the family Vespidae, are encountered for the first time in the upper Oligocene. Larger wasps are generally scarce in the fossil record, and little can be said of their history (Burnham, 1978).

Bees. The earliest known fossil bee presumed to be eusocial is from Late Cretaceous amber, about 80 million years in age. It is a stingless bee of the modern subfamily Meliponinae (family Apidae) and – astonishingly – belongs to the modern genus *Trigona* (Michener and Grimaldi, 1988). By Late Oligocene times, members of the family Apidae, including the modern honeybee genus *Apis*, were abundant and diversified.

Termites. The termites have a fossil record roughly parallel to that of the ants. The earliest known fossil, a primitive species placed in the living family Hodotermitidae but constituting the extinct genus *Valditermes*, is from Lower Cretaceous deposits about 120 million years old (Jarzembowski, 1981). Thus the termites are likely to have originated sometime during early Cretaceous times or even further back, during the Jurassic. And like the ants, modern families were present and diverse by Eocene times, at least in the northern hemisphere.

We can thus assert with some confidence that on the basis of phyletic longevity social insects are relatively successful. Individual families such as the Formicidae (ants), Hodotermitidae (wet-wood termites), and Apidae (social bees) – by which I mean in each case the constellation of family level character states within monophyletic clades – have persisted for at least 100 million years. Each of these families (sets of synapomorphic traits) is older than 19 of the 20 *orders* of mammals; only the Marsupalia are older. And among the marsupial families originating during the Cretaceous or before, only one, the Didelphidae or opossums, have survived to the present time and hence is as old as the social insects. Even taking into account differences in the subjective evaluation of family-level and order-level character states by specialists, the disparity in turnover rate between social insects and mammals seems real.

But more to the point: how do social insects compare with solitary insects, and especially sister taxa among the solitary insects? The most meaningful comparison can be made within the Hymenoptera, which includes abundant social and solitary taxa. We find that the social

Hymenoptera, namely the ants, eusocial wasps and eusocial bees, are not exceptionally long-lived in this context. No fewer than 26 of the 37 hymenopteran families known from Cretaceous fossils, including the Formicidae (ants) and Apidae (bees), are still represented by living species. One group, the solitary sawflies of the family Xyelidae, have survived since the Triassic Period. Turning to the next lower level, only 1 of the approximately 10 ant genera thus far recorded from Cretaceous and Eocene deposits is extant. However, no fewer than 24 genera, or 56% of the 43 represented in the early Oligocene Baltic amber ant fossils (the most complete sample of fossil insects ever studied), still survive. A modern facies is even more evident in the Dominican amber, which is apparently early Miocene in age. Here no fewer than 34 genera, or 92% of the total 37, still survive. Moreover, the majority of species belong to living species groups, and a few are difficult to separate at the species level (Wilson, 1985c). Yet the solitary Hymenoptera may well be comparably long-lived and conservative at the generic and species-group level. Modern taxonomic studies of most solitary hymenopteran families in the Oligocene and Miocene deposits are still too incomplete to allow quantitative comparisons with the ants. Enough data are available on the Bethylidae and Braconidae, nonetheless, to indicate percentages of genus-level survival comparable to that of the ants (Larsson, 1978).

In summary, the Hymenoptera are overall a tenacious, slowly evolving group. Time and the fossil record are not adequate to evaluate definitively the macroevolutionary effects of eusociality within the order. It is nevertheless suggestive that no phyletic group of familial or greater rank, within or around the termites and the Hymenoptera, or for that matter involving any arthropod order, is known to have attained eusociality and then failed. No group comparable to the termites, ants, and apid bees in social order has gone extinct or even retreated to rare, relict status in isolated parts of the world. Furthermore, both the eusocial hymenopteran families first recorded from the Cretaceous Period, the Apidae and Formicidae, thrive today, whereas 11 of the 23 or one half of the hymenopteran families first recorded from the Cretaceous Period are extinct. The difference is not statistically significant, but it is consistent with the view that eusociality conveys evolutionary long life in the insects.

The Ecological Dominance of Social Insects

Whatever we may conclude about the geological longevity of the social insects, there is no question about their numerical superiority and the impact they have had upon the land environment and the evolution of other organisms. Eusocial insects, in other words, are dominant organisms. The point can be made vividly with the termites. A century ago Henry Drummond (1889) noted that Herodotus, who called Egypt the gift of the Nile, should have given partial credit to the "labours of the humble termites in the forest slopes about Victoria Nyanza." According to Wood and Sands (1978), the weight of soil in the mounds of African savanna termite species that build small nests vary according to abundance of the species from 10,000 kg to 45,000 kg per hectare. The soil composing large mounds of *Macrotermes* range between 100,000 and 2.4 million kg per hectare, in the latter case an equivalent of a uniform layer of soil 20 cm deep. The *Macrotermes* mounds directly blanket between 1 and 30% of the land surface. By metabolizing cellulose and some lignin as their main food source and depositing mostly lignin as the residue, termites alter the fine-grain physical structure and chemical composition of the soil down to at least several meters below the surface.

In most parts of the world the ants have a comparable or even greater impact on soil structure. In deciduous forest of Massachusetts (USA), where termites are much less common, ants turn approximately as much soil as earthworms (Lyford, 1963). In tropical forests they exceed earthworms and rival termites as soil builders. Because ants transport plant and animal remains into their nest chambers, mixing these materials with excavated earth, the nest environs are typically charged with high levels of carbon, nitrogen, and phosphorus. The upper soil layer is broken into a mosaic of nutrient concentrations, which in turn generates patchiness in the distribution of plant species. The great earthen nests of the leafcutter ants have a particular importance in the forests and savannas of the New World tropics, where native mammalian herbivores are relatively scarce. Each mound, which covers up to 600 square meters, contains as much as 40,000 kg of excavated earth and overlays a vast network of galleries and chambers that penetrate six meters or more below the surface. Each colony harvests and processes hundreds of kilograms of vegetation yearly, equaling the consumption of a cow. In rain forests, where less than

0.1% of nutrients normally penetrate deeper than 5 cm beneath soil surface by ordinary filtration, the *Atta* are the principal agents of deep fertilization. Haines (1978) found that the flow of 13 elements through the underground refuse dumps of *A. colombica* was 16 to 98 times that in undisturbed leaf litter beneath equivalent sample areas. The enrichment of materials resulted in a fourfold concentration of fine tree roots in the dump.

Termites are the master brokers of the decomposition of dead plant material, which is largely a mixture of cellulose and lignin. They feed on the wood directly but do not digest it. Instead they bring the finely comminuted wood fragments into contact with protozoans and bacteria in their guts. These microorganisms catabolize 70% or more of the cellulose and up to half the lignin. The macrotermitine fungus-growers also cultivate a symbiotic fungus, *Termitomyces*, which breaks down cellulose and lignin and concentrates the products into protein-rich, thin-walled conidiophores easily digested by the termites.

Termites serve as decomposition brokers in other ways. Wood-dwelling species, as opposed to those that nest in soil and forage abroad for vegetation, carry soil into burrows they excavate through the wood. As a consequence they inadvertently transport bacteria and fungi specialized for wood decomposition and hasten the overall process of decay (Abe, 1982). Other phyletic lines have evolved elaborate foraging techniques that allow them to harvest cellulose and lignin at far distances from the ordinary sources of dead wood (Brian, 1983). Some members of the Hodotermitidae and Termitidae harvest grass. Other termites consume soil to acquire the humus within it. Among the extreme specialists in other directions are termitids of the Asiatic genus *Hospitalitermes* that collect lichens from the forest canopy, and inquilines such as species of *Adaiphrotermes* that feed on the nest carton of other termites.

Having preempted so many of the energy-productive niches available to terrestrial animals, termites and ants have attained extraordinary abundances. Among the highest estimates of density compiled by Baroni Urbani et al. (1978) are the following: 130,000 termites and 16.6 million ants per hectare in tropical forest litter alone on Barro Colorado Island, Panama; 47 million ants per hectare belonging to three arboreal ant species alone in East Africa; from 1.8 million to 180 million termites per hectare at several localities in Trinidad. These extreme figures and the variability they exhibit may be less surprising when it is considered that single colonies of macrotermitine termites and army ants often contain over a million individuals. Those of driver ants (*Dorylus*) in Africa occasionally attain populations in excess of 20 million. Each such colony is concentrated in an area of only a fraction of a hectare.

The energy consumption of social insect populations is correspondingly intense. Termites in the southern Guinea savanna of Nigeria, weighing up to 10.6 g/m^2, have a respiration rate of 442 kJ per m^2 per year. These figures are parallel to the biomass and metabolism of ungulates in a savanna game reserve in Tanzania, namely 17.5 g/m^2 and 649 kJ per m^2 per year (Wood and Sands, 1978).

Ants impact energy flow heavily at several trophic levels (Hölldobler and Wilson, 1990). In most terrestrial environments they are among the leading predators of other invertebrates. They scavenge a substantial majority of dead arthropod and small vertebrate remains. *Pogonomyrmex* and other harvester ants rank among the principal granivores, competing effectively with mammals for seeds in deserts of the southwestern United States. Around the world they serve as important agents of seed dispersal. Other ants live in varying degrees of symbiosis with plant species to the same end, attracted by the food bodies or elaiosomes of the seeds specialized to serve just this end.

Our appreciation of the role of social insects in the terrestrial environment has been improved in recent years by increasing knowledge of the multifarious devices by which great numbers of species exploit the social insects for food, shelter, and protection from enemies, as well as defend against their depredations. Much of this coevolution is epitomized in the internecine evolutionary race between ants and termites. These two "superpowers" of the insect world have undoubtedly been locked in a struggle for the greater part of the 100 million years of their coexistence, with ants as the active aggressors and termites the prey and resisters. They also contend for the same nest sites.

A convincing field demonstration to illustrate the continuous hostile tension between ants and termites can be had by breaking open a log that contains both. Before the intrusion the termite colony will be found to have sealed its portion of the log off with walls made of lignin-impregnated excrement. No exits open to the outside. The termite workers cautiously extend their domain by tunneling a millimeter at a time, sealing the newly formed walls as they go. If by accident they break through to an ant gallery, the small perforation is quickly covered. But when their nest is ruptured by a break in the log, the termites are exposed for a dangerously long time. The ants, provided they are one of the great majority of species that accept termites as prey, rush in and engage the termites, killing and carrying off as many as possible. The termites fight back as they retreat into the intact portions of their nest. Workers, some bearing eggs and first-instar nymphs, pull back quickly. Soldiers move out toward the break, attack the ants for a time, and then gradually retreat. Within an hour or two the survivors are relatively secure, and the workers are busy sealing off the last of the openings to the outside.

In the tropics and subtropics of every continent are found ant species that feed exclusively on termites. *Paltothyreus tarsatus*, illustrated in Figure 7, is one of a guild of large ponerine ants that organize raids on termite nests, conducted with such élan and concentrated force as simply to overwhelm the defenses of their prey. A scout leads a party of her giant nestmates to the termite nest by laying chemical trails with secretions from the intersegmental glands of the abdomen. The group digs into the nest wall, and each raider proceeds to stack as many termites in its mandibles as it can carry before returning home. An entirely different strategy is employed by the Malaysian myrmicine ant *Eurhopalothrix heliscata*. The workers hunt singly through rotting wood housing termite colonies. They use their peculiar wedge-shaped heads, heavily sclerotized bodies, and short legs to press into tight spaces. Upon breaching a nest gallery they seize the appendages of the termites with their sharp-toothed mandibles, clasping these body parts of the prey even more tightly with the aid of hardened labra that project like forks from between the bases of the mandibles (Wilson and Brown, 1984).

Termites have responded to the intense pressures from ants and other predators with formidable armaments and tactics of their own. In most species the soldiers possess large sclerotized heads that work like helmets, together with sharp, elongate mandibles used like scissors to slice and chop enemies. The mandibles of *Termes* and several other higher termite genera are shaped like scimitars, with points as sharp as needles. The soldiers of the kalotermitid genus *Cryptotermes* have cylindrical heads that are used to plug the nest entrances. The "snapping" soldiers of *Capritermes, Neocapritermes*, and *Pericapritermes*

Fig. 7. Some species of ants are specialized predators of termites. Here a large raider of the genus *Paltothyreus* emerges from a termite nest gallery with several termites stacked in its mandibles. (From Hölldobler and Wilson, 1990.)

possess mandibles that are twisted, asymmetrical, and arranged so that their flat inner surfaces press against each other as the adductor muscles contract. When pulled strongly enough, the mandibles slip past each other convulsively, in the same way we snap our fingers by pulling the middle finger with just enough pressure to make it slide off the thumb with sudden force. When the mandibles strike an ant or other insect in this manner, they deliver a stunning blow.

Even more sophisticated chemical techniques are employed by other termites. Some disgorge poisonous droplets of saliva or frontal gland secretions and daub them onto the bodies of their enemies. *Globitermes sulfureus* soldiers occasionally burst their own bodies by violent abdominal contractions, spreading toxic secretions in all directions. Soldiers of the nasutitermitines possess the equivalent of a "gun," a conical organ projecting from the front of the head like a long nose, from which the termites fire frontal gland secretions over

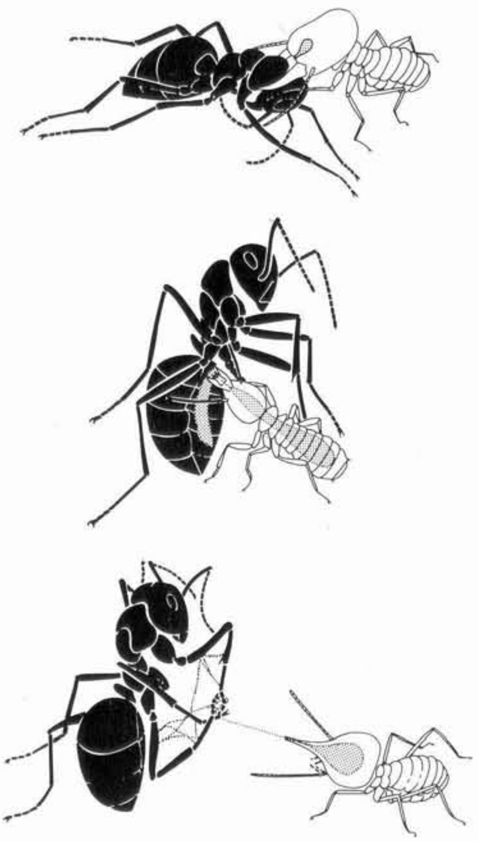

Fig. 8. Defenses of termites against ants, illustrating the highly varied techniques employed by different species. Top: a *Cubitermes* soldier seizes an ant behind its head while emitting noxious secretions from the frontal gland (indicated in outline by stippling). Center: a *Schedorhinotermes* soldier daubs frontal gland secretion on an ant with the aid of its labral brush. Bottom: a nasute soldier immobilizes an ant with a jet of sticky fluid fused from its elongated nasus. (From Hölldobler and Wilson, 1990; adapted from Grassé, 1986.)

distances many times their own body length. Even though they are blind, their aim is quite accurate (see Figure 8).

How Closely are Success and Dominance Linked?

There are good reasons to believe that dominance is one of the principal factors promoting longevity. However, such enhancement is likely to occur only if dominance by a given clade generates certain populational traits that directly lessen the chances of extinction (Wilson, 1987c). These traits, which are well developed in the ants and termites, are the following:

(1) Number of species generated through time.
A dominant clade that speciates and penetrates many adaptive zones is on average better off than one that continues as a single species, because as an unintended effect it has "balanced its investments" and *ceteris paribus* will probably persist longer into the future. If the cluster includes both generalists and specialists, it is all the more likely to ride out perturbations in the physical environment as well as invasions by new enemies. And if some of the species come to occupy multiple major adaptive zones, survival of the clade is enhanced still further (Boucot, 1978). The ants (8800 known species) and termites (2200 species), with their spectacular adaptive radiations, are notable examples of all these qualities. On the other hand, if the rate of species turnover is high within a clade (speciation more or less balanced by extinction) total extinction of the clade is more likely in a given interval of time (Stanley, 1979). Compared with mammals at least, social insects have a low species turnover rate.

(2) One or more species hold exclusive or nearly exclusive occupancy of a major adaptive zone.
If an innovation of this kind has occurred, the phyletic assemblage as a whole is less likely to suffer extinction through competitive exclusion. Partly as a consequence of their colonial existence, ants and termites have accomplished the feat several times, creating new adaptive types. The fungus-growing ants (tribe Attini) and macrotermitine termites, for example, are among the few animals of any kind that utilize symbiotic fungi or yeasts as food, sharing the trait with only a few taxa in the beetle families Anobiidae, Brenthidae, Curculionidae, Lymexylidae, and Scolytidae. One apparently monophyletic group within the Attini, the leafcutter species of *Acromyrmex* and *Atta*, are unique within the animal kingdom in their ability to convert large quantities of fresh vegetation into a fungus substrate (Weber, 1972). Many ant species keep aphids, scale insects, pseudococcids, and other homopterans as "cattle" in their nests, moving them from one site to another in response to danger or food shortage. The Malaysian *Doli-*

choderus (= Diabolus) cuspidatus is a true herder, since its colonies have no permanent nests but move in toto with their coccids from one tree to another at frequent intervals (Maschwitz and Hänel, 1985).

(3) The homeostatic maintenance of large populations.
Mathematical models confirm as robust the intuitive principle that the larger the population and the less the numerical fluctuations through time, the longer the waiting time to extinction (Frankel and Soulé, 1981; Pimm et al., 1988). Ant and termite species are celebrated for their high population densities, huge nuptial swarms, wide dispersal, and hence large effective breeding sizes. In addition, the population sizes may be generally more stable than those of most non social insect taxa, including solitary hymenopterans. The reason is that the basic breeding unit is the colony, or more precisely the single queen together with (in termites) the king, or at most the relatively few individuals composing these royal castes. As documented in the pioneering work by Pickles (1940) on British ants, a drastic reduction can occur in the overall number of workers in the population, thus lowering the average population of individuals per colony substantially, yet have little effect on the number of colonies or of functioning royal castes, in other words the effective breeding size. The colonies, in a phrase, absorb the blow by sacrificing their nonreproductive members. Although this homeostatic device is clearly an important potential factor in evolution, field studies have been too few to determine to what extent it occurs throughout the social insects.

(4) A large geographic range.
The wider the geographic range of the entire clade, the less likely the clade is to fall to extinction prior to microevolutionary adjustments and the renewal of population growth in one or more species. Similarly, the wider the ranges of each of the constituent species, the longer they are likely to persist. According to Jablonski (1987), to take a concrete example, a strong correlation existed between the size of the range of Upper Cretaceous mollusks and their longevity. The ants are one of the most widespread of all groups of organisms of comparable taxonomic rank. They range from above the Arctic circle to the southernmost reaches of Tasmania, Tierra del Fuego, and southern Africa. The only places free of native species are Antarctica, Iceland, Greenland, and a few of the most remote oceanic islands such as Hawaii and

St. Helena. Four genera (*Camponotus, Crematogaster, Hypoponera,* and *Pheidole*) extend separately over most of this range. The termites are only a short distance behind, falling away more rapidly in the cold temperate zones.

(5) Competitive preemption.
Dominant groups that exclude other groups with similar adaptations will inhibit the evolution of other forms like themselves. It seems plausible that the saturation of the terrestrial environment by the ant family Formicidae has made the subsequent independent origin of competing ant-like forms highly unlikely.

In conclusion, all that we know of the interrelation of species diversity, population size, density-dependent population regulation, and geographic spread indicate that ecologically dominant clades should persist longer than ecologically minor ones. There is, however, a countervailing trend: dominant clades that are speciose are more likely to generate new higher level taxa capable of replacing them. More precisely, suites of diagnostic traits belonging to dominant clades that adaptively radiate are more likely to evolve new suites of traits capable of driving the old traits out, thus producing chronotaxon extinction. So the problem of the relation between dominance and success is not simple. It requires a great deal more theoretical and empirical study than has been devoted to it so far, before a satisfying total picture can be put together.

Within the framework of biology, evolutionary success is best defined as the longevity of a clade, that is, the duration through geological time of a species and all its descendents. More precisely, the longevity of interest is the set of character states by which the clade is diagnosed, such as the metapleural gland and wingless worker caste in the case of ants. The end of the clade can then come from either absolute extinction, the death of all the populations, or from chronotaxon replacement, in which populations of the clade evolve a new set of diagnostic character states of sufficient distinction to rank the populations as a different genus or taxon of still higher rank.

Dominance, in contrast, is best measured at one or both of two levels: at any given time, by the relative abundance of the clade in *comparison with related clades, and over its entire history, by the ecological and evolutionary impact it has on the remainder of the fauna and flora. Dominance promotes success (longevity) to the extent that it enhances adaptive radiation, breadth of geographic range, and large, regulated population size. Dominance arises in individual species from the evolution by natural selection of particular sets of character states in response to local conditions, and it is sustained by the longevity that it confers on the acquirer species and its descendents.*

Other properties of clades, including raw speciosity, extent of adaptive radiation, breadth of geographical range, and the achievement of major evolutionary innovations, are loosely correlated with success and dominance but independent nonetheless.

The eusocial insects (i.e., the suites of traits defining each of the clades of eusocial insects in turn), have enjoyed at least moderate evolutionary success to date. Although not enough time has passed – about 100 to 150 million years – to say that major groups of social hymenopterans (ants, bees, wasps) outlast equivalently ranked taxa of nonsocial hymenopterans, the evidence is consistent with this trend. More importantly, no known major eusocial clade has ever gone extinct. In addition, eusocial insects are among the most dominant groups in the history of life. They compose a large part of the terrestrial biomass, channel much of its energy flow, and exercise a profound effect on ecosystems and the evolution of other terrestrial organisms.

IV Why are Social Insects Ecologically Dominant?

Eusocial insects are part of the evolutionary thrust that Geerat Vermeij (1987) has called escalation, a progressive elaboration of offensive and defensive devices in response to competition and predation. As Vermeij points out, colonial integration in particular steadily increased during Mesozoic and Cenozoic times. Contemporary marine colonial invertebrates, including bryozoans, corals, and sponges, prevail competitively over solitary invertebrates in stable hard-bottom communities below the tide line. Solitary animals predominate in the less stable and hence riskier intertidal zone. Numerous long-term studies, most featuring the experimental removal and addition of species, have documented the critical role that competitive replacement plays in creating this broad pattern on the marine floor (Schoener, 1983, 1986).

I will present documentation later, in Chapter 7, to show that competition has also been a powerful creative force in the evolution of the social insects. For the present let me give the reasons, as I have come to understand them from a lifetime of experience and from the writing of others, for the general competitive edge enjoyed by the social insects. It must be granted at once that such reasoning risks circularity. For if we know that the social insects are ecologically dominant and have a distinctive set of traits *X*, how do we know that *X* caused dominance, rather than the other way around? In other words, how do we know that dominance (due to some other unseen cause) did not promote the evolution of *X*? Or even that still other, unseen factors did not cause both? There are several reasons why the inferences I am about to propose support the conclusion that *X* led to dominance. First, the social insects are overwhelmingly dominant, among the most extreme in this trait in the history of animal life. Extreme effects imply extreme causes and vice versa, and so the cause-effect relation should be more obvious in this case than in most. And it is in fact. Second, due to the great diversity of solitary insects belonging to sister groups of the social insects, and the multiplicity of the origins of eusociality through the insects (at least 12 such origins produced the living eusocial stocks), it is possible to discern the causal factors of *X* with clearer definition than usual. Finally, a great deal is known from field and laboratory studies about the detailed actions of individual traits in *X* in creating a competitive edge over solitary insects.

The basis of eusocial insect dominance as I understand it can be epitomized with the following imaginary scenario. A hundred solitary, flightless wasps are pitted against an ant colony with the same number of workers. The two competing aggregations nest side by side. In a typical daily action, one of the wasps digs a nest, captures a prey, lays an egg on the prey, and closes the nest. If she fails at any one of these serial tasks, the entire operation fails. Since her genotype competes with those of other, independently working wasps, it will be less well represented in the future as a result of the failure. An ant nearby also commences to dig a burrow to be added to the colonial nest, where larvae will eventually be moved and fed. If the ant fails at any step of the sequence, a sister worker is likely to move in and complete the task. Other nestmates travel restlessly about the colony territory, addressing such contingencies as they arise. Sequences may be completed by an ant worker in the wasp manner, but they are generally much shorter in duration and transposable among many individuals.

In essence, the wasp is limited to what are called *series operations*. If we consider the entire wasp population as a single working unit, the ensemble can be said to be engaged in *parallel-series* operations, in which assemblies are more or less simultaneous and completely independent. Individual ants can also use parallel-series operations. Far more likely, however, they employ *series-parallel operations*, in which sisters switch back and forth across the assembly lines. The distinctions are illustrated in Figure 9. Under most conceivable circumstances, the ant colony is less likely to fail in any particular task than an aggregate of solitary wasps.

Consider next territorial disputes between the aggregation of solitary wasps and the colony of ants. The ants can throw workers into combat far more recklessly than can the wasps. If a wasp is killed or injured, the Darwinian game is over, just as if it could not complete the task of nest construction and provisioning. But this is not true of the ant, which is nonreproductive and will be quickly replaced by a closely

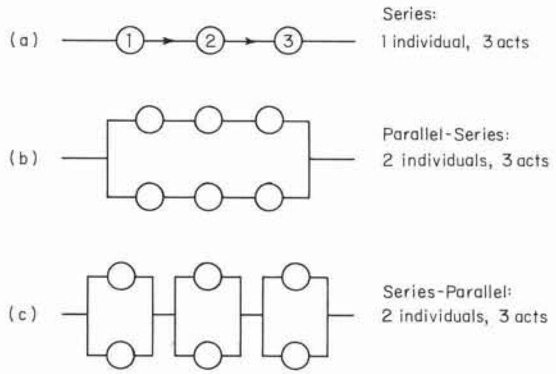

Fig. 9. The possible behavioral sequences in an aggregation of insects are illustrated in this diagram. The series-parallel operation, generally employed by social insects, is the most reliable. (Modified from Oster and Wilson, 1978.)

related sister back at the central nest. So long as the mother queen is protected, the loss of one or a few workers will have little effect on the representation of the colony members in the future gene pool. Suppose that the war of attrition continued until almost all of the wasps and ant workers are destroyed. So long as the queen survives, the ant colony will win. The queen and surviving workers will build up the worker population rapidly, restoring full representation of the original genotype. The wasps might also regain lost ground rapidly, but insofar as there was genetic variability among them subject to natural selection in combat, the population genotype will change, creating more timid wasps. In short, wasps are subject to *individual-level selection*. They tend to evolve in such a way as to avoid territorial combat, at least with ants and other eusocial insects. Ants, subject to *colony-level selection*, tend to evolve more expansive territorial defense. The result, I believe, is the denser, more aggressive populations of ants that exist in land environments around the world.

The greater defensive capability of an entire colony against solitary individuals means that prime nest sites and feeding areas can be passed from one generation to the next. The nests of mound-building termites and ants often last for decades, churning out new reproductives year after year. In the cases where new reproductives are retained within the nest, the colonies are potentially immortal.

Finally, because the ant colony builds larger nests than the solitary wasps and holds on to them for longer periods of time, it can introduce structures that regulate the microclimate. By using part of the worker force to patrol the nest perimeter, it can repair nest damage more quickly and respond more effectively to threats of invasion. The environment around the ants is held more closely to the ideal for growth and reproduction. The ant colony thus achieves a greater measure of homeostasis than does the wasp aggregation. It alone employs *social homeostasis*.

In summary, the following appear to be the key advantages of colonial life:

(1) Series-parallel operations, insuring fewer systems failures.
(2) Higher premiums paid to aggressive, dominant behavior.
(3) Superior resource inheritance.
(4) More efficient homeostasis.

I will now offer some examples to document these advantages, and then try to answer the obvious question that follows: if eusocial life is so superior in terms of genetic fitness to solitary life, why aren't all insects eusocial?

Series-parallel Operations

The significance of series-parallel operations can be more fully appreciated by considering how they contribute to the organization of the insect colony as a whole. The operations shape the colony into a special kind of hierarchy (Wilson and Hölldobler, 1988). A hierarchy, it will be recalled, is a system comprising interrelated subsystems, each of the latter being in turn hierarchical until the lowest level of subsystem is reached. The hierarchy can be defined in structure, function, or causal connection, or any combination of the three. It can be said to be decomposable, which means that the linkages within the components at a given level are stronger than the linkages between those same components. Thus an ant colony distributed over multiple nest sites can be decomposed into the occupants of the different nests, because members of each nest are more fully associated with each other than they are with members of other nests. Moving downward in the hierarchy, the members of each nest can be decomposed into various castes and, finally, each caste can be decomposed into individual ants.

The ant colony, while a hierarchy in the broad sense, is not at all like the conventional hierarchy of military or industrial command, where instructions emanate from the top and are elaborated and passed downward until they reach the final, functioning individual. Instead, the colony is a special assemblage that can be usefully called a heterarchy. This means that the properties of the higher levels affect the lower levels to some degree, but induced activity in the lower units feeds back to influence the higher levels. The heterarchy is also highly connected or "dense," meaning that each individual member is likely to communicate with any other. Groups of workers specialize as castes on particular tasks, and their activities are subordinated to the needs of the whole colony, but they do not act as part of a chain of command independent of other, parallel chains of command. They are open at all times to direct influence by most or all of the other colony members. They also switch specific jobs back and forth in the series-parallel pattern. If a nurse worker departs before completely feeding a larva, a second nurse worker soon moves in to complete the job. In so doing it may abandon another job, which is likely then to be taken over by yet another worker.

The insect colony is a genetically prescribed republic. The members of the community are in frequent communication, and they segregate according to caste and to the local conditions each one encounters around the nest. The heterarchy comprises a nested system of labor categories that progress (by definition) from narrowly defined to progressively more broadly defined. An example of this expansion is the following: major workers defending the nest entrance are distinguishable from major workers in the nest interior storing liquid food in their crops, then these two labor groups taken together compose a higher general category of major workers, and so on up through progressively inclusive categories to the entire colony population.

It follows that the highest level of the heterarchy is the complete membership, rather than any set of "bosses" who direct nestmates. The queen is not at the head of the heterarchy. So far as is known, she does not integrate any more information than do individual workers, nor does she direct specific actions unilaterally. The highest level of the dense heterarchy composing the colony is the colony itself.

Worker Sacrifice

The readiness of workers to sacrifice their personal safety on behalf of the colony is revealed strikingly in the phenomenon of castes. The more familiar trait of insect societies is the possession of physical castes. First and fundamentally, the eusocial insect colony is divided into reproductive members, the queens and males, and nonreproductive members, the workers. In the case of ants and termites, the workers may be divided into soldiers (often designated in ants by the neutral term major workers) and ordinary workers, or minor workers. These several physical castes, from queens to minor workers, are easily distinguished by size and other anatomical features.

In addition, the vast majority of social insects possess temporal castes, based on the different roles assumed by the same workers as they age. Each species has its own pattern of role progression as a function of aging, but in general – indeed, almost as an absolute rule across the social insects – workers begin as nurses and end as foragers. A typical example from the ants is illustrated in Figure 10. The myrmicine *Pheidole dentata* depicted there is one of the most abundant ants in forests of the southern United States. Its colonies nest in rotting logs and stumps and less commonly in the soil. Each colony has 5 adult castes: three temporal stages during the life of the minor workers, a large-headed major worker (which has only one temporal caste), and the queen (Wilson, 1976b). The male does not perform labor of any kind that qualifies it as a caste. The larva may convert protein into sugars for use by the workers, a function documented in several other myrmicine genera, but the possibility has not yet been investigated in *Pheidole*. As *P. dentata* minor workers age, their repertory passes through two stages of brood care and then increasingly to nest guarding and foraging outside the nest for food. The latter *Aussendienst*, as it is neatly labeled in the German literature, exposes the aging worker to a greatly increased risk of injury or death from enemies. In both the field and laboratory, I have noted that the older *Pheidole* workers are the first to die when fire ants and other alien species invade the nest environs. Foragers are also far more likely to be picked off by predators.

A general increase in mortality of older workers by natural causes has been documented widely among the social insects. Foragers of the Idaho harvester ant *Pogonomyrmex owyheei*, which compose fewer

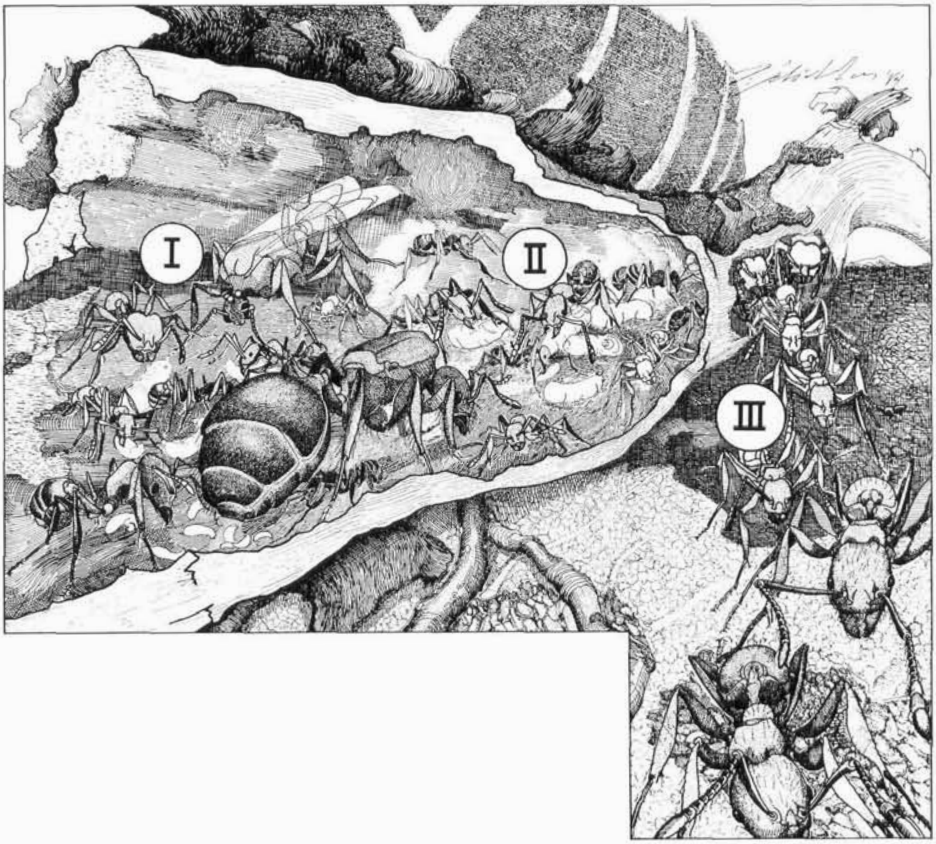

Fig. 10. The temporal division of labor of workers of the ant *Pheidole dentata*. As they age, the minor workers pass through three stages: *I*, concentration on the care of queen, egg, and pupa; *II*, attention to the care of larvae and other quotidian tasks within the nest; and *III*, foraging. Also shown are the mother queen and a winged male, as well as a scattering of the large-headed major workers. This species nests in rotting logs and stumps in forests of the southern United States. (From Wilson, 1985a, copyright 1985 by the American Association for the Advancement of Science.)

than 10% of the worker population at any given time, undergo substantial mandible wear and a weight loss of 40%. They are subject to intense predation and live an average of only 2 weeks after they commence expeditions away from the nest. As a result Porter and Jorgensen (1981) have referred to them as a "disposable caste." According to DeVita (1979), colonies of the related species *P. californicus* suffer an average of 0.06 death per worker foraging hour due to fighting with neighboring *P. californicus* colonies alone. Equally suicidal levels are accepted by the formicine *Cataglyphis bicolor*, a scavenger of dead arthropods in North African deserts. At any given time about 15% of the workers are engaged in long, dangerous sorties away from the colony, where they are frequently seized by spiders, robber flies, and other predators. Their life expectancy is only 6 days, but during that time each one retrieves 15 to 20 times its body weight in food (Schmid-Hempel and Schmid-Hempel, 1984). Aging workers of the queen weaver ant in Australia (*Oecophylla smaragdina*) are the chief occupants of "barracks nests" around the periphery of the colony territory. When alien weaver ants or workers of other species invade the territory, these outermost guards are the first to rush to the attack (Hölldobler, 1983).

The self-sacrificial role of social insect workers in general is enhanced by a peculiarity in the construction of their bodies. Space is saved by the reduction or elimination of reproductive organs and filled in good part by poison glands used in combat. Perhaps the most extreme known case in ants is found in workers of a Malaysian species of the *Camponotus saundersi* group. Huge mandibular glands filled with a sticky secretion run the entire length of their bodies. In the midst of a fight, they are able to rupture their own body walls, ejecting the secretion onto their adversaries (Maschwitz and Maschwitz, 1974). An evolutionary convergent "bomb defense" occurs in the termite genus *Globitermes*. Other glands in ants and termites produce pheromones, chemical substances used by the colony members to communicate with one another. Each individual is a walking battery of such glands and specialized chemicals, a formidable adversary able to spray formic acid or some other toxic material while summoning nestmates to its side.

Resource Inheritance

Superiority in the defense of resources is a major benefit of colonial life. A typical scene of the kind often documented in ants is the following: a minor worker of the imported fire ant *Solenopsis invicta* discovers a cockroach corpse too large for her to carry home. She runs back to the nest laying an odor trail. Excited by the pheromone, both minor workers and larger media and major workers follow the trail back to the cockroach. As some cut away pieces and drink the hemolymph, many others mill around the perimeter, alert and ready to attack intruders. Solitary insects and scouts of other colonies are quickly driven off. On a wholly different scale visualize the nest of a typical colony of leaf cutting ants (*Atta*). The vast system of subterranean galleries and chambers holds hundreds of fungus gardens and more than a million ants. The invested labor of the colony includes the excavation of over 10,000 kg of soil and hundreds of millions of sorties by individual workers to cut and retrieve the fresh vegetation used as fungal substrate. *Atta* colonies seldom abandon this enormous resource. When a nest is disturbed, workers of all sizes swarm out to defend it. Prominent among them are soldiers with heads more than 5 mm wide, making them Goliaths in the ant world. Their mandibles are heavy and sharp, and closed by muscles packed into the swollen posterior half of the head – altogether hard and powerful enough to cut through leather. Deeply entrenched and heavily defended, the nests are almost indestructible.

The most aggressive social insect species are those with large investments that are difficult or impossible to replace. The colonies have their backs against the wall, so to speak. Pseudomyrmecine ants specialized to live entirely on trees in the genera *Acacia, Barteria*, and *Triplaris* are notably more vicious than other pseudomyrmecine ants not so specialized. To lean against one of the trees is to be quickly covered by stinging ants, as though brushing against a nettle. Equally ferocious is *Camponotus femoratus*, one of the most abundant ants found in the ant-gardens of the South American rain forest canopy. The gardens are spherical masses of epiphytes belonging to a variety of species. Their growth is enhanced by the presence of the ants, while the ants depend on the shelter provided for their existence. *C. femoratus* is far more aggressive than any of the hundreds of other *Camponotus* species I have encountered around the world. When a garden is disturbed in the slightest, its surface is quickly covered by a seething blanket of large workers ready to bite and spray formic acid. In yet another category of symbiosis, ants that tend herds of aphids and other homopterous insects for their honeydew treat these aggregations just as they do their own nests. They cluster around the aggregations and drive off potential parasites and predators, as well as competitor ants that try to take over their herdsman role. Some ants, such as members of the genera *Crematogaster* and *Solenopsis*, build shelters of soil and carton around the homopterans. Field experiments have repeatedly confirmed that groups of the guardian ants are superior in such conflicts to solitary adversaries.

For primitive termites in the families Kalotermitidae and Termopsidae that inhabit wood, resource monopoly may not only be of great benefit to colonies but the key to the origin of their eusociality. A rotting log is a bonanza for these insects, as a mile-high granary might be for a tribe of human beings. Because they can digest cellulose with the aid of intestinal protozoans, they use the wood for both home and food. Often a single colony occupies the same large piece for years, raising generation after generation of winged reproductives that go forth in search of other, similar bonanzas. Myles (1988), drawing on the work and concepts of C. Noirot, J. A. L. Watson, and others, as well as his own recent research, has argued persuasively that the first termite castes were neotenics, individuals able to reproduce but not capable of flight and long-distance dispersal. Their appearance allowed the prototermite aggregations to continue occupying pieces of dead wood across two or more generations with a minimum of risk. Flight dispersal to suitable new logs is dangerous, while log inheritance is a valuable stroke of luck. Neotenics are, in effect, opportunistic nest inheritors. The newly evolved colonies in early termite evolution nevertheless continued to produce generations of full, winged reproductives as an alternative tactic. Few such individuals succeed, but when they do the reward in reproductive fitness is very high. In Myles' view, neotenics, the first evolved caste, represent the low-risk low-payoff tactic, and winged reproductives, the "ordinary" individuals of the prototermite aggregations, exemplify the high-risk high-payoff tactic. Soldiers and true workers then evolved as part of the more highly diversified and integrated termite colonies that exist today. These castes are highly effective in defending the nests against intruders while simultaneously rearing new generations of nymphs.

Abe (1987) has noted that the caste systems of termites appear to be adjusted so as to attain a balance between the low- and high-risk strategies, in accordance with the amount of resource investment. At one extreme, dry-wood termites (Kalotermitidae) typically occupy the dead branches of living trees, nest sites that are easily broken and thus unstable and relatively short-lived. When food becomes scarce as a result, all individuals in the colony except for the soldiers become winged reproductives. In reflection of this *r*-strategy, kalotermitids are good overseas colonists, their maturation time is relatively short, and their caste differentiation is generally very flexible. At the opposite end of the spectrum are the mound-building termites (Termitidae subfamily Macrotermitinae) of the Old World tropics. Their huge colonies occupy heavily fortified soil nests for years or even decades at a stretch. Large numbers of reproductives are generated, but the caste system is rigidly determined and a majority of the members remain soldiers and workers throughout the life of the colony.

The analogs of the high-risk kalotermitids among the social wasps are the Neotropical polistines of the genus *Mischocyttarus*. The life span of colonies of *M. drewseni* studied by Jeanne (1972) in Brazil averaged only 86 days. If left unmolested, colonies decline relatively early due to an increasingly heavy investment in males and large females ("queens"), which contribute little to the welfare of the colony and leave the nest early. The key advantage of this *r*-strategy seems very likely to be the heavy mortality of the colonies due to external causes, especially ants and other predators. It is better for *Mischocyttarus* colonies to reach maturity quickly and to invest almost totally in reproductives, rather than to take the chance of producing reproductives at a lower rate over a longer span of time. As in the kalotermitids, the developmental time of colony members is short and the caste system flexible. In marked contrast are the large, long-lived colonies of other Neotropical polistines such as *Chartergus* and *Polybia*, which build heavily fortified arboreal nests that are relatively immune to all but the most powerful predators.

To summarize, social insect colonies dominate nest sites and long-lived food sources through numbers and social cooperation. The amount and durability of these resources has had a profound effect on the evolution of the colony life cycle, including colony longevity and programs of caste production. In termites but probably not the social Hymenoptera, resource monopoly and inheritance may have been the critical factor in the origin of sociality itself.

Social Homeostasis and Flexibility

By employing mass labor to produce novel structures and magnify effort, social insect colonies are able to maintain more nearly constant nest environments than solitary insects. Social homeostasis has evolved to control virtually every conceivable component of the environment, as illustrated by the following array of techniques:

o In rain forests of Central America, colonies of the primitive ponerine ant *Prionopelta amabilis* nest in very moist rotting logs. The workers line the chambers of nest cells containing living pupae with fragments of discarded pupal cocoons. This "wallpapering" protects the pupae from excess moisture (Hölldobler and Wilson, 1986).

o Colonies of ant species use remarkable social devices to escape drowning when the nest is flooded. *Pheidole cephalica* minor workers are extremely sensitive to water near the nest. A single drop placed next to the nest entrance is enough to cause nearby foragers and guards to race inward into the galleries through the nest, and then out to alternate exits, laying trails as they go. The trail pheromones alert other adult colony members and cause them to move away from the water, some carrying brood pieces for possible rescue (Wilson, 1986). In a wholly different tactic, *Solenopsis* fire ants form living rafts. As flood waters rise, the ants move upward through their nests to ground level and then press together in large groups that float on the water surface. The queens and immature forms are sequestered in the centers of the masses. The colonies eventually anchor themselves to grass stems or bushes sticking out of the water and return to the soil when the flood recedes (Hölldobler and Wilson, 1990).

o Under ordinary circumstances the division of labor between the minor and major castes of ants of *Pheidole* is nearly total. The large-headed majors are inactive most of the time. When they do work they usually concentrate on either defense, milling, or liquid food storage in their expandable crops, with the specialization varying according to species. In marked contrast, minor workers take full responsibility for most of the ordinary tasks, including nest construction, brood care, and foraging. However, when the minor to major ratio is lowered to below 1:1 (from a norm of 3:1 to 20:1 that varies according to species), so that minors are abnormally scarce, the repertory of the majors suddenly and dramatically expands to cover most of the tasks of the minors. Similarly, when older minor workers specialized for foraging (see Figure 10) are removed, younger workers act to fill their places. In the reverse experiment, older workers quickly fill in as nurses. In other words, *Pheidole* colonies as a whole have the flexibility to maintain a division of labor by using well-defined and narrow specialization in normal times, but shifting labor assignments in radical fashion to maintain equilibrium during emergencies (Wilson, 1984).

o With impressive ingenuity, honeybee colonies maintain the temperature of their hive at or near the ideal level for brood development during the summer and well above freezing during winter. The first line of thermoregulation is achieved by nesting in a tree hollow or other protective enclosure and calking it with plant gums and resins. A finer control is attained by minute-by-minute shifts in worker behavior. As the nest cools during the winter, the workers cluster more tightly on the combs to form a living blanket, thus raising the immediate ambient temperature with their own metabolic heat. The effect not only protects them from freezing but provides a faster start-up for flight as soon as the weather is suitable for foraging. When the hive overheats in summer, the bees follow three procedures: they space out their bodies on the comb, increasing the dissipation of metabolic heat; they fan their wings to improve air circulation; and they cool the air with water evaporation. The last effect, cooling by evaporation, is achieved by spreading water droplets over the comb surface and by extending films of water out between the mandibles. If overheating continues for long, foragers bring in additional water. They gauge the colony's overall need by the rapidity with which their nestmates accept the water (Lindauer, 1961; Seeley, 1985). Similar techniques are employed by free honeybee swarms during emigration away from the mother nest, and in this circumstance the geometric pattern is even more striking (Figure 11).

o Fungus-growing termites of the genus *Macrotermes* equal the honeybees in the degree of microclimate regulation, but they have achieved it by means of architectural innovation. The entire nest, in essence, has been turned into an air-conditioning system. It consists mostly of a huge mound housing a million or more workers and one to several queens. The central core of the nest, where the termites and their symbiotic fungus live, sits atop pillars separated by large air spaces. Above the core is another large air space, and around it is a wall permeated by numerous flat chambers. As air within the core warms from the metabolism of the termites, it rises by convection to the large upper chamber and passes laterally to the capillary-like network of outer chambers, where it is cooled and freshened. Then as the air cools it sinks to the lower passages of the nest around the pillars beneath the core. The continuous slow circulation, center up and

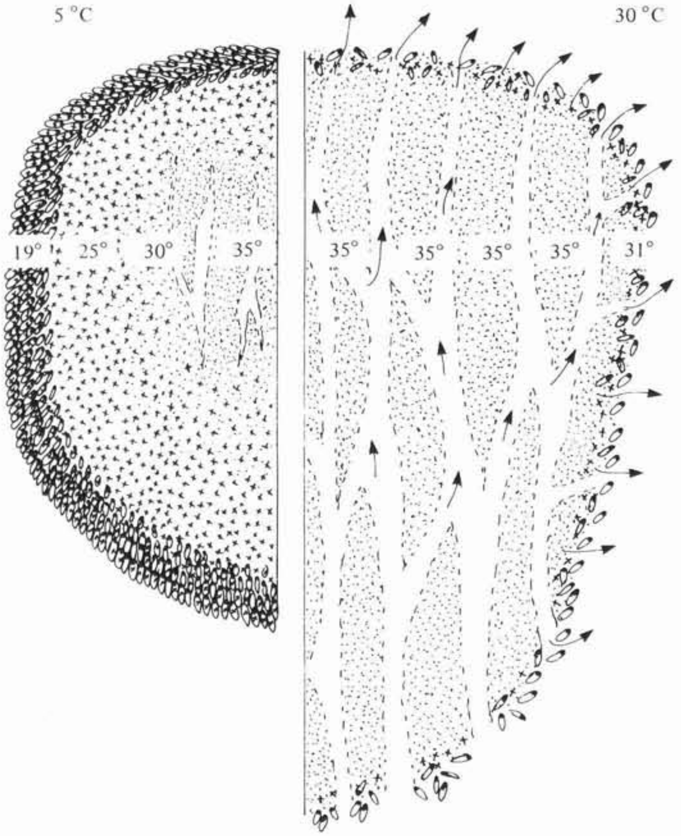

Fig. 11. Thermoregulation in a free swarm cluster of honeybees is achieved in part by the spacing of the workers. This diagram shows a typical cluster at a low temperature, on the left, and a high temperature, on the right, with indications of the position of the worker bees, channels among them kept open for ventilation, heat loss (arrows), areas of active metabolism (crosses), areas of resting metabolism (dots), and approximate temperatures at different points. (From Heinrich, 1981.)

periphery down, holds the temperature of the core to within several degrees of 30 °C and its carbon dioxide level close to 2.7% (Lüscher, 1961).

To the extent that the homeostatic devices work, colonies of social insects containing a sizeable worker force should live much longer on the average than individual insects. Such has proved to be the case (Wilson, 1971; Hölldobler and Wilson, 1990). We should also expect to find that populations of social insect colonies fluctuate less widely in density. We expect it, but data to test the idea are sparse. Pickles (1940) as noted previously, found that densities of ant colonies at a British site varied less through time than did densities of worker ants. E. A. Oinonen (cited by K. Vepsäläinen, personal communication) provided evidence of extreme longevity in Finnish populations of *Formica aquilonia*. Because single colonies of this species have multiple queens, build multiple mounds, and control extensive territories, they are potentially immortal. Oinonen estimated one "mound complex" to be over 500 years old. However, as Vepsäläinen has pointed out, forest fires might kill a particular colony, which could soon be replaced by new propagules of the same species. If a *F. aquilonia* colony dies, there is a good chance that the more opportunistic species *F. fusca* or *F. lemani* would settle in the mound remnants, but then these colonies are likely to be invaded by *F. aquilonia* queens, which are temporary social parasites. Even if such turnover occurred frequently, however, the relative stability of local populations is undeniable.

In general, it appears that colony mortality of perennial social insects (in other words, all but the annual social wasps) is very heavy at the earliest stages, but mature colonies are relatively very persistent, and populations of colonies are therefore changing in density slowly in comparison with populations of solitary insects. Population stability through colonial homeostasis has the additional effect of permitting entire faunas of social insects to survive in habitats with severe, irregularly fluctuating environments. For example, ants survive the long and uncertain periods of drought in the arid zone of Australia, whereas mammals as a rule do not. According to Morton and Baynes (1985), this difference is the reason that ants are far more abundant and diverse.

Why Aren't All Insects Eusocial?

Colonial life is a relatively recent development in the overall evolution of the insects, covering only about half of their time on earth. Insects arose at least as far back as the Devonian and radiated extensively during the late Carboniferous. By the Permian Period, about 290 million years ago, several modern orders, including the cockroaches (Blattaria), true bugs (Hemiptera), and beetles (Coleoptera) were present. The first termites probably arose in the Jurassic or early Cretaceous, roughly 200 million years ago, and ants, social bees, and social wasps in the Cretaceous some 100 million years later. The social insects as a whole, particularly the termites and ants, became dominant elements no later than the beginning of the Tertiary Period, approximately 65 million years ago.

If colonial life has great intrinsic advantages, as the evidence strongly suggests, why was its appearance so long delayed, and why aren't insects now exclusively eusocial? The two questions can be turned around, with the better chance of an answer, as follows: What advantages, under what conditions, do solitary insects enjoy over social insects? The answer, I believe, is that solitary insects reproduce faster and upon a smaller resource base. Ecologically, they fill in the cracks left by the eusocial insects.

It may seem odd to say that eusocial insects breed more slowly than their solitary counterparts. Colonies are after all growth factories teeming with workers devoted to the production of new nestmates. But it must be remembered that the colony, not the worker, is the unit of reproduction. In order to create new propagules, in other words additional queens that can disperse and start new colonies, the colony must first produce a crop of workers large enough to attain reproductive capacity. And the larger the colony, the fewer new individuals (worker or queen) will be produced per worker per unit time. This last, "reproductivity" effect is due variously to reduced efficiency in larger masses, the smaller number of eggs available for rearing as the worker population outpaces the queen's oviposition capacity, and the falling energetic yield per forager as the surrounding terrain becomes more heavily exploited.

Consider a terrain newly invaded by both solitary and eusocial insect species that are dependent on the same diet. The environment presents them with a mosaic of resources of variable size and persistence. If they live and forage in rotting wood, for example, they can exploit an array of pieces ranging from logs to tiny twigs. The social insect colonies can live in and dominate the larger pieces but not the smallest, which they concede to solitary insects. Also, they are slower at spreading from one suitable site to another, because their propagules are created only after a period of colony growth that consumes multiple generation times of individuals, whereas their solitary competitors need only one generation. Consequently, the solitary insects arrive earlier on the average and utilize some of the resource before being displaced by social insect colonies. Many solitary insects can persist even in the most favored sites by intercalation: through small size, exceptional swiftness, or specialization on near-impenetrable resting sites, they can avoid fatal attacks by ants and termites.

In competition among species where there is direct aggressive confrontation or the concurrent exploitation of stable resources in a well-defined space, social insects can be expected to prevail over solitary insects. Models and empirical studies show that they gain their edge through (1) series-parallel operations, which allow them to conduct many tasks simultaneously to successful completion by switching labor roles back and forth among colony members; (2) the option of individuals to risk or throw away their lives on behalf of the colony with a gain in inclusive fitness; and (3) the ability of colony members to control nest sites and rich food sources and bequeath them to later generations. Social insects can also be expected to prevail where control of the microclimate permits longer occupancy of nest sites near stable resources.

Social insects, and particularly the ants and termites, do prevail in terms of biomass in most terrestrial habitats. Yet solitary insects still abound, and in some environments they outweigh the social insects. I suggest that ecologically they "fill the cracks" left by the social insects, dispersing to places less accessible to the more ponderous colonies and their propagules and breeding faster on smaller amounts of resource.

V The Superorganism

Viewed from afar and slightly out of focus, the raiding column of an African driver ant colony seems a thing apart, a giant pseudopodium reaching out. A closer look discloses a mass of several million workers flowing out from the bivouac site, at first in an expanding sheet, then tree-like, with the trunk growing from the nest, the crown an advancing front, and numerous anastomosing branches connecting the two. The swarm is leaderless. The excited workers rush back and forth at an average speed of 4 cm per second. Those in the van press forward for a short distance and then turn back into the tumbling horde to give way to other advance runners. The feeder columns resemble thick black ropes lying along the ground. The frontal swarm, advancing at 20 m an hour, engulfs all the ground and low vegetation in its path, gathering and killing almost all the insects and even snakes and other larger animals too sluggish to crawl away. After a few hours the direction of flow is reversed, and the column drains backward into the nest holes.

To speak of a colony of driver ants or other social insect as more than a tight assembly of individuals is to speak of a superorganism, thereby evoking more detailed comparisons between the society and a conventional organism. The comparisons are justified only if the metaphor is heuristic, and in the present context especially when it helps to explain the dominance of the social insects. In 1968 I argued that the superorganism concept had outlived its usefulness, that the analysis between colonies and organisms in the old style had been pushed too far. I suggested that what was needed was a period of close analysis of individual behavior in order to construct a precise picture of the inner workers of the colony, free of metaphor. In other words, the analysis should be bottom-up instead of top-down. Twenty years later I believe we have progressed quite well in that direction, with a virtual encyclopedia of new information on caste, division of labor, communication,

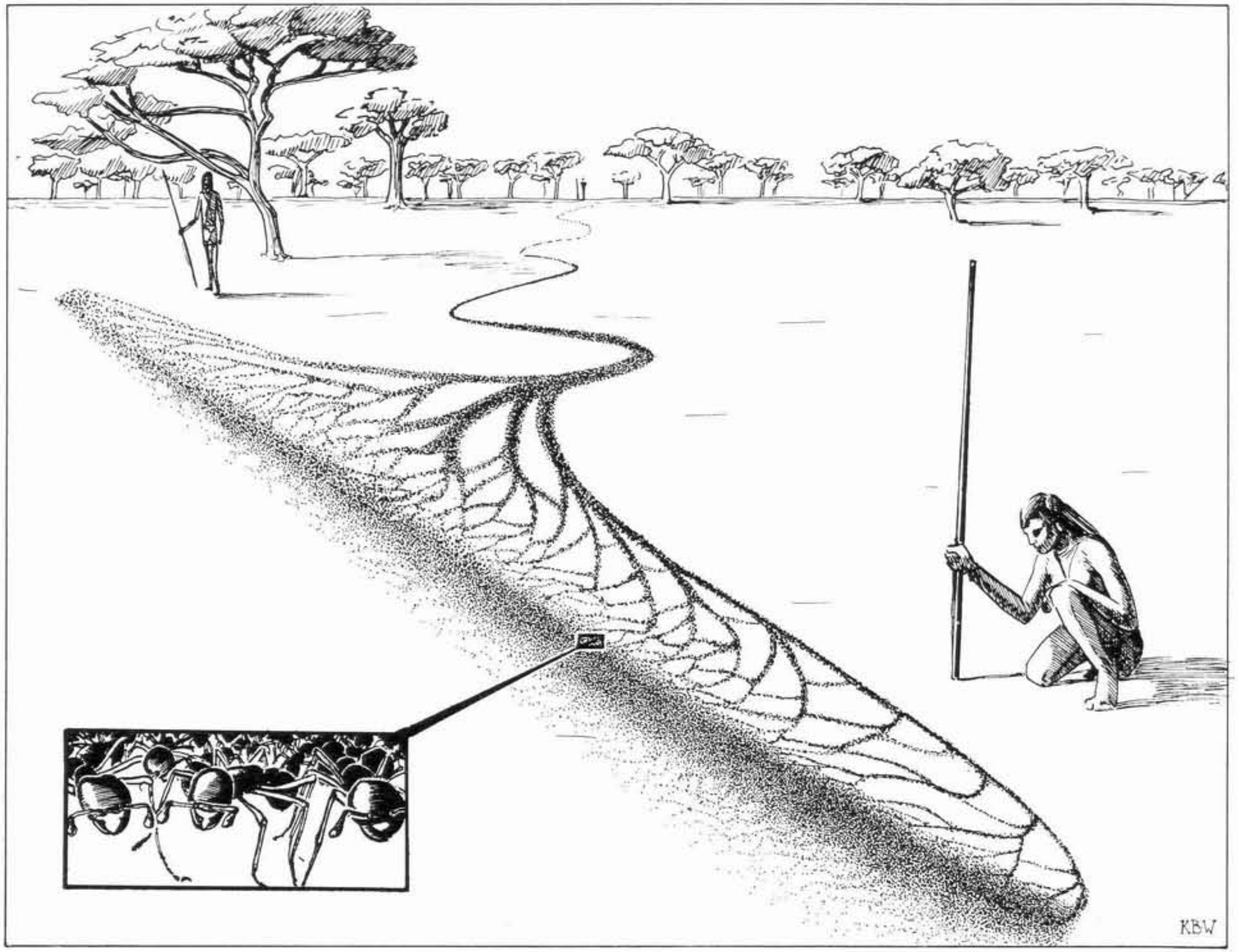

Fig. 12. A foraging swarm of *Dorylus* driver ants. This stylized original drawing by Katherine Brown-Wing is based on diagrams from the field by Raignier and Van Boven (1955).

dominance, and learning now at hand. The comparisons between organisms and colonies can be made a good deal more precise, and they are heuristic in the sense of stimulating research at both levels.

The typical colony has the following organismic attributes:

- The workers are equivalent to cells in the manner if not degree of their specialization for particular forms of labor, including most importantly a division between reproductive and nonreproductive elements.
- The activities of the workers are coordinated by intricate modes of communication.
- The unit of natural selection is the colony, or more precisely the mother queen operating through the daughter workers, rather than the individual workers tested by selection one by one. This is of course not perfectly true, since a few workers of some species lay viable eggs and even compete with their nestmates for the privilege. But in general the colony is indeed the prevailing selection unit, and this preponderant focus of natural selection is reflected in the homeostatic regulation of caste ratios. The age- and size-frequencies of the colony members are adaptive traits, not epiphenomena as they are in a population of noncolonial organisms.

The comparison of colonies and organisms has a larger goal than amusing analogy: the meshing of comparable information from developmental biology and sociobiology to reveal more general and exact principles of biological organization (Wilson, 1985a). The definitive process at the level of the organism is morphogenesis, the set of procedures by which individual cells or cell populations undergo changes in shape or position incident to organismic development. The definitive process at the level of the colony is sociogenesis, the procedures by which individuals undergo changes in caste and behavior incident to colonial development. The question of interest for general biology is the nature of the similarities between morphogenesis and sociogenesis. The question of interest for ecology particularly is the way in which superorganisms fit themselves more efficiently to the environment by means of social mechanisms.

How the Superorganism Works

It is an interesting exercise to define the exact means by which eusocial insects are fitted into the superorganism. Put another way, how does one identify an isolated individual as a social insect, as an element to be fitted into a colony? There are surprisingly few anatomical features that can be called diagnostic in this sense. In most respects a single termite looks very much like a cockroach nymph, and in fact is astonishingly close to a young nymph of the subsocial cockroach *Cryptocercus*. There are few if any clear-cut outward traits to separate social halictine bees from solitary halictine bees, or social polistine wasps from subsocial polistine wasps. Indeed, the gradual transformation from solitary to eusocial states among the species of halictines and polistines has been the principal source of our knowledge of the origin of advanced social behavior within the insects generally. For their part, worker ants are characterized by the absence of a spermatheca, the tiny globular bag near the base of the ovarioles in which sperm are stored, and by the reduction or absence of ovaries. As a rule they also have a notably complex exocrine gland system used in combat and communication, although such is not the case for the most primitive ants in the genera *Amblyopone, Myrmecia,* and *Nothomyrmecia*. Only two glands, the postpharyngeal gland of the head and the metapleural gland of the alitrunk (middle portion of the body), are diagnostic for the ants as a whole, in other words widespread enough to characterize the entire family Formicidae. Of these two, only the postpharyngeal gland has a primarily social function, as a source of special foods for the queen and larvae. (The metapleural gland produces antibiotics or defensive secretions.) So close are worker ants to the wingless wasps in external anatomy that a disagreement has arisen on the status of the earliest known ant worker fossils, which date from the late Mesozoic (see Figure 6). Dlussky (1983) placed these specimens in the Sphecomyrmidae, which he regards as a side branch of the winged Armaniidae, the "true" ancestors of modern ants. In contrast, I consider the Armaniidae to be the queens of the Sphecomyrminae and the entire complex to fit comfortably in the single, probably eusocial genus *Sphecomyrma* (Wilson, 1983). This conclusion is supported by the fact that the abdomens of the *Sphecomyrma* and those of modern ant workers are smaller relative to the rest of the body than is the case for modern wingless solitary wasps. In whatever manner the problem of the Mesozoic ants is eventually resolved, the important point here is that most ants are outwardly little modified as part of their adaptation to an extreme social existence.

Overall, then, life within the superorganism does not modify the social insect worker nearly so drastically as life within the organism modifies the cell. The reason may be simply that however tightly integrated the colony members may be, the individual worker must continue to function as an organism fully endowed to run, orient, feed, and eliminate on its own. The most distinctive properties of the superorganism are behavioral, not anatomical. They comprise mass communication and adaptive demography, by which the behavioral repertories of individual workers are integrated to create emergent properties.

Mass Communication

Mass communication is the transfer of information among groups of individuals of a kind that cannot be transmitted from one individual to another individual. Excellent examples are provided by the imported fire ant *Solenopsis invicta*, which because of its economic importance is one of the most thoroughly studied of all insect species. The flow of food into the colony is regulated by communication between groups. When the foragers of laboratory colonies were starved as a group by Sorenson et al. (1985), they collected disproportionately more honey. When they were well fed but the nurse workers and larvae were starved instead, the foragers collected a larger proportion of vegetable oils and egg yolk. The significance of this shift is that sugars are used mainly by adult ant workers, lipids by workers and some larvae, and proteins by larvae and egg-laying queens. Hence the foragers respond to the nutritional needs of the colony as a whole and not just to their personal hunger. Sorenson and her co-workers found that the ants monitor this generalized demand by a form of mass communication. A large group of individuals, the reserve workers, receive most of the food soon after it is carried into the nest by the foragers. They then pass it on to other colony members, including the nurses. When the demand encountered by the reserve workers declines anywhere in the colony, they accept the corresponding food (honey, oils, or yolk) less readily from the foraging workers. The foragers are unable to dispose of their loads as quickly as before, and they reduce their efforts to collect more of the same kind. As a result, they shift their emphasis as a group among carbohydrates, oils, and proteins, according to the needs of the colony. In this fashion the colony as a whole blindly impresses its needs on the individual, and the individual blindly responds until the needs of the colony are met. Furthermore, the mass response is more precise than if each worker were to attempt to assess the overall requirements of the colony on its own.

Mass communication is also employed during recruitment. Individual fire ant workers arriving at a large food find, such as an animal carcass, lay odor trails consisting of secretions from the Dufour's gland of the abdomen paid out through the extruded sting. Some individuals lay trails and others do not. They base their decision on the nutritional needs of the colony as a whole and the richness of the food. These variables also affect the speed with which a forager inspects the food and returns to the nest, as well as the amount of trail substance she deposits. The number of workers crowding the food sites is determined by both the quality and quantity of food, which are evaluated through mass communication in the following way. As food retrieval proceeds, the number of recruiting workers determines the amount of recruitment pheromone in the trail, which in turn fixes the number of workers answering the call. As the colony as a whole approaches feeding satiety, or the food becomes saturated with worker bodies, the responses by individual workers diminish and the growth of the worker population at the food site decelerates. The flow of the food stabilizes and finally declines. As a result, the colony reacts more quickly and precisely to food discoveries than would be the case if workers searched for food and harvested it as individuals (Wilson, 1962).

Arguably the most dramatic form of mass communication in social insects is the tournaments of the honeypot ant *Myrmecocystus mimicus*, discovered by Hölldobler in Arizona (Hölldobler, 1986a; reviewed in Hölldobler and Wilson, 1990). One of the principal food sources of *Myrmecocystus mimicus* is termites. When a scouting ant encounters a rich source of these insects, she summons nestmates by means of odor trails consisting of hindgut fluid. She stimulates them further with ritualized movements of her body. If another colony of *M. mimicus* is located near the food source and is detected by the foragers, some of them rush home and recruit an army of 200 or more workers to the foreign colony. The raiders swarm over the nest and engage all of the workers emerging from the alien nest entrance in an elaborate mass display, the "tournament." The performance is taken up by both sides. It consists of contacts among pairs or combinations of several ants during which the ants rise high on their legs and run about as though on stilts, jerking their bodies rapidly during close approaches and often bending sideways toward the opponents. During their presentations the ants sometimes mount small stones, as though trying to increase the impression of large size. Mandibular nipping and formic acid spraying, the deadly forms of direct assault available to *Myrmecocystus*, are rare or absent. The entire performance appears to be a means of mutual assessment of overall colony strength. Almost invariably the colony with the smaller number of displaying foragers retreats from the scene.

Hölldobler found that territorial tournaments occur not only on food sites but also in the zone between two adjacent *Myrmecocystus* nests, and especially when both colonies are active at the same time. By this means alien foragers are blocked from the respective foraging areas of each colony. The tournaments sometimes drag on for several days, ending only at night as the workers become inactive. When one colony is considerably stronger than the other and can summon a much larger worker force, the tournaments end quickly and the weaker colony is invaded. During these terminal raids the queen is killed or driven off, and the larvae, pupae, callow workers, and honeypot workers (abdomens swollen with stored liquid food) are carried or dragged to the nest of the raiders. The kidnapped individuals are largely incorporated into the raiders' colony as full members. In other words, the *Myrmecocystus* practice true slavery.

Using mass communication in combination with ritualized combat, honeypot ants settle territorial disputes with little shedding of hemolymph. What signals pass back and forth during the tournaments? And how do individual ants measure the numbers of their opponents? Hölldobler adduced evidence of two methods used by the ants. Individual workers "count heads" to gain a rough measure of the enemy's strength. They also determine whether a low or high percentage of the opponents are major workers, since a high percentage of such large individuals is a reliable index of mature colony size. The ants may also use a queuing technique. A long wait before meeting an unengaged opponent means a small colony, while a short wait means a large colony.

The group assessment procedure has been extended to long-term maintenance of territorial boundaries by *Myrmecocystus* colonies of similar strength. Small groups of workers post themselves at locations intermediate between the two nests. These guards stand "at attention" on stilt-like legs, often posing on top of little stones. Neighboring colonies also contribute guard contingents to the posts, where they conduct mini-tournaments with opposing workers. The contacts can continue indefinitely – a kind of formicid 38th parallel. But if the number of workers of one party at the guard-post suddenly increases, the other party responds by summoning a large counterforce, and a full-scale tournament ensues.

The importance of mass communication in ecological dominance is made clear by these examples from the ants. The individual colony member does not have to perform in an extraordinary manner. Quite the contrary, it can have a simpler repertory than that of an otherwise similar solitary insect. It can even be "degenerate." The worker need operate only with cues, or rules of thumb, which are elementary decisions based on local stimuli that contain relatively small amounts of information.

The cues I have cited in the previous paragraphs are the following: *continue hunting for a certain foodstuff if the present foraging load is accepted by nestmates, and do so avidly if the load is accepted quickly; follow an odor trail if sufficient pheromone is present; and retreat if many enemy workers are encountered in a short time, especially if a high proportion of them are large individuals.*

Each of these cues is easily followed by individual workers. The required actions are performed in a probabilistic manner with limited precision. But when put together in the form of heterarchies involving large numbers of workers engaged in mass communication, a larger pattern emerges that is strikingly different and more complicated in form, as well as more precise in execution.

Adaptive Demography

Adaptive demography is defined as the programmed schedules of individual birth, growth, and death resulting in frequency distributions of age and size in the colony members that promote survival and reproduction of the colony as a whole. An aggregate of organisms turns more decisively into a superorganism to the extent that its demography is adaptive at this higher level of organization (Wilson, 1968b; Oster and Wilson, 1978).

Ordinary demography of the kind found in nonsocial organisms is a function of the parameters of growth, reproduction, and death. These parameters and the schedules of the life cycle they determine are clearly direct adaptations shaped by natural selection operating at the level of the individual. On the other hand the age-frequency distribution and the size-frequency distribution are epiphenomena, in the sense that they reflect the individual-level adaptations but do not constitute adaptations in their own right. Thus a sharply tapered age distribution in a local population of fishes results from a high birth rate and a high mortality rate throughout the life span, but in itself does not contribute to the survival of either the population or the individual members. The exact reverse is the case of the eusocial insect colony. The demographic parameters and the resulting age-size frequency distributions are directly adaptive. Because the workers are for the most part sterile, their birth and death schedules have meaning only with reference to the queen. Hence the unit of selection is the colony as a whole. What matters at this level is the percentage of soldiers, nurses, nest workers, and so forth available to meet the minute-by-minute contingencies and bring the group as safely as possible to the point of maximum queen and male production. Adaptive demographies serve to generate the greatest possible number of new colonies in the next generation, not the greatest number of workers in the current generation.

A striking example of adaptive demography is provided by the early colony development of the leafcutter ant *Atta cephalotes* (Wilson, 1983). The first group of workers, produced by the nest-founding queen from her own body reserves, must include workers as small as those with head width 0.8 mm. This "minim" caste cares for the delicate growing hyphae of the *Leucocoprinus* fungus that serve as the colony's principal food source. The first group must also include workers with head widths at least 1.6 mm, the smallest size capable of cutting the vegetation on which the fungus is grown. Older colonies regularly produce large numbers of workers with head widths well over 1.6 mm, in fact sometimes exceeding 5 mm. A founding queen must be very precise in choosing the size range of her first brood. If she were to rear just one overly large worker, say a media with head

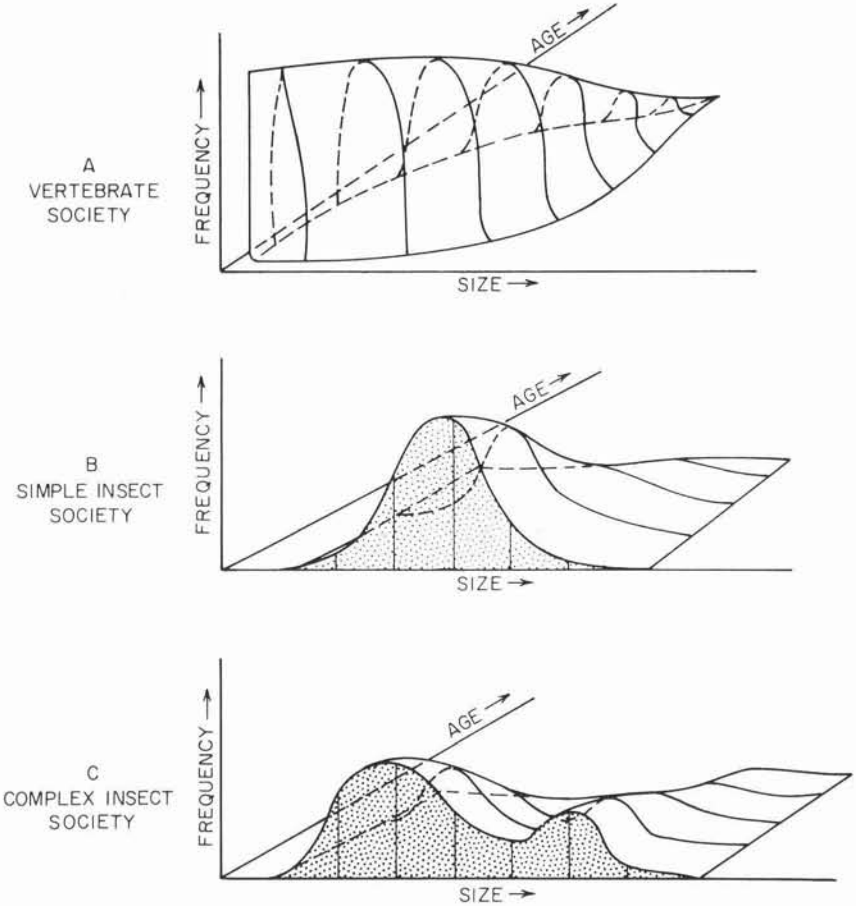

Fig. 13. The concept of adaptive demography in colonies of ants and other advanced eusocial insects is illustrated in the distinctive properties of their age-size frequency distributions. In a typical vertebrate society and in the simplest insect societies, whose members are able to assume important reproductive roles, the distributions are adaptively neutral at the level of the group. In complex insect societies, however, the relative numbers of individuals of various sizes and ages determine the efficiency of the division of labor and thus are positively or negatively adaptive at the level of the entire colony. (From Wilson, 1975.)

width 3 mm, she would use up most or all of her body reserves and lose the ability to create enough members of all of the rest of the required castes. Conversely, if she raised only minims (the usual practice in ants other than leafcutters), the colony would have no one to gather vegetation. In fact, beginning colonies of *Atta cephalotes* almost always have a nearly uniform size-frequency distribution across the head width range of 0.8 to 1.6 mm, exactly the configuration needed to succeed.

This fortunate peculiarity in the sociogenesis of *Atta* leads us to the question of whether the size of the colony or its age determines the size-frequency distribution. To learn the answer, I selected four colonies of *A. cephalotes* 3 to 4 years old with about 10,000 workers, and reduced the population of each to 236 workers, giving them a size-frequency distribution characteristic of natural young colonies of the same size collected in the wild. The worker pupae produced at the end of the first brood cycle possessed a size-frequency distribution like that of small, young colonies rather than larger, older ones. Thus colony size proved to be more important than age. The exact physiological feedback mechanisms mediating the control are still unknown, but the final phenotypic result is quite clear.

Extreme Castes

In many ant species belonging to the subfamilies Ponerinae and Myrmicinae, the subordination of worker anatomy and behavior to colony needs is less than total. The workers are able to lay eggs and occasionally compete to do so. They form dominance hierarchies, with the highest ranking individual acting more like a queen than a worker (Bourke, 1988). But in other species, perhaps a majority of ant species as a whole, the subordination is total, and the superorganism can therefore be said to be uncontaminated by individualism.

In the myrmicine genera *Pheidole* and *Solenopsis*, for example, workers lack ovaries altogether. *Pheidole* is notable for the universal presence among its hundreds of species of two discrete castes: a small-headed minor worker that conducts most of the nursing, foraging, and other quotidian tasks of the colony, and a large-headed major caste, which is highly specialized (see Figure 10). The majors in fact are so specialized that those of some species have the most limited repertories known in the social insects. Most of the time they do very little beyond eating and grooming themselves. According to species, they also perform one or two of the following three functions: storing liquid food in their enlarged crops, milling seeds collected by the minor workers, and defending the nest and food sites.

The roster of highly specialized castes in other ants and termites includes some of the more bizarre of known ambulatory organisms:

- Major workers of the Oriental ant genus *Acanthomyrmex*, which are specialized for milling seeds, possess massive heads that are about as large as the entire rest of the body. They are literally "walking heads."
- The soldiers of *Eciton* army ants and the formicine desert ant *Cataglyphis bombycina* have bizarre, scimitar-shaped mandibles used, so far as known, only during combat.
- The minims of the fire ant *Solenopsis invicta* and many other ants, produced by colony-founding queens, are smaller than even the smallest workers of larger colonies, short-lived, exceptionally timid, and evidently designed to be numerous enough to produce a second, larger brood at the cost of their own reduced longevity.
- The "honeypot" workers of ants in the formicine genus *Myrmecocystus* and a few species in the formicine genera *Camponotus, Melophorus, Leptomyrmex*, and *Plagiolepis* consume so much liquid food that their crops swell grotesquely and locomotion becomes difficult. They regurgitate the liquid to nestmates upon demand.
- Phragmotic soldiers occur in the ant genera *Camponotus, Colobopsis, Pheidole*, and *Zacryptocerus* and in the termite genus *Cryptotermes*. Their heads are thick-walled, heavily pitted, and truncated in front, and are used by the soldiers to serve as living doors: they plug nest entrances and narrow galleries, and prevent invasion by enemies.

In general, insect colonies are not like siphonophores and other extreme colonial invertebrates. They do not reduce their members to mere inanimate appendages of the corporate body. The modes of foraging and emigration from one nest site to another require that social insects remain separate ambulatory entities. But specialization of individuals has in the extreme known cases proceeded nearly as far as can be imagined. Many species have evolved colonies so differentiated as to deserve designation as superorganisms by even the strictest definition.

Penetration of New Adaptive Zones

Colonial existence has allowed social insects to exploit the environment in wholly new ways, adding to their total competitive advantage over solitary insects. The insect colony is able to blanket a relatively huge area all at once, monitoring and extracting large quantities of food. Of honeybees Seeley (1985) wrote:

> Each colony can be thought of as an organism which weighs 1 to 5 kg, rears 150,000 bees and consumes 20 kg of pollen and 60 kg of honey each year. To collect this food, which comes as tiny, widely scattered packets inside flowers, a colony must dispatch its workers on several million foraging trips, with these foragers flying 20 million km overall.

The achievement of the honeybee colony can be visualized even more graphically by enlarging honeybees to human scale in the imagination, so that each worker is 1.8 m long. Then a colony would be roughly the equivalent of the town of Brownwood, located near the center of Texas. On good days its foragers would patrol most of the state of Texas. To achieve this steady monitoring its inhabitants would travel each year a total of 3.5 billion km – 100 thousand times around the earth. The bees communicate with one another continuously, so that the main foraging battalions are shifted quickly as old nectar sources decline and new ones appear.

The leafcutting ants of the New World tropics and subtropics, comprising 24 known species of *Acromyrmex* and 15 of *Atta*, are the only members of the animal kingdom to cultivate fungi for food on fresh vegetation. A few other ants, beetles, and termites raise fungi for food, but they use rotting wood or insect excrement as a substrate. Only the leafcutters collect and process pieces of leaves and flowers for this purpose. To live as agriculturists on such a rich fertilizer source represents impressive sophistication for small instinct-driven creatures. They must overcome two major obstacles. First, the living plants attacked by the ants are relatively tough and difficult to cut. (They are also loaded with chemicals poisonous to insects. The chemicals do not affect the fungi, however, which are used by the ants to bypass the poison.) Second, the symbiotic fungi are microscopic, delicate, and easily overgrown by fungus species unsuitable for the ants.

The leafcutters have overcome these obstacles by means of an assembly line based on caste. I noted previously that the minimum size range in *Atta* is head width 0.8 to 1.6 mm, which is precisely spanned in the first brood by the colony- founding queen. In larger colonies the actual size range is expanded to achieve a more efficient operation as opposed to a minimal operation. First, relatively large workers with powerful mandibles (head width 1.8 to 2.8 mm) climb shrubs and trees and cut off circular fragments of leaves and flowers, which they then carry back to the nest. Inside the subterranean garden chambers, successively smaller workers slice the pieces into tiny fragments and then chew them into pulp. Still smaller workers insert them into the spongy substrate masses. The next smallest workers plant strands of fungi onto the new pulp, and finally the smallest workers of all, the gardeners, cultivate the fungus and distribute it as food to other colony members (see Figure 14). Such an assembly line is necessary because the foragers are too large to care for the fungus, while the tiny gardeners are too small to cut leaves. The caste system had to evolve along with the separate, sequential acts of behavior to facilitate the complete process of fungus cultivation, and it appears to have been fine-tuned in the course of evolution (Wilson, 1980a, b).

Evidently as a consequence of their superorganismic innovation, the leafcutters have become dominant elements of the Neotropical environment. The colonies of some species live more than 10 years and contain at any given time in excess of a million workers. The vast systems of chambers and galleries extend as much as 6 m beneath the surface of the ground. The ants are the principal herbivores of the New World tropics, consuming more vegetation than mammals, caterpillars, or beetles. Colonies of the more abundant genus, *Atta*, have been calculated on the basis of twelve studies to appropriate between 12 and 17% of leaf production in tropical forests (Cherrett, 1986). They also consume large quantities of grass in more open habitats. The ants adapt readily to crop vegetation and are consequently the leading pests of agriculture in the American tropics. At the same time they enrich the soil of forests and grasslands with the deposits of dead workers and exhausted fungal substrate abandoned in deep nest chambers.

Army ants, defined as species whose workers change the nest site at frequent intervals and forage in groups, have been notably successful at preying on large or otherwise formidable prey. By operating in organized groups they are able to overcome defenses impenetrable to ordinary solitary predators. Among ponerine ants utilizing group hunting, for example, are the species of *Onychomyrmex* and the *Leptogenys diminuta* group that prey heavily on large beetle larvae and other outsized arthropods. *Simopelta* and *Cerapachys* raid colonies of

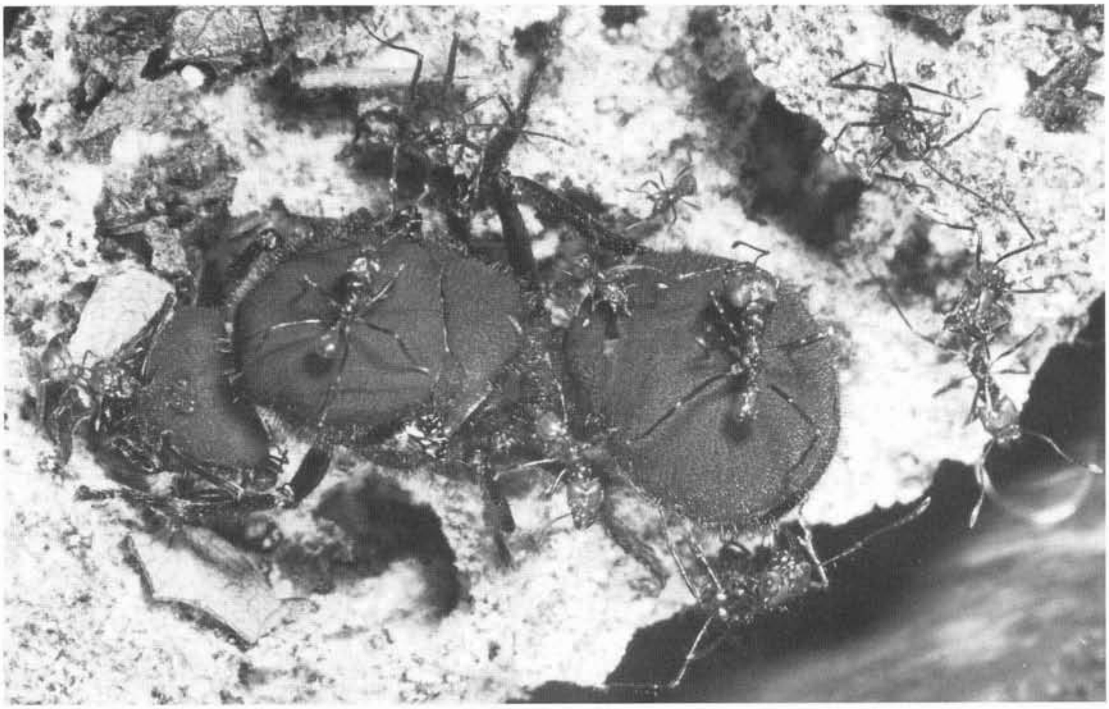

Fig. 14. A queen of the leafcutter ant *Atta cephalotes* rests on a fungus, surrounded by workers of several castes. The two larger workers on her abdomen are at the lower limit of the leaf harvesting caste. The smallest workers, on the queen's abdomen and just above it (the latter carrying a larva), are members of the gardening caste. Most of the garden is covered by the fluffy white mycelium of the *Leucocoprinus* fungus. Fresh fragments of leaves, used as the substrate for fungal growth, are seen in various stages of preparation in the upper half of the figure. (Photograph by C. W. Rettenmeyer.)

other kinds of ants, and *Megaponera foetans* and *Pachycondyla laevigata* hunt termite colonies. Driver ants (*Dorylus*) of Africa and army ants (*Eciton*) of the American tropics prey on a wide variety of arthropods that include wasps and other ants. In the case of *Eciton burchelli*, not only are large prey routinely captured by mass action but the biggest items are carried by teams of workers – the key single member of which is a submajor, a forager only a bit smaller than the long-mandibled soldier caste. Franks (1986), who first noted this phenomenon, showed that the *Eciton burchelli* teams are "superefficient." They can carry items that are so large that if they were fragmented, the original members of the group would be unable to carry all of the fragments. This surprising fact is explained at least in part by the ability of the teams to overcome rotational forces; in other words, the pieces do not swing away from the center line as if carried by a single ant. Cooperating individuals can support an object so that these forces are balanced and diminished.

A wholly different niche has been opened by several ant clades through the invention of new kinds of high arboreal nests. Nest sites are relatively scarce in the tropical forest canopy. Most ant species living there depend on preformed cavities in twigs and branches, especially those excavated by beetle larvae and other wood-boring insects, and space among the roots and leaf axils of epiphytes. Bigger ants, with body lengths of 5 mm or more, have an especially difficult time finding preexisting cavities large enough to accommodate them. Weaver ants of the genus *Oecophylla*, comprising two species found in tropical Africa and Asia to Australia respectively, have solved the problem by constructing their own large nests out of leaves, twigs, and larval silk. This operation, one of the most intricate in the animal kingdom, has been described by Hölldobler and Wilson (1990) as follows:

> Individual workers explore promising sites within the colony's territory, pulling at the edges and tips of leaves. When a worker succeeds in turning a portion of a leaf back on itself, or in drawing one leaf edge toward another, other workers in the vicinity join the effort. They line up in a row and pull together, or, in cases where a gap longer than an ant's body remains to be closed, they form a living chain by seizing one another's petiole (or "waist") and pulling as a single unit. Often rows of chains are aligned so as to exert a powerful combined force. The formation of such chains of ants to move objects required intricate maneuvering and a high degree of coordination. So far as we know, the process is unique among the social insects. When the leaves have been maneuvered into a tent-like configuration, workers form rows and hold the leaves together. Another group of workers carries larvae from the interior of the existing nests and uses them as sources of silk to bind the leaves together. . . . The worker holds the larva in her mandibles between one-fourth and one-third of the way down the larva's body from the head, so that the head projects well out in front of the worker's mandibles. The larva keeps its body

stiff, forming a straight line when viewed from above but a slightly curved, S-shaped line when seen from the side, with its head pointing obliquely downward. Occasionally the larva extends its head for a very short distance when it is brought near the leaf surface, giving the impression that it is orienting itself more precisely at the instant before it releases the silk.

Weaving countless silk threads day by day, the *Oecophylla* colonies build large pavilions throughout their territories. With their large individual size and ability to erect nests almost anywhere, they have achieved a close control of their tree-top environment. Each mature colony, containing a single queen and hundreds of thousands of workers, extends throughout the canopies of one to several trees. The ants are extremely aggressive and drive off or eat all but a small number of insect species.

Two weaver ants in the genus *Camponotus* have the same habits except that they lack the ability to form chains and pull leaves together. Occurring in the forests of Central and South America, they are far less abundant than *Oecophylla* in the Old World tropics. Instead, the dominant ants in the canopy are often the inhabitants of ant gardens, which represent an equally ingenious invention. These structures, as noted earlier, are aggregates of epiphytes assembled by ants. Foraging workers carry the seeds of the epiphytes into foundation nests made of carton. As the plants grow, nourished by the carton and detritus brought home by the ants, their roots become part of the framework of the nests. The ants also feed on the fruit pulp, the elaiosomes (food bodies) of the seeds, and the secretions of the extrafloral nectaries. The ants construct irregular nest chambers divided by carton walls among their roots. The garden plants are specialized species belonging to at least 16 genera in the families Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Moraceae, Piperaceae, and Solanaceae, with the piperaceous *Peperomia macrostachya* as the principal element. The dominant ants in South America, which are also among the most abundant ants of the canopy generally, are *Camponotus femoratus* and two or more species in the *Crematogaster parabiotica* complex. These species typically live together in close symbiotic relationship in the same gardens.

A colony of eusocial insects is usefully conceptualized as a superorganism, because it resembles a traditional organism in several key *properties of organization. In particular, the colony members are divided into castes that specialize in labor roles, they integrate their activities through intricate communication systems, and they are directed toward the principal goal of rearing new reproductive forms. For the most part, the unit of selection is the colony rather than each of its individual members.*

Superorganisms are expected to manifest emergent properties beyond the capacity of organisms, and eusocial colonies possess two that confer superior competitive power. Mass communication, the first, is transmission of information among groups of individuals within the colony of a kind that cannot be exchanged between individuals alone. In such procedures as the regulation of recruitment to food and response to enemy colonies, it allows the colony as a whole to make decisions that are beyond the scope of single workers. Adaptive demography, the second emergent property, defined as the adaptive regulation of caste proportions by differential birth and mortality schedules of the separate castes (such as major and minor workers), brings the colony closer to an optimum division of labor.

The efficient systems of integration of eusocial insects, culminated by mass communication and adaptive demography, have allowed various species to penetrate wholly new adaptive niches closed to their solitary counterparts. Examples include the simultaneous monitoring of vast foraging areas (honeybees), culturing of fungi on processed fresh vegetation (leafcutter ants), the capture of unusually large and difficult prey (army ants), and the domination of arboreal habitats by construction of silken pavilions and epiphyte gardens (weaver ants and others).

VI Social Optimization

Given that colonies of eusocial insects have been the units of selection for tens of millions of generations, we should expect to find that the key organizational properties of colonies should be at or close to those providing maximum survival and reproduction. The optimum conceived in this case, as in the remainder of theoretical biology, exists within a local neighborhood of phenotypes. It is a constrained optimum. There is no evidence that any ant species has ever taken a macroevolutionary leap, such as exchanging one caste system for a radically different system, or cultivating fungi on fresh leaves, or building a silken pavilion, or any other principal organizational change, in a single step. The large number of known living and fossil species allows close species comparisons, and in case after case discloses gradual transitions from one major adaptive zone to another. The evidence suggests strongly that ant social organization has generally proceeded by small, microevolutionary steps. Ant species "feel their way" in evolution.

An example is the use of larval silk in the communal weaving of arboreal nests, which reaches its apogee in species of *Oecophylla*. Here in briefest form are the differing degrees of complexity among living species of formicine ants likely to represent the steps that led to the *Oecophylla* state (Hölldobler and Wilson, 1983):

(1) The larvae spin their personal cocoons in typical fashion, except that they also lay some strands onto the floor of the carton nest, thus strengthening it (species of the Neotropical genus *Dendromyrmex*).

(2) Workers pick up the larvae and hold them in position while the larvae turn their heads back and forth to apply silken threads to the nest; the larvae still spin personal cocoons (the Neotropical species *Camponotus senex*).

(3) Workers and larvae behave as in (2) except that the larvae no longer spin cocoons (many species of the Old World genus *Polyrhachis*).

(4) Workers hold the larvae, which are anatomically modified for their communal role, and move them back and forth during the release of the silk; the larvae do not perform weaving movements nor do they spin cocoons (the Old World tropical genus *Oecophylla*). The evidence from such species comparisons does not entirely eliminate the possibility that *Oecophylla* evolved from an ordinary ant to an extreme weaver in one leap but it makes such a jump far less plausible and certainly unnecessary in any phylogenetic scheme. In the absence of evidence to the contrary, gradual microevolutionary change is the more parsimonious, logical inference.

Optimization, then, is not global nor does it proceed to extrema. Instead, it is local, and often very local. The most realistic procedure in assessing optimization is therefore to examine alternative caste ratios, patterns of division of labor, nest structures, and other limited domains through which species are moving by microevolution. Relatively few attempts have been made at this mode of analysis, but the results clearly justify the hypothesis of adaptation resulting in settlement near local optima, with the occasional movement to other optima.

Caste Ratios in Leafcutter Ants

In my introduction to adaptive demography in Chapter V, I showed how queens and workers of the leafcutter genus *Atta* regulate the size-frequency distributions of young colonies so as to achieve the exact minimum coverage of necessary tasks in fungus cultivation with a simultaneous spread of resources to create at least approximately the largest possible number of workers. In order to achieve this effect in the youngest colonies, it is necessary for the actual leafcutter caste, the one that goes out of the nest and harvests fresh vegetation, to have a head width of 1.6 mm, no more and no less. As colonies grow, however, leafcutting is taken over by larger workers, with head widths 1.8 to 2.8 mm and especially those with head widths 2.0 to 2.2 mm. Why does the colony commit this particular size cohort and not some other? In approaching the problem, I envisioned three selection pressures that could be posed as competing hypotheses: the reduction of defense and evasion during foraging, the minimization of foraging time through skill and running velocity during foraging, and the maximization of net energetic yield (Wilson, 1980a, b).

In order to measure the performance of various size groups of *Atta sexdens* workers, I next devised the "pseudomutant" method. As workers left a laboratory nest each day to forage, I removed all but one size group. Thus one day only workers with head widths of 1.6 mm were allowed out, the next day only those with head widths of 2.0 mm got exit passes, and so on across all the size cohorts (at intervals of 0.4 mm) that normally leave the nest at all. During the experiments measurements were made of the performance of the different size cohorts in finding and cutting vegetation, their velocity in returning to the nest, their body weight, and their oxygen consumption. The pseudomutant method in effect altered the colony repetitively so that it had to respond as an entire series of mutants would, committing foragers of differing sizes instead of the usual ensemble with a peak at 2.0 to 2.2 mm head width. The method illustrates one advantage in the use of a superorganism rather than an organism in experimentation: it can be taken apart and put back together again with ease. To illustrate the advantage more clearly, suppose that we wished to test the hypothesis that the human hand is optimized for tool use. If the human body (organism) could be treated like an ant colony (superorganism), we would be able to remove one finger painlessly in the morning, test performance with a four-fingered hand through the day, and restore the missing finger in the evening; then next morning we would trim off all the terminal joints, or add a sixth finger – and so on through all desired configurations.

Using this technique, I found that the natural *Atta sexdens* foraging size group, that is the group with modal head width 2.0 to 2.2 mm, is also the one with the highest net energetic yield. The difference between the predicted and actual modal size groups specializing on leaf cutting is 10% or less of the total size range (0.8 to 5.6 mm) of the *sexdens* worker caste. More precisely, the maximally efficient group is 2.2 to 2.4 mm. A model was next constructed in which attraction and initiative of the ants were allowed to "evolve" genetically to uniform maximum levels across all the size groups, so that only mechanical properties such as cutting ability and oxygen consumption were left unaltered. The theoretical maximum efficiency levels obtained by this means were found to reside in the head-width 2.6 to 2.8 mm size class, or 8% of the actual maximally efficient class. *Atta sexdens* can therefore be said to be not only at an adaptive optimum but also, within at most a relatively narrow margin of error, to have been optimized in the course of evolution.

Number of Queens in Honeypot Ants

Experiments by Bartz and Hölldobler (1982) on the honeypot ant *Myrmecocystus mimicus* have allowed an assessment of the advantages of cooperation among queens during colony founding. In the natural Arizona environment, the most frequent group size of founding queens in newly dug burrows is 2 to 4. Under laboratory conditions, the maximum production of workers per founding queen is attained when the number of associated queens is 3, corresponding very closely to the modal group size in nature. It also turns out that the mortality rate among the founding queens is lowest when the group is 3 to 4. Hence both reproductive and survival rates are maximized at the group size actually favored by the ants themselves.

The particular selection factors that led to the association level of *Myrmecocystus mimicus* remain to be identified. They may include convex curves of efficiency in brood care, by which is meant that several queens are better able to attend a cluster of brood than a single queen, whereas a great many queens interfere with one another as the volume-to-area ratio of the brood pile reaches unwieldy levels. The selection pressures keeping the optimal group size low may also include a steadily rising frequency of egg cannibalism among competing queens, some of which has actually been observed, together with reduction of resistance to disease in the crowded brood chambers. Yet another selection factor is competition among new colonies. Bartz and Hölldobler discovered that when the first *Myrmecocystus* workers appear, they start to raid nearby incipient colonies by transporting brood to their own nests. As strength in the losing colonies wanes, workers often abandon their own mothers in favor of the raiding colonies. In 19 of 23 laboratory experiments, the winners were the ones with the largest initial worker force. Since that total number per colony (as opposed to the number per queen) is attained by 5 to 6 foundress queens, it would appear that between-colony competition alone favors the evolution of colony founding by intermediate-sized groups of queens. A closely similar result concerning multiple-queen founding was obtained independently in the fire ant *Solenopsis invicta* by Tschinkel and Howard (1983).

Multiple Nest Sites in Lasius Ants

A puzzling behavior displayed by many ant species is polydomy, the occupation of multiple nest sites. Even when just one queen is present and the ants nest in the open soil, so that space is not a problem as it is for species that nest in small twigs or soil beneath stones, the colonies spread out through the establishment of outposts. Traniello and Levings (1986) found that in *Lasius neoniger*, a North American formicine ant that nests in the soil in fields, polydomy allows the colony to approach maximum foraging efficiency. During the early and middle summer, workers construct increasing numbers of little crater nests, which expands the foraging area of the colony as a whole. At the study site used by Traniello and Levings, the nests were more uniformly distributed than they would have been had chance alone dictated their distribution. Workers emerging from a given nest entrance were most successful at retrieving prey items over distances of less than 20 cm. The average distance between nest entrances was 38 cm, that is, about twice the most effective foraging range. In other words, the nests were spaced in a manner close to optimal for foraging efficiency. In late summer, as the season drew to a close, the number of nests declined and the colony contracted toward a central core.

The Discretization of Labor Assignments

As minor workers of the ant *Pheidole dentata* age, their repertory changes in a discretized manner. As shown in Figures 10 and 15, virtually all of the 26 behavioral acts recorded in the caste under laboratory conditions can be divided according to three age periods within which the acts are performed approximately in concert. During the first nine days of adult life, after the worker has eclosed from the pupa as a six-legged insect, she attends the mother queen and cares for the eggs, smallest larvae, and pupae. For the next week she concentrates on the care of larger larvae. Then she switches dramatically to a complex set of mostly outside activities, which she continues for the remainder of her life: excavating the nest, guarding the nest entrance and food sites, and foraging. The tasks within each of these three sets have only one thing in common that also distinguishes them from the other sets. No matter how different they are from one another in the

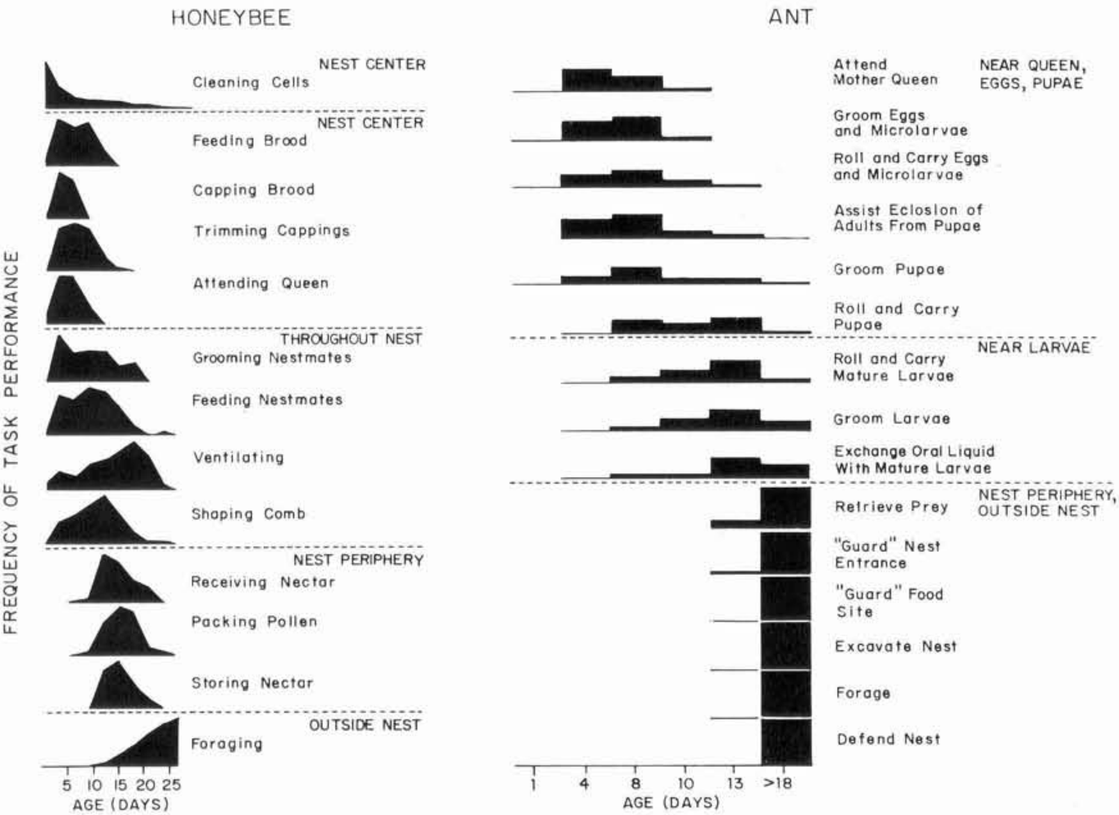

Fig. 15. A discretization of labor occurs during aging in workers of the honeybee *Apis mellifera* and ant *Pheidole dentata*: the insects shift from one linked set of tasks to another as they age and move their activities outward from the nest center. The similarities between the two species are evolutionarily convergent and believed to be adaptive. From Wilson (1985a, copyright 1985 by the American Association for the Advancement of Science), modified from Wilson (1976b) and Seeley (1982).

behavior performed and the function served, they are close together in space. Attending to all as a set minimizes the energy and time spent in travel. For example, eggs and pupae are kept close to the queen, so that the mean distance between the three objects is less than, say, between the queen and the large larvae. A closely similar discretized sequence occurs in the honeybee *Apis mellifera* (Seeley, 1982). The similarities between the two patterns can only be due to convergent evolution, since ants and bees arose during late Mesozoic times from widely different stocks of aculeate wasps.

Size Matching Within Bee Colonies

Waddington (1988) reasoned that in honeybees, a colony's yield from food sources should increase to the extent that the foragers are similar in size. The reason is the enhancement of precision during communication. From the viewpoint of a very small bee, a very large bee is likely to give poor information on the distance and quality of a patch of flowers to a very small bee. The reason is that the profit in energy yielded from each visit of a particular bee depends on the kind of flowers the bee will encounter and the energy it must expend to reach its goal, both variables dependent on its body size.

The inference is supported by the fact that size variance within colonies of honeybees and stingless bees is less than within colonies of bumblebees and halictid sweat bees. Workers of the first two groups recruit nestmates to food sources, while those of the last two groups do not recruit. Also, among the species of stingless bees, composing the apid tribe Meliponini, the size variance decreases as the complexity of recruitment communication increases. Waddington further discovered that within single honeybee colonies the rate of nectar flow increases as worker size variance decreases. This correlation exists even though workers tend to follow and receive signals from nestmates closer to themselves in size. In other words, the variance between honeybee dancers and followers is less than the variance of the worker population as a whole.

The evidence for colony-level selection provided by such optimization studies of bee communication and other key social phenomena reinforces the conclusion that eusocial insect colonies face their competitors and penetrate new niches as superorganisms. In effect, solitary insects and other small organisms are forced to compete with relatively gigantic "insects" possessed of thousands of antennae, legs, and mandibles, well integrated in movement hour by hour, and able to control large areas of terrain at near-optimum levels.

An expected consequence of natural selection at the colony level is the local optimization of colony-level traits. When tested by field and laboratory studies in various aspects of foraging, colony founding, division of labor, and communication, this inference has received substantial support.

VII Competition and Community Organization

Species belonging to the same community are said to be organized when the species interact in such a way as to make certain subsets more frequent than expected from chance alone. In Elton's terms (1933), the community has "limited membership." At the outset only some of the species in the surrounding pool have the dispersal ability to reach the habitat, so that admission is restricted. And of those that colonize, some fit in less well and pass into extinction sooner, making expulsion from membership discriminatory. Although studies in the behavioral ecology of ants are still in an early stage, it has become clear that the overwhelming abundance of these insects has made competition a hallmark of their existence. They possess some novel features of community organization as well as a startling variety of social mechanisms that adjust species to one another and hence contribute to organization.

Competition and Species Hierarchies

For more than twenty years interference competition and dominance hierarchies have been known to play key roles in the organization of ant communities (Brian, 1965, 1983; Wilson, 1971; Hölldobler and Wilson, 1990). In their treatment of northern European ants, for example, Vepsäläinen and Pisarski (1982) derived a useful three-tiered classification from general winners at the top to general losers at the bottom. On the Tvärminne Archipelago off the Finnish Baltic coast, the hierarchy is as follows:

(I) The lowest level comprises species that defend only their nests, e.g., *Formica fusca* and three species of *Leptothorax*.

(II) At the intermediate level, species defend their nests and food finds; examples include *Tetramorium caespitum, Camponotus herculeanus*, and small colonies of *Lasius niger*.

(III) At the top level species successfully defend their nests and all of their foraging areas as absolute territories. These are the "large-scale conquerors" recognized in a separate study by Rosengren and Pamilo (1983), and include *Formica aquilonia* and *F. polyctena.*

Intermediate (Level II) species are often extirpated entirely from the extensive domains of colonies belonging to Level III. On the other hand colonies of Level I species, which fight with alien workers only in the immediate vicinity of their own nests, are able to survive better in the presence of the dominants. Since the dominants patrol large foraging areas, extending as far as 100 m from the nests, local faunas are often profoundly influenced by relatively few colonies. Entire communities can be closed against some species. *Formica rufibarbis*, for example, is absent from the Tvärminne Archipelago, evidently because its favored habitat, open dry pine forests, is preempted by the dominant competitor *F. sanguinea*. As Vepsäläinen and his co-workers have demonstrated (see also, for example, Savolainen and Vepsäläinen, 1988), it is possible to translate from dominance orders among competing worker ants at food baits upward to local faunal lists. Thus the workers of *Formica fusca* are adept at finding new food but abandon it when confronted by more aggressive ant species; and the density of their colonies is depressed within the foraging ranges of the dominant ants.

As one proceeds from small to large islands in various archipelagoes around the world, the number of ant species increases roughly as the logarithm of the island area, more precisely as some value between the fifth to third root of the area (Wilson and Taylor, 1967). It is further true that the growing assemblages tend to form nested sets. On extremely small islands only species A-C might be present, on somewhat larger islands A-F, on still larger islands A-H, and so on. The sequence is seldom if ever of the form A-C, D-I, K-X, and so forth. This regularity, which is far from perfect and evidently subject to considerable stochasticity, reflects the fact that larger islands offer a greater array of microhabitats in which specialized ant species can settle. But it is also likely to be shaped in part by the kind of rank-ordering and preemption illustrated in the Finnish studies. The nested-set phenomenon is unusually clear-cut in very small mangrove islands in the Florida Keys, as shown by Cole (1983). The five species of arboreal ants normally occurring on the islets accumulate in a regular manner as the volume of foliage increases from one island to the next. Each species has a minimum island volume it requires for indefinite survival, which for some species at least is the amount of plant surface needed to protect the colony from lethal wind and wave action. Two species, *Crematogaster ashmeadi* and *Xenomyrmex floridanus*, are dominant. When a colony of either one is established first, it precludes the colonization of the second. When one of these two species is present on islands with volumes of less than 5 m^3, it also precludes an invasion by a colony of the other three species. Workers of the two dominant species are consistently aggressive toward workers of all other species, while those of the subordinate species (*Camponotus* sp., *Pseudomyrmex elongatus*, and *Zacryptocerus varians*) almost invariably run from the dominant workers. When Cole removed dominant species from islands less than 5 m^3 in volume, the subordinate species were able to invade the trees and persist indefinitely.

Dominance hierarchies among ant species are a worldwide phenomenon. In the arid and semi-arid regions of Australia, the dominant species belong to the genus *Iridomyrmex*, including the large meat ants and many other species with smaller workers (Andersen, 1986). Most are diurnal and tend to displace one another, so as to form interspecific mosaic distributions on the ground. *Camponotus* species are subordinate, such that their workers usually forage at night and run when contact is made with the *Iridomyrmex*. Species of *Melophorus*, on the other hand, tend to be specialized for foraging in places and at times of day too hot for the *Iridomyrmex*. In the canopies of African forests, the dominant species also displace one another, forming what Dennis Leston and others have called "ant mosaics" (Room, 1971; Leston, 1973; Majer, 1976). Each dominant is the center of a positive association of particular species of other insects, including non-dominant ants, as well as spiders, and a negative association – that is, reduced abundance or absence – of other such species. The dominance order identified by Majer was successively, *Oecophylla longinoda, Crematogaster striatula, C. depressa,* and *Tetramorium (= Macromischoides) aculeatus*. He proved competitive displacement by removing colonies of some of the dominants and watching the competitor species move in along with their favored ant and other arthropod associates. Similar shifts have been observed in other, nonmanipulated ant communities in Australia and the Solomon Islands (Greenslade, 1971, Fox and Fox, 1982).

The Dominance-Impoverishment Rule

Hölldobler and Wilson (1990) noticed what appears to be a worldwide 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.* The relation holds in the relatively species-poor canopies of Africa (Room, 1971; Leston, 1973), Australia (Hölldobler, 1983), and the Solomon Islands (Greenslade, 1971); the boreal faunas of northern Europe (Vepsäläinen and Pisarski, 1982); the mangrove islets of the Florida Keys (Cole, 1983); the small islands of the West Indies (Levins et al., 1973); and some of arid and semiarid as opposed to mesic environments of Australia (Greenslade, 1976; Greenslade and Halliday, 1983; Andersen, 1986). It is not true of at least some surface-dwelling communities of Australia. Alan N. Andersen (personal communication), for example, observed domination by *Iridomyrmex* species in a 24 × 18 m plot at Kakadu, Northern Territory, in which 112 ant species were recorded.

What is cause and what is effect in this rule, assuming that it will be sustained by further censusing? Are some ant faunas impoverished because of the suppressing effect of the "large scale conquerors," or have the large scale conquerors originated in environments that already had impoverished ant faunas? At first it might seem that the first alternative is the more likely, because the dominant species have been repeatedly shown to reduce species diversity and abundance within the individual colony territories. When the populations of colonies of such species are dense, the effect can be widespread or even total throughout a habitat. However, initial intuition appears to be wrong in this case. Hölldobler and Wilson concluded that the opposite is true, that impoverished faunas promote dominant species. Their reasoning is as follows. If the appearance of dominant species were to impoverish faunas (the first alternative), the loss should occur only in alpha diversity, that is, the number of species found in the particular habitat sites where dominant species are present, and it should not occur in beta diversity, the number of species occurring across many habitat sites with and without dominants. Put another way, the faunas of whole regions and habitats in which dominants prevail should be rich even though the local, individual sites in which they occur are poor. But this usually appears not to be the case. In some instances the dominants occur in regions where the faunas as a whole are small, such as boreal Europe and small tropical islands. Elsewhere they typically occur in major habitat types with few species relative to nearby habitat types. For example, arboreal ant faunas in tropical forests are generally much less diverse than the terrestrial faunas just beneath them; and they are also the ones dominated by species with large aggressive colonies and absolute territories. Diversity is low even in trees lacking dominant species. This appears particularly to be true in West African forests, which were hard hit during the Pleistocene dry periods (Carroll, 1979). Finally, the difference exists even though the leaves and branches on which the arboreal ants live are the same geological age as the litter and humus of the terrestrial zone.

Thus the primary causal chain is from impoverishment to dominance rather than from dominance to impoverishment. Some habitats have relatively few species because they are physiologically harsh and offer a limited number of niches in the form of nest sites and food items. The opportunity exists in such places for a few other, generalist species to expand ecologically and to exploit a variety of such nest sites and food items, taking over from specialists unable to make a living in such stringent circumstances. They will tend to evolve a large colony size as well as behavioral mechanisms, such as absolute territories, insuring control of the larger, eclectic set of niches into which they have moved.

Active Species Displacement

Interference competition sometimes results in the displacement of foraging activity of one or more species to different times of the day. In Australia, *Iridomyrmex purpureus* and *Camponotus consobrinus* utilize the same food sources, and they often nest in close association. The *Iridomyrmex* forage mostly during the day and the *Camponotus* mostly at night, with the two species replacing each other at particular homopteran aggregations and other persistent food sources. Where either of the species occurs alone, its foraging period is usually longer by one or two hours. And where the *Iridomyrmex* and *Camponotus* occur together, they shorten each other's foraging period by direct interference. In the morning *Iridomyrmex purpureus* workers gather around the nest exits of *Camponotus consobrinus* and close them with pebbles and clumps of soil. At dusk the situation is reversed: the

Camponotus gather to prevent the *Iridomyrmex* from leaving the nest (Hölldobler, 1986b). In Costa Rica, Swain (1977) observed that workers of the dolichoderine *Monacis bispinosus* ceased tending scale insects at night when large workers of a *Camponotus* species appeared. In an attempt to recreate the displacement experimentally, he lured *Monacis* workers to a sugar bait in a nearby site. At first, the *Monacis* workers continued feeding after dusk, the normal activity of the species in other localities. But as soon as *Camponotus* workers found the new bait, the *Monacis* retreated. Those who hesitated were attacked and killed. A diel displacement of the kind originally observed was quickly established.

The retreat of subordinate species before dominant ones in the boreal and African species hierarchies has also been documented. In the Siberian steppes, colonies of *Formica subpilosa* are usually most active during midafternoon. However, in the presence of *Formica pratensis* they shift the peak of their activities to the evening. Stebaev and Reznikova (1972) were able to induce the change by moving nests of *F. pratensis* to the vicinity of those of *F. subpilosa*. In forests of Ghana the arboreal myrmicine *Tetramorium aculeatus* has been observed to space out its foraging time and to become more nocturnal in the immediate presence of the dominant *Crematogaster clariventris* and *Oecophylla longinoda* (Leston, 1973; Majer, 1976).

Enemy Specification

Given the widespread occurrence of ecological displacement and exclusion by direct behavioral interference in ants, how do the interacting species fit together to build organized communities? It is not surprising to find that ants have evolved mechanisms of social behavior to identify and confound their most dangerous adversaries. This phenomenon of "enemy specification" was first noted in *Pheidole dentata*, a small myrmicine ant abundant in woodland over most of the southern United States (Wilson, 1976a). The dominant native fire ant *Solenopsis geminata* occurs in many of the same habitats and to some extent utilizes the same nest sites as *P. dentata*. It forms large and aggressive colonies that are strongly territorial. Fire ant scouts recruit masses of workers to food sites. They also treat *P. dentata* as food and are able to destroy a colony within an hour. The *Pheidole* can avoid this fate by intercepting the scouts before the *Solenopsis* are able to mount an invasion. The *Pheidole* minor workers respond to the presence of as few as one or two *Solenopsis*. Within seconds, some of them start to run swiftly back and forth to the nest, dragging the tips of their abdomens over the ground. The trail pheromone thus deposited attracts major workers ("soldiers") from the nest in the direction of the invaders. Upon arriving at the battle scene these specialized individuals become even more excited, rushing about and snapping at the fire ants with their powerful mandibles and chopping them to pieces. In this manner the *Pheidole* are able to "blind" colonies of fire ants by destroying the scouts before their opponents can report back to their own nest. As a consequence they are able to insinuate themselves into the otherwise absolute territories of the fire ants. The *Pheidole* do not react to other potential adversaries in the same way. Ants of a wide variety of species in other ant genera that have been tested proved neutral or required a large number of workers to induce the response. Recently, enemy specification to *Solenopsis* has been discovered in other species of *Pheidole* (Feener, 1987).

Enemy specification appears to be a widespread phenomenon in ants. At the Shimba Hills in Kenya, for example, only a few ant species coexist with *Oecophylla longinoda* on the same tree. Some of these, including a large species of *Polyrhachis*, are occasionally hunted and attacked by the weaver ants. Others, including a common *Camponotus* of the region, are never found on the same trees. When *Camponotus* workers are placed in an *Oecophylla* territory, the weaver ants react by recruiting masses of defending workers. Still other ants are treated indifferently and are able to coexist with the weaver ants. Because weaver ants are abundant over large stretches of terrain, this differential treatment has a profound effect on the distribution of the ant fauna (Hölldobler, 1979, 1983).

Enemy specification may prove to be a key process in the organization of communities of ant species. On the one hand it provides the means whereby a vulnerable species can live alongside a dominant one, in the way *Pheidole dentata* manages to coexist with the *Solenopsis* fire ants. Alternatively, it can lead to the opposite effect by excluding one species from within the territories of other species, thereby sharpening the patterns of the ant mosaics. A case of this second effect is provided by *Oecophylla longinoda* and its co-dominants.

Competition in Other Social Insects

Comparatively few studies have been conducted on competition in eusocial insects other than ants, but they suggest that aggressive, even lethal interactions play an important role. Combat among termite colonies of the same species has been observed on repeated occasions. Pickens (1934) observed that workers of *Reticulitermes hesperus* attack and kill founding pairs and incipient colonies of the same species that settle close to their nests. Thorne (1982) suspended three nests of the arboreal *Nasutitermes corniger* close to one another and observed colonial wars of relentless ferocity:

> As they reached the ground groups fanned out: termites from a single colony divided into several ribbons heading in different directions. Because of the close proximity of the ramp exits, it was inevitable that encounters occur between trails from different colonies. The meetings were not passive. Soldiers oriented towards (and apparently squirted) termites from other colonies, but this did not seem much of a deterrent to recipients. The major defense stemmed not from the soldiers, but from the *Nasutitermes* workers. Workers from different colonies grabbed each other with their mandibles and locked in one-on-one conflict. Pairs of termites squirmed and bent with vigor, often until the death of both. Occasionally a third or fourth worker would join the engagement, but usually only temporarily. Workers avidly attacked soldiers as well, grabbing at the legs and occasionally biting the abdomen. The next morning worker carcasses littered the arena over an area of approximately 1,500 cm^2, with some battle "patches" as far as 1.5 m from the center of the ramp triangle. The density of bodies was often quite high (25 to 50 dead in a 4.0 cm^2 area). Surviving termites did not appear to cannibalize the dead. Ants, flies, staphylinid beetles, and wasps began scavenging the termite carcasses.

In addition, the *Nasutitermes* were observed to adjust their foraging trails so as to avoid those of hostile colonies. When scouts encountered alien workers, they changed direction. In Thorne's experiment none of the trails of any colony crossed that of another, even though together they spanned half or more of the compass around the cluster of three nests.

Aggression among colonies of termites is probably a general phenomenon. In laboratory experiments that brought alien workers into contact, Thorne tested the responses within and between species of *Nasutitermes, Amitermes,* and *Armitermes.* All interspecific encounters resulted in fighting, with certain species tending to dominate others. Aggression among colonies belonging to the same species was also general but varied in intensity according to species.

Competition and local species displacement also occur widely among social bees. Workers of *Trigona* stingless bees use various strategies to avoid or defeat members of other species at flowers, resin patches, and other resource sites. According to species, they either avoid such enemies, use rapid recruitment to arrive at the sites first, confront them in combat, or habitually arrive late and glean the leftovers (Johnson, 1983). Competitive displacement among species of the honeybee genus *Apis* and between *Apis* and *Trigona* occurs in Asia and South America, entailing both aggressive interactions at food sites and differences in foraging ability (Roubik, 1982; Brian, 1983).

The Impact on Other Organisms

Competitive exclusion and other organizational processes at the community level in social insects have a profound effect on the distribution and abundance of other kinds of terrestrial organisms. Dominant ant species influence which nest sites receive the most detritus, which seeds are transported, which plants are protected, which prey are targeted, which predators are fed, and which insects are tolerated or (in the case of honeydew-producing homopterans and lycaenid caterpillars) which are cultivated.

In extreme cases, the intrusion of a single highly competitive species can alter the entire ecosystem. In South Africa, for example, the notorious Argentine ant *Iridomyrmex humilis* has invaded a portion of the fynbos, a local form of scrubland. This unusual habitat possesses one of the largest number of endemic plants found anywhere in the world. Hundreds of the species produce elaiosomes, appendages of the seeds that are attractive to ants and serve as food for them. After the ants have stripped off the elaiosomes, they discard the seeds, which are capable of germinating. Frequently, the ants carry the seeds into their underground nests before removing the elaiosomes. Thus the plants are dependent on the ants for their dispersal and interment in the soil. *Iridomyrmex humilis*, a dominant species of South American origin, has replaced the native ants where it has invaded the fynbos of the Kogelberg State Forest. In field tests Bond and Slingsby (1984) found that the *Iridomyrmex* are much slower than the native ants in removing seeds of the proteaceous *Mimetes cucullatus*, a representative elaiosome-bearing species of the fynbos. The *Iridomyrmex* also move the seeds shorter distances and leave them on the soil surface more often, where they are quickly eaten by invertebrate and small vertebrate granivores. In one trial 35% of the *Memetes* seeds disseminated from depots germinated in *Iridomyrmex*-free sites, but fewer than 1% germinated in a nearby infested site. It is quite likely that the *Iridomyrmex* will alter the composition of the fynbos species and may even cause the total extinction of some of the most vulnerable species.

Competition within and among species is the hallmark of social insect ecology. Species hierarchies based partly on competitive exclusion are a commonplace in ant communities. Many species adjust to one another by displacement in the times they forage during the 24-hour cycle, and by enemy specification, a disproportionately strong social response to species that are major enemies. The overall result is some degree of community organization. The overwhelming abundance and active community organization of social insects, especially ants, has an important effect on the distribution and abundance of other terrestrial organisms.

VIII Hawaii: A World Without Social Insects

In order to assess the impact of a dominant group of organisms, it would be extremely useful to have biotas free of the dominant group that can serve as evolutionary controls. This baseline is not easily found, because dominant groups are also as a rule very geographically widespread. The eusocial insects in particular have almost completely filled the terrestrial world. But there is one place to look. They did not, prior to the coming of man, inhabit the easternmost archipelagoes of the Pacific. In particular, they did not reach Hawaii. This most isolated of all archipelagoes evolved a rich endemic fauna and flora in the absence of termites, ants, and eusocial bees and wasps (Zimmerman, 1948; Wilson and Taylor, 1967; Williamson, 1981).

The massive weight of the social insects was therefore lifted from the plants and animals that departed from their midst and colonized Hawaii. Insects and other arthropods were freed from predation by ants and social wasps. Conversely, predators and scavengers did not have to compete with ants and social wasps; and invertebrate decomposers of wood did not have to contend with termites in the rotting logs and stumps. On the negative side, plants were deprived of the protection of ants and the pollination services of social bees.

How did the Hawaiian biota respond to this release? Unfortunately, we cannot directly read off the results, because there is an additional force working in Hawaii that is easily conflated with the absence of social insects: the disharmonic nature of the biota as a whole. The Hawaiian biota, as expected from its extreme remoteness, has evolved from a limited number of stocks, which have radiated extensively thereafter. By 1980, 6500 endemic insect species had been described, and these are believed to have evolved from about 250 original immigrant species (Williamson, 1981). A typical case is the oecanthine tree crickets, comprising 3 genera and 54 species, or 43% of the entire known oecanthine fauna of the world, all derived from a single species that colonized the islands no more than 2.5 million years ago (Otte, 1989). Disharmony of this kind means that not just social insects but many other major stocks of invertebrates are absent in the native fauna. Their absence as predators, herbivores, and decomposers must also be taken into account when assessing the histories of the sweepstakes winners.

The problem, while not readily soluble, is nevertheless tractable. Given the great ecological importance of social insects and the general significance of dominance in community evolution, the Hawaiian biota deserves a new look with social insects in mind. It is entirely possible that certain traits of the Hawaiian fauna usually ascribed to disharmony and reduced dispersal opportunity, such as extreme local abundance and flightlessness, are due at least in part to the lack of pressure from social insects, especially ants. What I offer now as a first analysis is a set of properties of biotas expected from the absence of social insects, without the attempt (or even the capacity, given the present scarcity of ecological knowledge) of disentangling the effects from those due to the absence of other, ecologically equivalent invertebrate groups as a reflection of disharmony in the fauna.

Scale insects and other honeydew-producing insects protected by ants elsewhere will be scarcer relative to related groups. This prediction is confirmed but vitiated by the disharmonic nature of the fauna. There are no native coccids, fulgorids, or aphids, among the groups most avidly attended by ants elsewhere. Their absence could be ascribed either to the absence of ant protectors or bad luck in the dispersal sweepstakes. The latter hypothesis seems somewhat less likely in view of the fact that aphids are excellent dispersers. There is only one butterfly species belonging to the Lycaenidae, a family whose caterpillars are heavily attended by ants, but the native butterfly fauna of Hawaii is, inexplicably, very small overall. Mealybugs (Pseudococcidae), also much favored by ants, are represented by 3 endemic genera and 14 species, but are heavily outweighed in diversity by the homopterous families Cixiidae, Delphacidae, and Psyllidae, which are not attended by ants (Zimmerman, 1948).

Both herbivores and predaceous insects will occur in denser, less protected populations. This prediction is dramatically confirmed. A very high percentage of the endemic insect species are flightless, and also generally "sluggish," to use Perkins' (1913) term, with populations persisting on the same tree or bush for years. Otte (personal communication) has referred to the conspicuous abundance of endemic crickets and their "lackadaisical" behavior. Many of the species walk about in the open where they can be easily picked up with the fingers, in sharp contrast to the cryptic, fast-moving species that occur in other faunas. Caterpillars such as those of the pyraustid moth genera *Margaronia* and *Omiodes*, the extremely diverse drosophilid flies, and a few other dominant groups are comparably abundant and accessible, or at least were so in the last century in the less disturbed habitats. These are the kinds of insects most vulnerable to ant predation. No fewer than 36 ant species have been introduced by man, including the notorious omnivore and pest species *Pheidole megacephala*. The widespread destruction of native Hawaiian insects by ants is well known. Zimmerman (1948) states that "the introduction of a single species of ant, the voracious *Pheidole megacephala*, alone has accounted for untold slaughter. One can find few endemic insects within that scourge of native insect life. It is almost ubiquitous from the seashore to the beginnings of damp forest." Otte has observed the same displacement in the case of native crickets on Hawaii and the Society Islands, which also lacked ants before they were introduced by human commerce. There are other major causes of extinction of Hawaiian native insects, including habitat destruction and the incursion of alien parasites and diseases. But the important point with reference to the question of social insect dominance is the documented extreme vulnerability of the native insects to introduced ants in both disturbed and undisturbed habitats, which is consistent with observations in other parts of the world where ants are native. (Ants may also have played a key role in the retreat of the rich and abundant Hawaiian land snail fauna, comprising over a thousand species, although I am not aware of studies addressing this possibility.) The converse conclusion is equally important: the local abundance of behaviorally vulnerable, epigaeic insects is consistent with the absence of native ants, whether or not it explains the phenomenon entirely.

The non-formicid predators in the mesofauna (0.2 to 2.0 mm body length range), especially carabid beetles and spiders, should be more diverse and abundant. Also, predators should have evolved in mesofaunal arthropod groups that are not predaceous in other parts of the world. I call attention here especially to carabid beetles and spiders, because it is my experience in many other parts of the world that large numbers of species belonging to these two predatory groups have similar microhabitat preferences to ants. They occur abundantly in the litter and soil and especially under rocks not yet colonized by ants. In the summit forest of Mt. Mitchell in North Carolina, USA, where ants are very scarce, I found carabids and spiders to be more abundant, or at least more conspicuous, than at lower elevations. Darlington (1971) and Cherix (1980) present evidence that ants generally reduce the abundance of ground-dwelling carabids and spiders in both the tropics and temperate zones, especially those species specialized to live in soil and rotting vegetation. And as expected, carabids and spiders are both very diverse and abundant in the native forests of Hawaii. Other mesofaunal predatory groups that have radiated include the nabid bugs, staphylinid beetles, dolichopodid flies, and muscid flies of the genus *Lispocephala*. Groups that have moved into the ant predator zone include the geometrid moth *Eupithecia*, whose caterpillars ambush insects like praying mantises, and the damselfly *Megalagrion*, whose predator nymphs have left the aquatic environment entirely to hunt on the ground, especially under clumps of ferns. As I have stressed, these adaptive radiations and major ecological shifts may have been favored by the absence of competing predators in addition to ants, due to the general disharmonic nature of the fauna. Yet it is hard to imagine their occurring at all if a well-developed ant fauna had been present.

Non-formicid scavengers should be diverse and prominent relative to those in ecologically otherwise comparable faunas. Ants are strongly dominant as the scavengers of small arthropod corpses in most parts of the world. It is to be expected that this largely empty niche was filled by other groups on Hawaii, perhaps (at a guess) staphylinid and histerid beetles, but I know of no studies addressing the matter.

Wood borers other than termites should be very prominent. In the absence of termites, we should expect to find a greater diversity and abundance of insects that bore through dead wood, especially the softer, rotting "wet" wood favored by so many termite species elsewhere in the world. Again, studies appear not to have been directed specifically to this hypothesis. Candidate groups include beetles of the families Anobiidae, Cerambycidae, Curculionidae, Elateridae, and Eucnemidae, which have in fact radiated extensively on Hawaii.

Solitary wasps and bees should be relatively diverse and very abundant. The solitary eumenid wasp genus *Odynerus* is represented by over 100 endemic species on Hawaii and, until the last century at least, was extremely abundant. The solitary hylaeid bee genus *Hylaeus* contains at least 50 endemic species, all derived from a single ancestor. The relation of these minor evolutionary explosions to the absence of social wasps and bees is an intriguing possibility but has not yet been explored.

Extrafloral nectaries and elaiosomes will be reduced or absent in the native flora. In general, extrafloral nectaries serve to attract ants, which in turn protect the plants from herbivores. Extrafloral nectaries are substantially scarcer in the Hawaiian flora than elsewhere, in agreement with the prediction (Keeler, 1985). Eleven endemic species and 6 indigenous species do have the nectaries, which may be attended by protector arthropods other than ants or simply reflect phylogenetic inertia. Significantly, three other indigenous (but not endemic) species having extrafloral nectaries elsewhere lack them on Hawaii, again supporting the prediction. Elaiosomes are seed appendages attractive to ants that induce the ants to disperse the seeds. No study has been made to my knowledge of their relative abundance on Hawaii.

To conclude, Hawaii has long fascinated biologists for its superb adaptive radiations, and depressed conservationists for the continuing destruction of those same evolutionary wonders. I suggest that the value of the biota is enhanced still further by the realization that it is a natural laboratory, the unique site of an experimental control, for the assessment of the impact of social insects on the environment. These insects are so dominant in almost all other parts of the world that their absence in the original, native Hawaiian fauna and flora provides an exceptional opportunity to study the effects of ecological release on the part of taxa that would otherwise have interacted with them most strongly. At the very least, the absence of social insects should be taken into more explicit consideration in future studies of the biota. What is clearly needed are deeper studies of the life cycles of native Hawaiian taxa in comparison with sister taxa elsewhere, and especially on other islands with and without key elements such as social insects.

Hawaii, the most remote archipelago in the world and home of a rich endemic fauna and flora, was evidently never colonized by social insects before the coming of man. The absence of these dominant elements means that the Hawaiian native biota is a controlled experiment in which we can observe the effects of freedom from social insects, especially ants and termites. It seems probable that the circumstance was a major contributor to some of the tendencies characterizing the Hawaiian biota *as a whole, including flightlessness, lack of evasive behavior, increased abundance and diversity of carabid beetles and spiders, adaptive shift to predation in some terrestrial insect groups, and the loss of extrafloral nectaries in flowering plants.*

IX General Summary

Success is most heuristically defined as an evolutionary concept: the duration of a clade (a species and all its descendents) through geological time. Dominance on the other hand is an ecological property: the relative abundance of a clade, especially as its numbers cause it to appropriate energy, accumulate biomass, and affect the life and evolution of the remainder of the biota. Species numbers, the breadth of adaptive radiation, geographic range, and the magnitude of evolutionary innovations are enhanced by dominance, and they in turn are likely to increase success, but they nevertheless remain separate properties of clades.

The causes of success and dominance are best elucidated by detailed studies of living organisms that most strikingly display them. This is the rationale here for addressing the subject through the "eusocial" insects, which include the termites, ants, and several clades of bees and wasps. Eusociality is defined as the combination of three traits: care of young, overlap of adult generations in the same colony, and a division of labor between reproductive and nonreproductive castes.

The eusocial insects, which date from Cretaceous times, have already attained moderate longevity in comparison with sister groups. Their tenacity is further indicated by the fact that so far as known no major eusocial clade, at the rank of family or above, has ever gone extinct. Far more important, however, is the overwhelming dominance of the eusocial insects. In some habitats, especially tropical forests, they make up 30% or more of the animal biomass, and comparable figures may hold in grassland, deserts, and even some temperate forests. Ants are the major predators and scavengers in the mesofauna (0.2 to 2.0 mm body length range), while termites are the premier brokers of wood decomposition. Together the two groups turn more soil than other animals. Their impact is evident in the life cycles and behavior of many kinds of organisms. In a most general sense, ants and termites hold the central microhabitats where interference competition allows the control of stable resources, while solitary insects "fill the cracks" of less stable, accessible resources.

It is possible to identify the sources of dominance in the eusocial insects with some confidence because these insects, especially the ants and termites, are so conspicuously abundant, their abundance is manifestly tied to competitive superiority, and this superiority clearly arises from unique traits in social organization. The inferences made are strengthened by the comparison of large numbers of species of eusocial insects and nonsocial insects in sister taxa, and the direct establishment of the links between competitive superiority and social organization through field and laboratory studies.

The advantages of colonial life leading to dominance in the social insects are evidently the following: (1) series-parallel operations of multiple workers, insuring a higher percentage of success in the completion of tasks; (2) the ability to engage in more aggressive, even suicidal behavior with positive payoff in terms of inclusive fitness; (3) a superior ability to protect and bequeath resources such as nest sites and large or sustainable food sources; and (4) more efficient homeostasis and control of the nest microenvironment.

The existence of a worker caste, which is largely or entirely nonreproductive, has allowed colonies to evolve such advanced division of labor and high levels of integration as to constitute superorganisms. The small number of studies of efficiency and fitness conducted to date suggest that at least some of the colonial properties have approached evolutionarily local optima. The eusocial insect colony thus faces its competitors as a proportionately huge organism, blanketing a substantial trophophoric field with nearly continuous exploration and defense.

An ideal circumstance in the analysis of dominance by a group of organisms would be the existence of an ecosystem free of the group that could serve as a control. Hawaii is such a place, having never been colonized by eusocial insects, and its biota appears to have evolved in the direction expected in an environment free of social insects. However, this conclusion is vitiated, or at least complicated, by the generally disharmonic nature of the Hawaiian biota, so that important groups ecologically similar to eusocial insects are also missing.

References

Abe, T. 1982. Ecological role of termites in a tropical rain forest. *In* M. D. Breed, C. D. Michener, and H. E. Evans, eds., *The biology of social insects*, pp. 71–78. Westview Press, Boulder, Colo.

Abe, T. 1987. Evolution of life types in termites. *In* S. Kawano, J. H. Connell, and T. Hidaka, eds., *Evolution and coadaptation in biotic communities*, pp. 125–148. University of Tokyo Press, Tokyo.

Andersen, A. N. 1986. Patterns of ant community organization in mesic southeastern Australia. *Australian Journal of Ecology*, 11(1): 87–97.

Baroni Urbani, C., G. Josens, and G. J. Peaken. 1978. Empirical data and demographic parameters. *In* M. V. Brian, ed., *Production ecology of ants and termites*, pp. 5–44. Cambridge University Press, New York.

Bartz, S. H., and B. Hölldobler. 1982. Colony founding in *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae) and the evolution of foundress associations. *Behavioral Ecology and Sociobiology*, 10(2): 137–147.

Bond, W. J., and P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology*, 65(4): 1031–1037.

Bonner, J. T. 1988. *The evolution of complexity, by means of natural selection*. Princeton University Press, Princeton, NJ. xii + 260 pp.

Boucot, A. J. 1978. Community evolution and rates of cladogenesis. *Evolutionary Biology*, 11: 545–655.

Bourke, A. F. G. 1988. Worker reproduction in the higher eusocial Hymenoptera. *Quarterly Review of Biology*, 63(3): 291– 311.

Brandão, C. R. F., R. G. Martins-Neto, and M. A. Vulcano. 1989. The earliest known fossil ant (first southern hemisphere Mesozoic record) (Hymenoptera: Formicidae: Myrmeciinae). *Psyche*, 96(3–4): 195–208.

Brian, M. V. 1965. *Social insect populations*. Academic Press, London. vii + 135 pp.

Brian, M. V. 1983. *Social insects: ecology and behavioural biology*. Chapman and Hall, New York. x + 377 pp.

Burnham, L. 1978. Survey of social insects in the fossil record. *Psyche*, 85(1): 85–133.

Carroll, C. R. 1979. A comparative study of two ant faunas: the stem-nesting ant communities of Liberia, West Africa and Costa Rica, Central America. *American Naturalist*, 113(4): 552–561.

Cherix, D. 1980. Note preliminaire sur la structure, la phenologie et le régime alimentaire d'une super-colonie de *Formica lugubris* Zett. *Insectes Sociaux*, 27(3): 226–236.

Cherrett, J. M. 1986. History of the leaf-cutting ant problem. *In* C. S. Lofgren and R. K. Vander Meer, eds., *Fire ants and leaf-cutting ants: biology and management*, pp. 10–17. Westview Press, Boulder, Colo.

Cole, B. J. 1983. Assembly of mangrove ant communities: patterns of geographical distribution. *Journal of Animal Ecology*, 52(2): 339–347.

Darlington, P. J. 1971. The carabid beetles of New Guinea, Part IV: General considerations; analysis and history of fauna; taxonomic supplement. *Bulletin of the Museum of Comparative Zoology, Harvard University*, 142(2): 129–337.

DeVita, J. 1979. Mechanisms of interference and foraging among colonies of the harvesting ant *Pogonomyrmex californicus* in the Mojave Desert. *Ecology*, 60(4): 729–737.

Dlussky, G. M. 1983. A new family of Upper Cretaceous Hymenoptera: an "intermediate link" between the ants and the scolioids. *Paleontologischeskii Zhurnal*, 3(3): 65–78. [In Russian with English summary.]

Drummond, H. 1889. *Tropical Africa*. Scribner and Welford, New York. 228 pp.

Elton, C. S. 1933. *The ecology of animals*. Methuen, London. 97 pp.

Feener, D. H. 1987. Response of *Pheidole morrisi* to two species of enemy ants, and a general model of defense behavior in *Pheidole* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society*, 60(4): 569–575.

Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica*, 5(1): 2–14.

Fox, M. D., and B. J. Fox. 1982. Evidence for interspecific competition influencing ant species diversity in a regenerating heathland. *In* R. C. Buckley, ed., *Ant-plant interactions in Australia*, pp. 99–110. Dr. W. Junk, The Hague.

Frankel, O. H., and M. E. Soulé. 1981. *Conservation and evolution*. Cambridge University Press, New York. viii + 327 pp.

Franks, N. R. 1986. Teams in social insects: group retrieval of prey by army ants (*Eciton burchelli*, Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 18(6): 425–429.

Grassé, P.-P. 1986. *Termitologia: anatomie-physiologie-biologie-systématique des termites*, vol. 3. Masson, Paris. xii + 715 pp.

Greenslade, P. J. M. 1971. Interspecific competition and frequency changes among ants in Solomon Islands coconut plantations. *Journal of Applied Ecology*, 8(2): 323–352.

Greenslade, P. J. M. 1976. The meat ant *Iridomyrmex purpureus* (Hymenoptera: Formicidae) as a dominant member of ant communities. *Journal of the Australian Entomological Society*, 15(2): 237–240.

Greenslade, P. J. M., and R. B. Halliday. 1983. Colony dispersion and relationships of meat ants *Iridomyrmex purpureus* and allies in an arid locality in South Australia. *Insectes Sociaux*, 30(1): 82–99.

Haines, B. L. 1978. Element and energy flows through colonies of the leaf-cutting ant, *Atta colombica*, in Panama. *Biotropica*, 10(4): 270–277.

Heinrich, B. 1981. The mechanisms and energetics of honeybee swarm temperature regulation. *Journal of Experimental Biology*, 91: 25–55.

Hölldobler, B. 1979. Territories of the African weaver ant (*Oecophylla longinoda* [Latreille]): a field study. *Zeitschrift für Tierpsychologie*, 51(2): 201–213.

Hölldobler, B. 1983. Territorial behavior in the green tree ant (*Oecophylla smaragdina*). *Biotropica*, 15(4): 241–250.

Hölldobler, B. 1986a. Konkurrenzverhalten und Territorialität in Ameisenpopulationen. *In* T. Eisner, B. Hölldobler, and M. Lindauer, eds., *Chemische Ökologie,* *Territorialität, Gegenseitige Verständigung* (Information processing in animals, vol. 3), pp. 25–70. Gustav Fischer Verlag, New York.

Hölldobler, B. 1986b. Food robbing in ants, a form of interference competition. *Oecologia*, 69(1): 12–15.

Hölldobler, B., and E. O. Wilson. 1983. The evolution of communal nest-weaving in ants. *American Scientist*, 71(5): 490–499.

Hölldobler, B., and E. O. Wilson. 1986. Ecology and behavior of the cryptobiotic ant *Prionopelta amabilis* (Hymenoptera: Formicidae). *Insectes Sociaux*, 33(1): 45–58.

Hölldobler, B., and E. O. Wilson. 1990. *The ants*. Belknap Press of Harvard University Press, Cambridge, Mass. xii + 732 pp.

Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science*, 238: 360–363.

Jarzembowski, E. A. 1981. An early Cretaceous termite from southern England. *Systematic Entomology*, 6: 91–96.

Jeanne, R. L. 1972. Social biology of the Neotropical wasp *Mischocyttarus drewseni*. *Bulletin of the Museum of Comparative Zoology*, 144(3): 63–150.

Johnson, L. K. 1983. Foraging strategies and the structure of stingless bee communities in Costa Rica. *In* P. Jaisson, ed., *Social insects in the tropics*, vol. 2, pp. 31–58. Université Paris-Nord.

Keeler, K. H. 1985. Extrafloral nectaries on plants in communities without ants: Hawaii. *Oikos*, 44(3): 407–414.

Larsson, S. G. 1978. Baltic amber: a paleobiological study. *Entomonograph*, 1: 1–192.

Leston, D. 1973. Ecological consequences of the tropical ant mosaic. *Proceedings of the Seventh International Congress of the International Union for the Study of Social Insects* (London, 1973), pp. 235–242.

Levins, R., M. L. Pressick, and H. Heatwole. 1973. Coexistence patterns in insular ants. *American Scientist*, 61(4): 463–472.

Lindauer, M. 1961. *Communication among social bees*. Harvard University Press, Cambridge, Mass. ix + 143 pp.

Lüscher, M. 1961. Air conditioned termite nests. *Scientific American*, 205(1): 138–145.

Lyford, W. H. 1963. Importance of ants to brown podzolic soil genesis in New England. *Harvard Forest Paper* (Petersham, Mass.), no. 7: 1–18.

Magurran, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press. x + 179 pp.

Majer, J. D. 1976. The maintenance of the ant mosaic in Ghana cocoa farms. *Journal of Applied Ecology*, 13(1): 123–144.

Maschwitz, U., and H. Hänel. 1985. The migrating herdsman *Dolichoderus (Diabolus) cuspidatus*: an ant with a novel mode of life. *Behavioral Ecology and Sociobiology*, 17(2): 171–184.

Maschwitz, U., and E. Maschwitz. 1974. Platzende Arbeiterinnen: eine neue Art der Feindabwehr bei sozialen Hautflüglern. *Oecologia*, 14(3): 289–294.

Michener, C. D. 1974. *The social behavior of the bees: a comparative study*. Belknap Press of Harvard University Press, Cambridge, Mass. xii + 404 pp.

Michener, C. D., and D. A. Grimaldi. 1988. A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). *American Museum Novitates*, 2917: 1–10.

Morton, S. R., and A. Baynes. 1985. Small mammal assemblages in arid Australia: A reappraisal. *Australian Mammalogy*, 8(5): 159–169.

Myles, T. G. 1988. Resource inheritance in social evolution from termites to man. *In* C. N. Slobodchikoff, ed., *The ecology of social behavior*, pp. 379–423. Academic Press, New York.

Nitecki, M. H. 1988. *Evolutionary progress*. University of Chicago Press, Chicago. viii + 354 pp.

Oster, G. F., and E. O. Wilson. 1978. *Caste and ecology in the social insects*. Princeton, New Jersey. xv + 352 pp.

Otte, D. 1989. Speciation in Hawaiian crickets. *In* D. Otte and J. A. Endler, eds., *Speciation and its consequences*, pp. 482–526. Sinauer Associates, Sunderland, Mass.

Perkins, R. C. L. 1913. Introduction. *In* D. Sharp, ed., *Fauna Hawaiiensis*, vol. 1, pp. xv-ccxxviii. Cambridge University Press, Cambridge, England.

Pickens, A. L. 1934. The biology and economic significance of the western subterranean termite *Reticulitermes hesperus*. *In* C. A. Kofoid, ed., *Termites and termite control*, pp. 157–183. University of California Press, Berkeley.

Pickles, W. 1940. Fluctuations in the populations, weights and biomasses of ants at Thornhill, Yorkshire, from 1935 to 1939. *Transactions of the Royal Entomological Society of London*, 90(17): 467–485.

Pimm, W. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist*, 132(6): 758–785.

Porter, S. D., and C. D. Jorgensen. 1981. Foragers of the harvester ant, *Pogonomyrmex owyheei*: a disposable caste? *Behavioral Ecology and Sociobiology*, 9(4): 247–256.

Raignier, A., and J. Van Boven. 1955. Étude taxonomique, biologique et biométrique des *Dorylus* du sous-genre *Anomma* (Hymenoptera Formicidae). *Annales du Musée Royal du Congo Belge*, n.s. 4, Sciences Zoologiques, 2: 1–359.

Raup, D. M. 1984. Evolutionary radiations and extinction. *In* H. D. Holland and A. F. Trandell, eds., *Patterns of change in evolution*, pp. 5–14. Dahlem Konferenzen, Abakon Verlagsgesellschaft, Berlin.

Room, P. M. 1971. The relative distributions of ant species in Ghana's cocoa farms. *Journal of Animal Ecology*, 40(3): 735– 751.

Rosengren, R., and P. Pamilo. 1983. The evolution of polygyny and polydomy in mound-building *Formica* ants. *Acta Entomologica Fennica*, 42: 65–77.

Roubik, D. W. 1982. Ecological impact of Africanized honeybees on native Neotropical pollinators. *In* P. Jaisson, ed., *Social insects in the tropics*, vol. 1, pp. 233–247. Université Paris-Nord.

Savolainen, R., and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. *Oikos*, 51(2): 135–155.

Schmid-Hempel, P., and R. Schmid-Hempel. 1984. Life duration and turnover of foragers in the ant *Cataglyphis bicolor* (Hymenoptera, Formicidae). *Insectes Sociaux*, 31(4): 345–360.

Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist*, 122(2): 240–285.

Schoener, T. W. 1986. Overview: kinds of ecological communities – ecology becomes pluralist. *In* J. Diamond and T. J. Case, eds., *Community ecology*, pp. 467–479. Harper & Row, New York.

Seeley, T. D. 1982. Adaptive significance of the age polyethism schedule in honeybee colonies. *Behavioral Ecology and Sociobiology*, 11(4): 287–293.

Seeley, T. D. 1985. *Honeybee ecology: a study of adaptation in social life*. Princeton University Press, Princeton, N.J. x + 201 pp.

Sorenson, A. A., T. M. Burch, and S. B. Vinson. 1985. Control of food influx by temporal subcastes in the fire ant, *Solenopsis invicta. Behavioral Ecology and Sociobiology*, 17(3): 191–198.

Stanley, S. M. 1979. *Macroevolution: pattern and process*. W. H. Freeman and Company, San Francisco. xi + 332 pp.

Stebaev, I. V., and J. I. Reznikova. 1972. Two interaction types of ants living in steppe ecosystem in South Siberia, USSR. *Ekologia Polska*, 20(11): 103–109.

Swain, R. B. 1977. The natural history of *Monacis*, a genus of Neotropical ants (Hymenoptera: Formicidae). Ph.D. thesis, Harvard University. 258 pp.

Thorne, B. L. 1982. Termite-termite interactions: workers as an agonistic caste. *Psyche*, 89(1–2): 133–150.

Traniello, J. F. A., and S. C. Levings. 1986. Intra- and intercolony patterns of nest dispersion in the ant *Lasius neoniger*: correlations with territoriality and foraging ecology. *Oecologia*, 69(3): 413–419.

Tschinkel, W. R., and D. F. Howard. 1983. Colony founding by pleometrosis in the fire ant, *Solenopsis invicta. Behavioral Ecology and Sociobiology*, 12(2): 103–113.

Vepsäläinen, K., and B. Pisarski. 1982. Assembly of island ant communities. *Annales Zoologici Fennici*, 19(4): 327–335.

Vermeij, G. J. 1987. *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, N.J. xv + 527 pp.

Waddington, K. D. 1988. Body size, individual behavior, and social behavior in honey bees. *In* R. L. Jeanne, ed., *Interindividual behavioral variability in social insects*, pp. 385–417. Westview Press, Boulder, Colo.

Weber, N. A. 1972. *Gardening ants: the attines*. American Philosophical Society, Philadelphia. xx + 146 pp.

Williamson, M. 1981. *Island populations*. Oxford University Press, New York. xi + 286 pp.

Wilson, E. O. 1962. Chemical communication among workers of the fire ant *Solenopsis saevissima* (Fr. Smith), 1: The organization of mass-foraging; 2: An information analysis of the odour trail; 3: The experimental induction of social responses. *Animal Behaviour*, 10(1–2): 134–147, 148–158, 159–164.

Wilson, E. O. 1968a. The superorganism concept and beyond. *In* R. Chauvin and Ch. Noirot, eds., *L'Effet de Groupe chez les Animaux* (Colloque Internationaux du Centre National de la Recherche Scientifique, no. 173, Paris, 1967), pp. 27–39. Centre National de la Recherche Scientifique, Paris..

Wilson, E. O. 1968b. The ergonomics of caste in the social insects. *American Naturalist*, 102: 41–66.

Wilson, E. O. 1971. *The insect societies*. Belknap Press of Harvard University Press, Cambridge, Mass. x + 548 pp.

Wilson, E. O. 1975. *Sociobiology: the new synthesis*. Belknap Press of Harvard University Press, Cambridge, Mass. x + 698 pp.

Wilson, E. O. 1976a. The organization of colony defense in the ant *Pheidole dentata* Mayr (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 1(1): 63–81.

Wilson, E. O. 1976b. Behavioral discretization and the number of castes in an ant species. *Behavioral Ecology and Sociobiology*, 1(2): 141–154.

Wilson, E. O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*), I: The overall pattern in *A. sexdens. Behavioral Ecology and Sociobiology*, 7(2): 143–156.

Wilson, E. O. 1980. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*), II: The ergonomic optimization of leaf cutting. *Behavioral Ecology and Sociobiology*, 7(2): 157–165.

Wilson, E. O. 1983. Caste and division of labor in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*), IV: Colony ontogeny of *A. cephalotes*. *Behavioral Ecology and Sociobiology*, 14(1): 55–60.

Wilson, E. O. 1984. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 16(2): 89–98.

Wilson, E. O. 1985a. The sociogenesis of insect colonies. *Science*, 228: 1489–1495.

Wilson, E. O. 1985b. Between-caste aversion as a basis for division of labor in the ant *Pheidole pubiventris* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*, 17(1): 35–37.

Wilson, E. O. 1985c. Invasion and extinction in the West Indian ant fauna: evidence from the Dominican amber. *Science*, 229: 265–267.

Wilson, E. O. 1986. The organization of flood evacuation in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Insectes Sociaux*, 33(4): 458–459.

Wilson, E. O. 1987a. The arboreal ant fauna of Peruvian Amazon forests: A first assessment. *Biotropica*, 19(3): 245– 251.

Wilson, E. O. 1987b. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology*, 13(1): 44–53.

Wilson, E. O. 1987c. Causes of ecological success: the case of the ants. *Journal of Animal Ecology*, 56(1): 1–9.

Wilson, E. O. 1988. The diversity of life. *In* H. J. de Blij, ed., *Earth '88*, pp. 68–81. National Geographic Society, Washington, D.C.

Wilson, E. O., and W. L. Brown. 1984. Behavior of the cryptobiotic predaceous ant *Eurhopalothrix heliscata*, n. sp. (Hymenoptera: Formicidae: Basicerotini). *Insectes Sociaux*, 31(4): 408–428.

Wilson, E. O., and B. Hölldobler. 1988. Dense heterarchies and mass communication as the basis of organization in ant colonies. *Trends in Ecology & Evolution*, 3(3): 65–68.

Wilson, E. O., and R. W. Taylor. 1967. The ants of Polynesia (Hymenoptera: Formicidae). *Pacific Insects*, no. 14, 109 pp.

Wood, T. G., and W. A. Sands. 1978. The role of termites in ecosystems. *In* M. V. Brian, ed., *Production ecology of ants and termites*, pp. 245–292. Cambridge University Press, New York.

Zimmerman, E. C. 1948. *Insects of Hawaii, vol. 1: Introduction*. University of Hawaii Press, Honolulu. xvii + 206 pp.

About the Author and the Book


Edward O. Wilson

Professor Edward O. Wilson is the recipient of the ECOLOGY INSTITUTE PRIZE 1987 in Terrestrial Ecology. Chaired by Professor Sir Richard Southwood (University of Oxford, England), the ECI Jury selected Edward O. Wilson among highly qualified nominees for his professional excellence in numerous publications, especially in the fields of population biology, biogeography, sociobiology, biodiversity, and evolutionary biology. Ed Wilson was born in Birmingham, Alabama (USA) in 1929. From Junior Fellow, he progressed at Harvard University, Cambridge (USA), to the Frank B. Baird Professorship of Science, also holding the Curatorship of Entomology in the University's Museum of Comparative Zoology.

The book addresses success and dominance in ecosystems with a mastership matured over decades of devoted, critical research. Defining 'success' as evolutionary longevity of a clade (a species and its descendents), and 'dominance' as abundance of a clade controlling the appropriation of biomass and energy, Wilson exemplifies his subject by referring to eusocial insects, especially termites and ants but also bees and wasps.

About the Ecology Institute (ECI)*

ECI is an international, not-for-profit organization of research ecologists. Director and staff – 41 marine, terrestrial and limnetic ecologists of high reputation – strive to honor excellence in ecological research; to further exchange between marine, terrestrial and limnetic ecologists; and to assist in bridging the gap between ecological science and its application for the benefit of nature and human societies.

In order to achieve this, a major ECI activity is to annually select – in a rotating pattern – a marine, terrestrial, or limnetic ecologist distinguished by outstanding performance who is able and willing to author a book taking into account ECI'S aims and addressing an audience beyond narrow professional borderlines. Published by ECI in the series 'Excellence in Ecology', the book is made available world-wide at cost price; a considerable number of books are sent free of charge to libraries in Third-World Countries.

---

* Nordbünte 23, D-2124 Oldendorf/Luhe, F. R. Germany; Tel. 04132/727, Fax 04132/8883