

Parasites in Social Insects

PAUL SCHMID-HEMPEL



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Parasites in Social Insects

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Parasites in Social Insects, by Paul Schmid-Hempel

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PAUL SCHMID-HEMPEL

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Preface and Acknowledgments

Social insects have fascinated people since very early times. For example, the most famous product of bees—honey—was cherished and used in large quantities by Egyptian priests for their religious rites. Sometimes even the dead were preserved in honey (Ransome 1986). On the other hand, social insects can be destructive to the human economy, as the examples of leaf-cutter ants or termites show. The double fascination of useful products and threats persists into modern times and gives social insects a prominent role in the living world.

To biologists, social insects have been fascinating for many different reasons. Darwin stumbled over the problem of sterile individuals and the problem of how altruism may evolve. The powerful tools of kin selection theory (Hamilton 1964) have not only answered some of these questions but social insects have also become a pivotal study subject for the evolution of social behavior in general (Wilson 1975). It is all too easy to forget that several milestones in animal physiology were reached by use of social insects as the test field. We need only mention Karl von Frisch's work on color vision in the honeybee, a milestone in the field of sensory physiology. Oster and Wilson (1978) added a further item to this menu: how the organization of complex biological systems may evolve and be maintained under natural selection. Indeed, the social organization and elaborate caste structure of ants and termites have few counterparts in other organisms. An additional reason social insects are a worthwhile study subject is that many of the relevant phenomena are analogous to those seen in single organisms. For example, there is a close correspondence between selection for insect colonies to be genetically diverse in the face of parasitism and the hypotheses for the evolution of sexual reproduction in single organisms. Throughout the history of biology, social insects have therefore not only fascinated passionate observers of nature but also provided manifold stimulation for developing general concepts. A great number of excellent monographs have been devoted to these subjects (Seeley 1985; Hölldobler and Wilson 1990; Itô 1993a; Bourke and Franks 1995; Crozier and Pamilo 1996), and I refer the reader to them for further study. It is perhaps less well known that social insects, especially the honeybee and its parasites, have also played an important role in the study of insect diseases (see McCoy et al. 1988 for a review).

Unfortunately, with the flurry of studies devoted over the last two decades to the problem of social evolution, kin selection, and within-colony conflicts, the

ecology of social insects has become somewhat neglected. The importance of such studies should not be minimized by noting that our view of social insects is therefore somewhat unbalanced. We know, for example, very little about the population biology of colonies in a given area, quite in contrast to the many details of how workers develop and shift through different tasks according to age inside the colony. A brief look at the many lifestyles and diets of social insects will show that the insects' ecology is not only fascinating in its own right, but also important in any given habitat. For example, social insects are prominent and sometimes dominant members in tropical ecosystems, and they are among the few insects that have successfully expanded into arctic or other extreme habitats. So, one aim of this volume is to correct a bias that I feel unhappy about and to highlight an important element in the ecology of social insects within an evolutionary-ecological-behavioral framework.

Research over the past two decades, almost completely outside the social insects, has shown that parasites are much more important factors for the ecology and evolution of their individual hosts, and for entire host populations and communities, than was previously believed (e.g., Andersson 1994; Grenfell and Dobson 1995). The role of parasites in the ecology and evolution of birds, for example, is a very active area of contemporary research. This has led to a more systematic approach to the general question of how parasites affect their hosts, ranging from sexual selection to the problem of trade-offs in host immunocompetence. Also, the broad area of research on how parasites could maintain sexual over asexual reproduction should be viewed in this light. The role of parasites in the biology of social insects has, in contrast, never been systematically addressed and is largely unknown, with the important exceptions of social parasitism, honeybee and fire ant studies, and some additional studies during the last few years. This is somewhat surprising given the attention social insects have received in general, and given the fact that social insects are prime targets for parasites due to their abundance, family structure, and persistent colonies.

This book is an attempt to fill this gap and to summarize the existing knowledge on parasitism in social insects. For reasons just alluded to, I have excluded the social parasites in this volume. Several excellent syntheses on this subject, in addition to the monographs mentioned above, exist (e.g., Buschinger 1986; Bourke and Franks 1991). Rather, the book will concentrate on "real" parasites, that is, infectious diseases, helminths, parasitoids, and the like. It is, however, not intended to duplicate the many excellent accounts on these different groups, such as Godfray's (1994) text on parasitoids. To my disappointment, however, I typically found that social insects hardly appear in these texts, as if they might be so very different from all others and not count in our view of nature. A second goal of this book is of a more conceptual nature—to help organize the field and to identify some basic problems that need further attention.

During my preparations, I have encountered a number of typical problems. First, much of the relevant literature is very widely scattered. Some sources

from highly specialized journals or obscure technical reports have remained unavailable. The synopsis provided in appendix 2 is therefore not complete but is almost so, and should contain all of the important reports to date. Second, frustratingly few of the ideas already found in the literature and those formulated here can actually be tested rigorously. This is due to the lack of empirical studies on parasites, but also because the basic knowledge on the population ecology of social insects has barely been collected. It is therefore inevitable that the cited comparisons are very crude and often make very bold assumptions. Nobody could be more painfully aware of the shortcomings than I. However, the ground is barren and therefore such attempts seemed justifiable to me. In several instances, a comparative study provides valuable insight. I have tried to carry this out wherever possible. Due to the scattered nature of the data and the poorly resolved phylogenies of many social insect groups, there is a clear limitation to this approach. I have restricted the use of comparative studies to ants and have used the phylogenies suggested by Hölldobler and Wilson (1990) and Baroni-Urbani et al. (1992). Finally, I have used a number of more explicit theoretical considerations, albeit simple ones. These are intended as starters for the discussion and not as an exhaustive treatment of the subject. As the reader will quickly realize, most of these models can be amended with additional constraints and complications, which would have been outside the scope of this volume and would also far outstrip the available data.

Furthermore, it is not always obvious whether a particular species is a parasite at all. By definition, parasites harm their host in some way. Ideally, this is defined by a reduction of host fitness compared to the unparasitized state. In birds, for example, one can safely assume that if a parasite causes damage to the organ it resides in, then its host will also suffer a fitness loss. In social insects, this is not always so clear-cut. Since workers usually do not reproduce themselves, they can often get diseased and drop out without any noticeable effect on colony performance and reproduction. It is also possible that some parasites, although they may be detrimental to their individual host, can actually benefit the colony in other ways. Mites pose a special problem, since their effects on individual hosts and colonies are sometimes hard to gauge. Most are probably just phoretic or commensalistic. In general, I have accepted the classification of a species as a parasite if an author has reported it as such; I have, however, excluded the mites in the more general, comparative studies. Similarly, the definition of a “social insect” is not always as universally accepted as it might seem. Here, the focus is more on advanced sociality and less on communally nesting species and more primitive associations. Last but not least, the subject of this book is quite complex because it touches a large variety of issues, from kin selection theory to population genetics to immunology or epidemiology. Therefore, these subject areas will have to be briefly exposed where necessary to help the reader appreciate the arguments. I hope that I have done some justice to the pivotal ideas in these fields.

The book is organized as follows. The first chapter is devoted to a summary of some relevant biological characteristics of social insects; it is intended mainly for readers who are not so familiar with social insects. Chapter 2 summarizes the relevant natural history of the parasites that are typically found in social insects. A short overview over special characteristics and some elements of the systematics of the different groups are given to facilitate the connection to the specialized literature on the subject. Chapter 3 is a second look at the natural history. However, this time a particular but crucially important aspect is considered: how parasites enter the colony and become transmitted further. Chapter 3 therefore complements the preceding ones by classifying and discussing the various attack routes of parasites. Chapter 4 is in some sense a reconsideration of Oster and Wilson's (1978) classical treatise on caste and ecology in social insects. Here, the consequences of social organization for the parasites and, vice versa, the effects of parasites on colony organization are considered. Chapter 5 is a major section, because the genetics of host-parasite interactions comes into play. Because social insects typically live together in genetically closely related groups, it seems particularly relevant to consider how parasitism blends with the breeding strategies of the social insect host. This field is probably one of the few where current research is quite active. Chapter 6 addresses the ecological dynamics of host-parasite interactions in social insects. Frustratingly little is known on this subject. The few studies on the spread of disease within honeybee colonies cannot count, because chapter 6 is concerned with the dynamics of populations of colonies. Hence, a large part of this section will be devoted to developing some preliminary ideas and concepts. Chapter 7 takes us down to the problem of how host and parasite coevolve. This is captured in the problem of parasite virulence and host resistance. Finally, chapter 8 touches on some of the areas that consider how parasites could select for sociality and how kin recognition comes into the picture.

When I started this adventure, I expected that it would be a short exercise since little is known on the subject and no meaningful patterns would be found. Fortunately, I was wrong. It is true that the database is small and widely scattered. But there are a number of excellent studies that needed to be discussed. It is also true that no elegant, unifying concept such as kin selection or sex allocation theory is available for studying disease in social insects. Perhaps some steps have now been taken in this direction. But the book will serve its purpose if it will stimulate others to dwell into this topic and to make most of its contents eventually superfluous. There are certainly more than just a few open questions left. Social insects are a study subject that has an enormous potential to understand how parasites coevolve with their hosts. In many respects, social insect societies are also a model of social organization in living organisms in general, including our own species. Hence, it is certainly more than worthwhile to tackle questions that unite two of the most successful strategies of life: sociality and parasitism.

I am grateful to the many people who have made this book possible. Dozens of very helpful comments on single chapters or all of the manuscript were provided by Brenda Ball, Koos Boomsma, Andrew Bourke, Deborah Gordon, Jukka Jokela, Stella Koulianos, Francis Ratnieks, David Roubik, Horst Schwarz, Regula Schmid-Hempel, and an anonymous reviewer. I have not always followed their advice and so the errors and shortcomings do remain my own. My students have kept me in a constant state of creative unrest and luckily helped me to resist the fatal attraction of an everyday university routine. I gratefully acknowledge the help of Renate Brunner, Kristine Campbell, Roland Loosli, Hanne Magro, and Christine Reber in gathering literature and for manuscript preparation. I would like to especially mention the financial support by the Swiss National Science Foundation, which has supported my research over the years and thus has added to the study of parasites in social insects. I am grateful to the editors of Princeton University Press's *Monographs in Behavior and Ecology*, John Krebs and Tim Clutton-Brock, for suggesting this contribution and for keeping an interest in the project that—as usual—took much longer than anticipated. Emily Wilkinson, Sam Elworthy, and Alice Calaprice from Princeton University Press were supportive in every way. Last but not least, I have to thank my wife, Regula, for her encouragement, support, and patience during the whole process.

Zurich, January 1998

Parasites in Social Insects

1

The Biology of Social Insects

Social insects are socially living insects. There are, however, controversial views about how to define and describe sociality (e.g., Sherman et al. 1995; Crespi and Yanega 1995). For the purpose of this book, these controversies add little but to remind us that “social insects” are very diverse. Moreover, many species of mammals, birds, fish, bryozoa, anthozoa, shrimps (Duffy 1996), and spiders are social, too. The biology of many social insect species is sometimes more reminiscent of group-living birds or mammals than of other social insects. For example, females of some halictid bees (Packer 1993) or wasps in the genus *Ropalidia* (Gadagkar et al. 1993) are not simply locked into an inflexible social behavior, but have quite similar options with respect to cooperation or selfishness as do birds or mammals (Brown 1987). Females can join other females, nest communally in groups, become a “queen,” or help as a “worker.” They may even breed alone and start a nest independently. On the other hand, leaf-cutter ants or fungus-growing termites possess highly evolved and sophisticated social behaviors that have no equivalent in any other group of organisms. Here, I consider social insects as those that are generally classified as primitively or advanced eusocial (table 1.1); yet I will occasionally look at other systems as well but will generally exclude communally nesting species (such as found in many andrenid bees). A hallmark of social insects as envisaged here is that they live in colonies and behave cooperatively.

Taxonomically, most social insects (some 19,000 known species) are found in the order Hymenoptera, this is, in the ants (all known species are social or parasites of other ants, Hölldobler and Wilson 1990), bees (Michener 1974), and wasps (Ross and Matthews 1990) (table 1.2). But truly social species are also known in the sphecid wasps (*Microstigma*s, Matthews 1991), in beetles (ambrosia beetles, Kent and Simpson 1992), and in the Thysanoptera (the thrips, Crespi 1992). Some authors include sphecid wasps in the superfamily Apoidea (e.g., Gauld and Bolton 1988). All known members of the order Isoptera (the termites) are social (ca. 2,300 species). Some excellent reviews of the biology of ants (Hölldobler and Wilson 1990), bees (Michener 1974, Roubik 1989), wasps (Spradbery 1973, Ross and Matthews 1990), and termites (Krishna and Weesner 1969, 1970) exist. The general treatise of Wilson (1971) on social insects is still unsurpassed. Hence, this first chapter is not intended to duplicate these works, but to provide a sketch of some prominent biological

Table 1.1
A Simple Overview of the Levels of Sociality in Insects

| <i>Level of Sociality</i> | <i>Trait</i> | | |
|---------------------------|-----------------------------------|--------------------------------|--|
| | <i>Cooperative Brood Care</i> | <i>Reproductive Castes</i> | <i>Overlap between Generations</i> |
| PARASOCIAL SEQUENCE | | | |
| Solitary | – | – | – |
| Communal | – | – | – |
| Quasisocial | + | – | – |
| Semisocial | + | + | – |
| Eusocial | + | + | + |
| SUBSOCIAL SEQUENCE | | | |
| Solitary | – | – | – |
| Primitively subsocial | – | – | – |
| Intermediate subsocial I | – | – | + |
| Intermediate subsocial II | + | – | + |
| Eusocial | + | + | + |

NOTES: The parasocial and subsocial sequences refer to two major evolutionary routes through which eusociality is thought to have arisen (after Wilson 1975). “+” means the trait is present, or “–” is absent. Reproductive castes refer to the fact that only some individuals are reproductive.

characteristics of social insects to introduce the subjects of the following chapters. I have arranged them by topic rather than by taxonomic group in order to emphasize how parasites will encounter social insects, independent of the taxonomic group of the host. The chapter should be useful primarily for readers who are not so familiar with social insect biology.

1.1 The Individual and the Colony Cycle

Parasites attack individual hosts. Even in social species, therefore, the individual and its life history are important. As a colony grows in number, the individuals inside are born, then develop and die (fig. 1.1). A typical social insect colony usually contains more than one class of individuals, i.e., it has several castes. A caste is a set of individuals of a particular morphological type and/or an age group that performs a distinguishable, separate task in the colony (Oster and Wilson 1978, p. 19). Such tasks can include nursing the brood, foraging, or

Table 1.2
The Taxonomic Distribution of Eusociality

| <i>Order</i> | <i>Family</i> | <i>Social Species</i> |
|--------------|--|---|
| INSECTS | | |
| Isoptera | Hodotermitidae | Ca. 2300 species, all eusocial |
| | Indotermitidae | |
| | Kalotermitidae | |
| | Mastotermitidae | |
| | Rhinotermitidae | |
| | Serritermitidae | |
| | Styloptermitidae | |
| | Termopsidae | |
| | Termitidae | |
| Thysanoptera | Phlaeothripidae | Subfertile soldiers in 1 genus (Crespi 1992) |
| Homoptera | Pemphigidae | 6 genera with soldiers known (Aoki 1977) |
| Hymenoptera | Anthophoridae | 7 genera (Allodapini) |
| | Apidae (honeybees, stingless bees, bumblebees) | 6 eusocial Apini (<i>Apis</i>) 4–500 eusocial Meliponini 300 primitively eusocial Bombini |
| | Halictidae (sweat bees) | 6 genera (Halictini, Augochlorini) |
| | Sphecidae (digger wasps) | 1 species (<i>Microstigmus comes</i>) (Matthews 1991) |
| | Vespidae | Ca. 9400 species (Polistinae, Stenogastrinae, Vespinae) |
| | Formicidae | Ca. 8800 species |
| Coleoptera | Curculionidae | 1 species (<i>Austroplatypus incompertus</i>) (Kent and Simpson 1992) |
| OTHER TAXA | | |
| Arthropoda | Aranea | 1 species? (<i>Anelosimus eximius</i>) (Vollrath 1986) |
| | Crustacea | 1 species (<i>Synalpheus regalis</i>) (Duffy 1996) |
| Mammalia | Rodentia | Several species of mole rats (Sherman et al. 1991; Burda and Kawalika 1993) |

SOURCES: After Wilson 1971, Spradbery 1973, Michener 1974, Snelling 1981, Ross and Matthews 1990, Crespi and Yanega 1995, Sherman et al. 1995, and Crozier and Pamilo 1996.

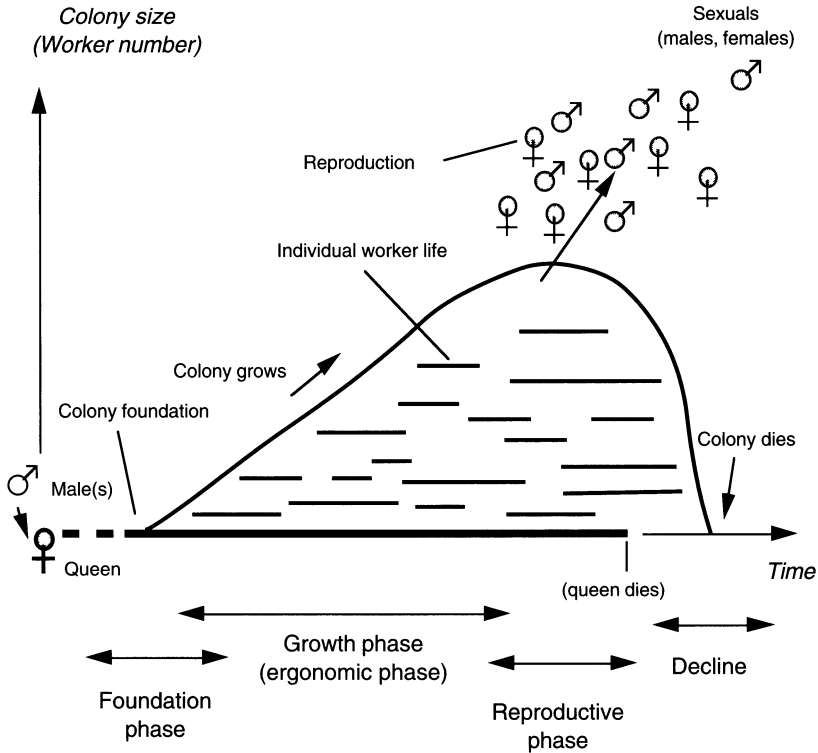


Figure 1.1 A schematic view of how individuals and colonies of social insects grow, mature, and die. The scheme depicted here is modeled after an annual species of social wasps (e.g., paper wasps) or bees (e.g., bumblebees). The queen founds the colony after the diapause (broken line) and produces workers. Toward the end of the cycle, sexuals (males and females) are produced. They (normally) leave the colony, mate, and start the next generation. The shorter horizontal arrows characterize the birth, life, and death of individual workers in the colony. The thick horizontal line indicates the life of the queen. Decline of the colony typically follows after queen death. The colony cycle is characterized by the number of workers present in the colony (colony size). The designation of the different phases follow Oster and Wilson (1978). Social insects show many variations on this basic scheme. Examples include more than one queen present (polygyny), perennial life cycles, and reproduction by fission.

milling leaves for the fungus garden (as in the leaf-cutter ants). Soldiers, usually large and behaviorally aggressive workers, are an example of a morphological caste, which is part of a polymorphic caste system. Young workers usually tend the brood—an instance of caste based on age rather than morphology. Although the significance of age, as compared to other factors such as opportunities to work, as a determinant of task attendance is controversial (see discussion

in Bourke and Franks 1995), age-related changes are widespread. Such differences lead to division of labor (polyethism) within the colony, a further hallmark of social insect biology. Most importantly, only some individuals actively reproduce (the reproductive division of labor). Variation in how fast the individuals develop or how many workers are produced are important determinants for the macroscopic differences in the lifestyle among species of social insects, for colony sizes, and for reproductive timing.

THE LIFE HISTORY OF INDIVIDUALS

The individual life of workers is characterized simply in figure 1.1 by arrows connecting birth and death. But these arrows hide important differences. In the social Hymenoptera (the bees, ants, and wasps), individuals have a holometabolous development (fig. 1.2). After the egg stage, several larval instars, dependent on being provisioned by adults, occur. In ants, there are usually four stages (3–6); in wasps there are five, and perhaps four or five in bees (Michener 1974). In some species, the larvae have been shown to actively contribute to the colony's economy by providing food or necessary digestive enzymes to the adults. Another larval function is the production of silk in weaver ants (*Oecophylla* spp.) for the construction of nest chambers from leaves (Hölldobler and Wilson 1990). Eventually, the last larval instar of hymenopteran insects pupates and ecloses as the adult (the imago)—the typical ant, bee, or wasp as we know it. However, imagoes are not necessarily “adult” in the sense of being fertile (the usual definition of adulthood in population biology). Rather, the colony produces adults that are either “workers” (typically nonreproducing adults) or reproductively competent sexual females (gynes, queens) and males (drones in hymenoptera). This developmental path also means that the adult ecloses with its final morphology. It no longer grows or changes shape, although many other age-related processes still occur. For instance, the fat body generally becomes smaller as the worker ages.

In contrast, development in the social Isoptera (the termites) is hemimetabolous (fig. 1.2). The juveniles live through a series of larval instars (the nymphs) and finally molt into the imago, the adult form. The nymphs already resemble the adults and engage in the colony's activities. The hemimetabolous development thus allows for high degrees of flexibility. In the termite *Trinervitermes*, for example, a male first instar larva can molt into a soldier larva, then into a small worker, and later again into a large soldier as it passes along its individual developmental sequence. A female larva can develop into a large worker and remain so until the final seventh instar (Watson et al. 1984).

The adult life span of workers (table 1.3) can be quite short and normally does not match queen longevity. Therefore, as the colony grows with the queen as the long-lived, permanent inhabitant, a turnover of workers occurs. Risks related to foraging activity are presumably the most important factors that set adult

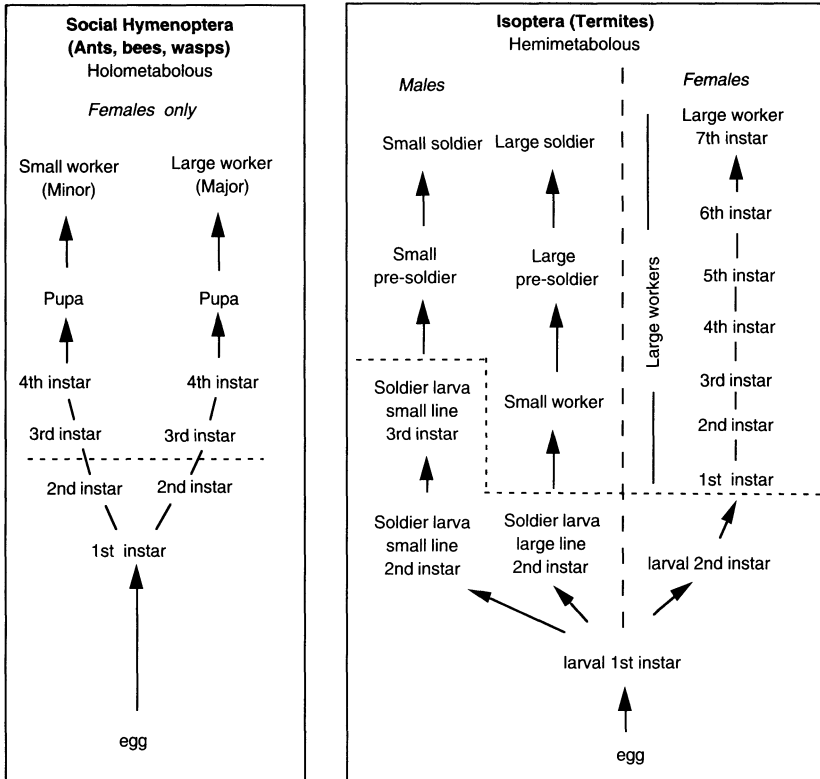


Figure 1.2 Sketch of developmental routes followed by (left panel) colony members of social Hymenoptera (holometabolous development in ants, bees, and wasps) and by (right panel) termites (Isoptera) (hemimetabolous development). In Hymenoptera, only females form the worker caste. They develop through a number of instars during which differentiation into small or large workers takes place, the exact stage varying among taxa (for example, as in ants). The system in termites is more complex: females can develop into large workers, males into small workers or soldiers (as in *Trinervitermes*). The stages below the dotted line are helpless and fully dependent on brood care; above the line, they can actively contribute to work in the colony, except for pupae (modified after Oster and Wilson 1978).

worker life span. In the desert-dwelling ant *Cataglyphis bicolor*, for example, workers live for about four weeks as adults in the nest before they start their foraging activities. The length of the subsequent foraging career is limited by predation of spiders and robber flies and is estimated to be around six days (Schmid-Hempel and Schmid-Hempel 1984). Life span is also often correlated with worker body size so that larger workers are usually longer-lived (e.g., in *Solenopsis*: Porter and Tschinkel 1985; Tschinkel 1993). In addition, as colony

Table 1.3
Longevity of Workers of Social Insects

| <i>Species</i> | <i>Life Span</i> | <i>References</i> |
|----------------------------------|------------------|---------------------------------------|
| ANTS | | |
| <i>Aphaenogaster rudis</i> | 3 years | Hölldobler and Wilson 1990 |
| <i>Cataglyphis albicans</i> | 32 days | Schmid-Hempel 1983 |
| <i>Cataglyphis bicolor</i> | 34 days | Schmid-Hempel 1983 |
| <i>Leptothorax lichtensteini</i> | 3 years | Hölldobler and Wilson 1990 |
| <i>Monomorium pharaonis</i> | 66 days | Hölldobler and Wilson 1990 |
| <i>Myrmecia nigriceps</i> | 2.2 years | Hölldobler and Wilson 1990 |
| <i>Myrmica rubra</i> | 2 years | Hölldobler and Wilson 1990 |
| <i>Pogonomyrmex owyheeii</i> | 42 days | Porter and Jorgensen 1981 |
| <i>Pogonomyrmex barbatus</i> , | Up to 30 days | Gordon and Hölldobler 1987 |
| <i>Pogonomyrmex rugosus</i> | | |
| BEES | | |
| <i>Allodape angulata</i> | 1 year | Skaife 1953 |
| <i>Apis mellifera</i> , summer | 32 days | Seeley 1985 |
| <i>Bombus fervidus</i> , | 20–30 days | Goldblatt and Fell 1987 |
| <i>Bombus pennsylvanicus</i> | | |
| <i>Bombus morio</i> | 54 days | Brian 1983, p. 175 |
| <i>Bombus terrestris</i> | 25 days | Pers. obs. |
| <i>Dialictus versatus</i> | 21 days | Michener 1969 |
| WASPS | | |
| <i>Mischocyttarus drewseni</i> | 21 days | Jeanne 1972 |
| <i>Polistes fadwigae</i> | 75 days | Yoshikawa 1963 |
| <i>Vespa orientalis</i> | 46 days | Ishay et al. 1968 |
| <i>Vespa simillima</i> | 13 days | Ross and Matthews 1990, p. 250 |
| <i>Vespa tropica</i> | 35 days | Ross and Matthews 1990, p. 251 |
| <i>Vespa vulgaris</i> | 25 days | Ritchie 1915 |
| TERMITES | | |
| <i>Coptotermes acinaciformis</i> | 2 years | Gay et al. 1955, cited in Wilson 1971 |
| <i>Coptotermes lacteus</i> | 2 years | Gay et al. 1955, cited in Wilson 1971 |
| <i>Cubitermes ugandensis</i> | 267 days | Williams 1959 |
| <i>Reticulitermes lucifugus</i> | 5 years | Buchli 1958 |

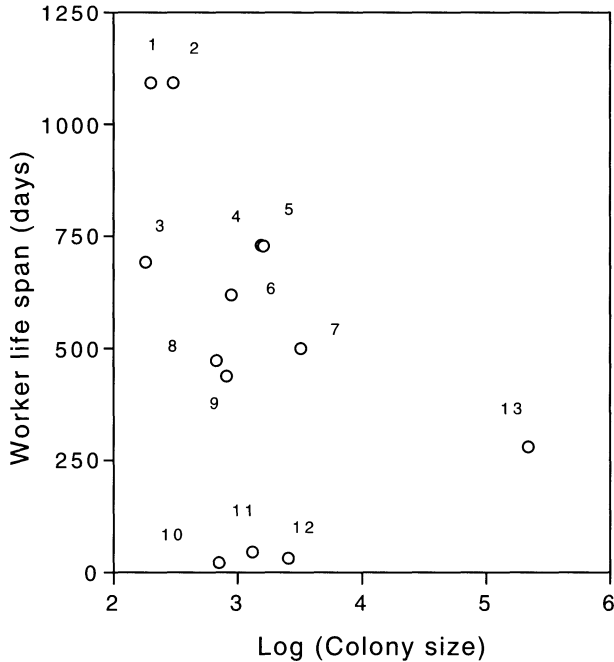


Figure 1.3 Relationship of life span of workers (in days) and typical size (worker number) reached by the mature colony for various ant species. (Data from Hölldobler and Wilson 1990 and table 1.3.) The formal statistics are as follows: Spearman's $r_s = -0.3824$, $N = 13$ species, $P = 0.19$. Species are: 1 *Leptothorax nylanderi*, 2 *Aphaenogaster rudis*, 3 *Myrmecia vindex*, 4 *Myrmica rubra*, 5 *Myrmica laevinodis*, 6 *Myrmecia gulosa*, 7 *Myrmica sabuleti*, 8 *Myrmecia pilosula*, 9 *Myrmecia nigrocincta*, 10 *Cataglyphis albicans*, 11 *Monomorium pharaonis*, 12 *Cataglyphis bicolor*, 13 *Solenopsis invicta*.

size increases, the egg-laying rate of the queen increases too, but worker longevity appears to decrease (e.g., Hölldobler and Wilson 1990, p. 170; Ross and Matthews 1990, p. 251) (see fig. 1.3 for ants). Matsuura (1991) noted the same trend when he compared five species of social wasps of the genus *Vespa* in Japan. Although there is no relation to the degree of sociality itself, highly advanced species tend to have larger colonies and thus have, on average, shorter-lived workers. These dynamical views of colony development, set by worker life span and turnover, will obviously become important when the spread of parasites within the colony is considered (chap. 4).

THE COLONY LIFE CYCLE

The colony life cycle is determined by the foundation of the colony, subsequent growth, and production of sexuals. The basic cycle depicted in figure 1.1 shows

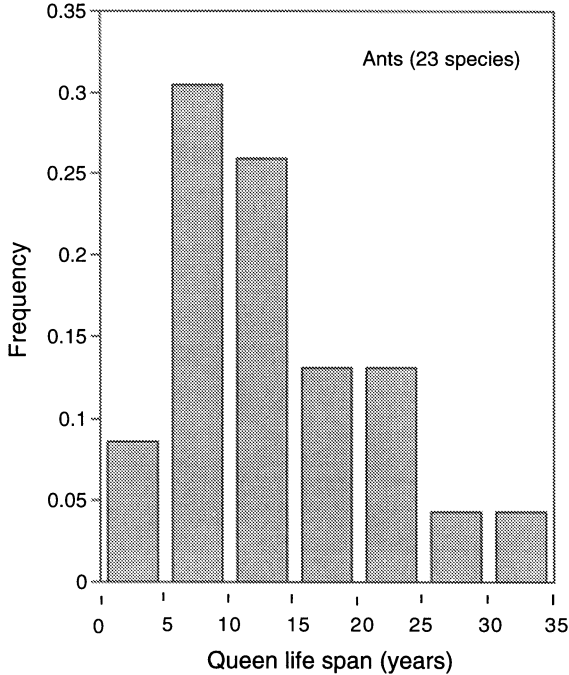


Figure 1.4 The distribution of life spans (in years) for ant queens ($N=23$ species). (Data from Hölldobler and Wilson 1990 and Brian 1965.)

many variations. For example, all ants and termites are perennial and have more than one reproductive season. Figure 1.1 also illustrates that the growth of the colony and its composition at any one time is affected, among other things, by how long its members live. Often, the longevity of the queen determines the longevity of the colony. Typically, queens are considerably longer-lived than workers (fig. 1.4). They can, in fact, live for several decades, e.g., in *Camponotus*, *Formica*, and *Lasius* up to 18–29 years (Hölldobler and Wilson 1990). Queens of the sweat bee *Halictus marginatus* have been recorded to live 5–6 years (Plateau-Quénu 1962), those of the stingless bee *Melipona quadrifasciata* around 3 years (Kerr et al. 1962). Queens of the honeybee live many years (Jean-Prost 1956; Seeley 1985; Winston 1987, p. 56). However, they are usually superseded after 1–2 years and leave their colony, i.e., the old queen is replaced by one of her daughters. When supersedure occurs, the colony changes its genetic profile. Interestingly, there seems to be no obvious relationship between queen longevity and degree of sociality achieved (Hölldobler and Wilson 1990, p. 170). Sometimes, real “queens” may not be present at all, as, for example,

among the approximately one hundred species of ponerine ants where all workers are fertile and cooperate (Peeters 1993).

Colony founding in social insects occurs in a number of different ways. Most species are capable of independent founding of their own, but some species depend on being able to occupy a host nest to start their own colony (“dependent founding,” as in several *Formica* or *Lasius* ants). For example, in the leaf-cutter ants (*Atta*), a single fertilized queen starts a colony on her own in a closed brood chamber (haplometrosis). She lives from her flight muscles that are metabolized during this time. She also carries a priming piece of the fungus from her parental nest to start the new colony’s garden. If successful, her colony will eventually contain several millions of workers, her daughters, all of them occupying an impressive nest several meters in height and diameter. In the termites, the reproductive male-female pair (the “king” and “queen”) starts the colony. In *Calotermes flavicollis*, the first 10–20 young workers emerge after 8 weeks of being fed with glandular secretions and wood paste, the latter being the normal diet of the species. After one year, 50–60 workers are present, two-thirds of which are soldiers. The proportion of soldiers later drops to 3% as the colony grows (Brian 1965). Across species, the time from nest foundation to first worker emergence varies considerably. Primitive ants, for example, usually take a long time to form a colony. In *Myrmecia forficata* the female lays eight eggs, of which usually only three survive, and which take 4 months to develop. *M. regularis* takes 8 months to produce the first workers (Haskins and Haskins 1950).

Colony founding by single queens (haplometrosis) is often reinforced by aggressiveness against potential cofounders. This period of colony foundation and early growth is particularly critical, since most colonies will not survive (table 1.4; see also fig. 6.1). Associations of foundresses (pleiometrosis) are therefore thought to have evolved to increase success during this period (e.g., Ross and Matthews 1990). This is not uncommon in wasps or ants (e.g., in *Acromyrmex versicolor*, where several unrelated females cooperate: Rissing et al. 1986; Rissing and Pollock 1987). If cofounding by several queens persists into the later life stage of the colony, and if it is combined with reproductive activity, it leads to polygyny, i.e., to the presence of several functional queens. Bourke and Franks (1995) provide an excellent discussion of life histories in ants. Pleiometrosis seems overall rarer in termites, perhaps because colony foundation already requires a couple, and hence further joiners may not be as valuable, or the conflicts of interest may be less likely to be settled through cooperation. Cofounding pairs in termites are in fact normally hostile toward each other.

The emergence of the first brood marks the start of the colony as a social group. The following early colony growth phase is also often characterized by the production of small workers (the nanitics). Soon afterwards, the colony enters a growth phase with the full economy of the society established (termed the “ergonomic phase” by Oster and Wilson 1978). During this period, the colony has a fully developed division of labor, often based on age-related polyethism,

Table 1.4
Colony Survival in Social Insects

| <i>Species</i> | <i>Observation on Colony Survival</i> | <i>References</i> |
|--|---|----------------------------------|
| BEES | | |
| <i>Halictus duplex</i> | 20% of started nests survive to social stage. | Sakagami and Hayashida 1961 |
| <i>Lasioglossum (Dialictus) zephyrum</i> | A few percent survive first 2–3 months. | Batra 1966 |
| <i>Bombus pascuorum</i> | Of 80 nests: 25 died early, 23 destroyed by predators or fire, 32 (29%) survived. | Cumber 1953 as <i>B. agrorum</i> |
| <i>Apis mellifera</i> | 78% of established (old) colonies survive winter in upstate New York, but only 24% of new (young) colonies. Mean colony longevity is 5.6 years. | Seeley 1978 |
| <i>Apis mellifera</i> | 45% of old colonies, only 8% of young colonies survive winter in Ontario. | Morales 1986, in Winston 1987 |
| WASPS | | |
| <i>Polistes</i> sp. | 3% (2 of 69) colonies survive to produce workers and sexuals. | Yoshikawa 1954 |
| <i>Dolichovespula</i> sp. | 1 out of 12 colonies survive to produce workers and sexuals. | Brian and Brian 1952 |
| <i>Vespula analis</i> | 36 of 59 colonies lost queens before growth phase, 3 ceased activity, 2 destroyed by predators; 30% (18) were successful. | Matsuura 1984 |
| ANTS | | |
| <i>Formica ulkei</i> | Of 56 mounds, 18 survived for 2 years, 13 for 6 years. | Talbot 1961 |
| <i>Formica exsecta</i> (= <i>F. opaciventris</i>) | Annual colony mortality: 8–9%; annual birthrate: 5–16%. | Scherba 1961, 1963 |
| <i>Lasius flavus</i> | 6 of 18 nests survived for 8 years. | Waloff and Blackith 1962 |
| <i>Pogonomyrmex owyheei</i> | Colonies live for 14–30 years (average 17 years). | Porter and Jorgensen 1988 |

and continues to grow in numbers (fig. 1.5). Where worker polymorphism exists, large workers are often more likely to forage while smaller ones will care for the brood. The large-sized workers (the majors) also serve as soldiers in the defense of the colony against enemies or of a foraging trail against competitors. Morphological castes are weak or absent in bees and wasps.

The number of workers that are typically found in a colony during the ergonomic phase is often taken as a measure of colony size (table 1.5). In an extensive review, Schmid-Hempel et al. (1993) found that colony size correlates not only with a number of fitness measures, but also with individual behavior or social organization. In particular, colony size at the time of reproduction, i.e., when sexuals are raised, is a good predictor of the number of sexuals that can be produced altogether, and thus a shorthand measure of reproductive success (Cole 1984; Schmid-Hempel et al. 1993; see also chap. 4). Obvious advantages to being a large colony involve competitive superiority or higher levels of resiliency against environmental fluctuations. In fact, in wasps (Jeanne 1991) and in ants (Kaspari and Vargo 1995) the typical colony size increases at higher latitudes. This has been interpreted as an adaptation to variable and harsh environments.

Toward the end of the cycle, the colony will reproduce (fig. 1.1). During this period, sexuals, i.e., drones and young queens (the gynes), emerge. This reproductive phase normally follows the ergonomic phase. In some perennial species, where growth is periodically interrupted by some kind of diapause, e.g., hibernation, the reproductive phase may come at other times (e.g., in the honeybee soon after hibernation). The sexuals of otherwise flightless groups, such as ants and termites, are winged and disperse to mate. In some cases, e.g., in slave-making ants, intranest mating seems to be the rule (Buschinger 1989). As in other organisms, only a few daughter queens will ultimately enjoy reproductive success. For instance, Wildermuth and Davis (1931, cited in Wilson 1971) estimated that only 0.1% of all queens of *Pogonomyrmex badius* will be successful at having offspring. In termites (*Nasutitermes*), where colonies typically release huge numbers of sexuals, the chances of success may be as low as 1 : 10,000 for any queen or king (Wilson 1971, p. 444). In other species, such as the honeybee, many fewer gynes are produced and hence the chances of success are considerably higher.

Some highly social species with elaborate colony structures and division of labor (e.g., army ants, honeybees, stingless bees) start new colonies by budding or fission. The swarming of honeybees is the best-known example of this kind. If the colony is large enough, the mother queen leaves the nest with a part of the worker force (the prime swarm). If the colony is strong enough, other, newly emerged daughter queens may leave the colony with additional parts of the worker force (afterswarms). These will find a new nest site, mate, and establish a colony. Finally, one of the daughter queens that stayed back in the old nest will manage to kill her remaining rivals and thus inherit the parental nest with its worker force.

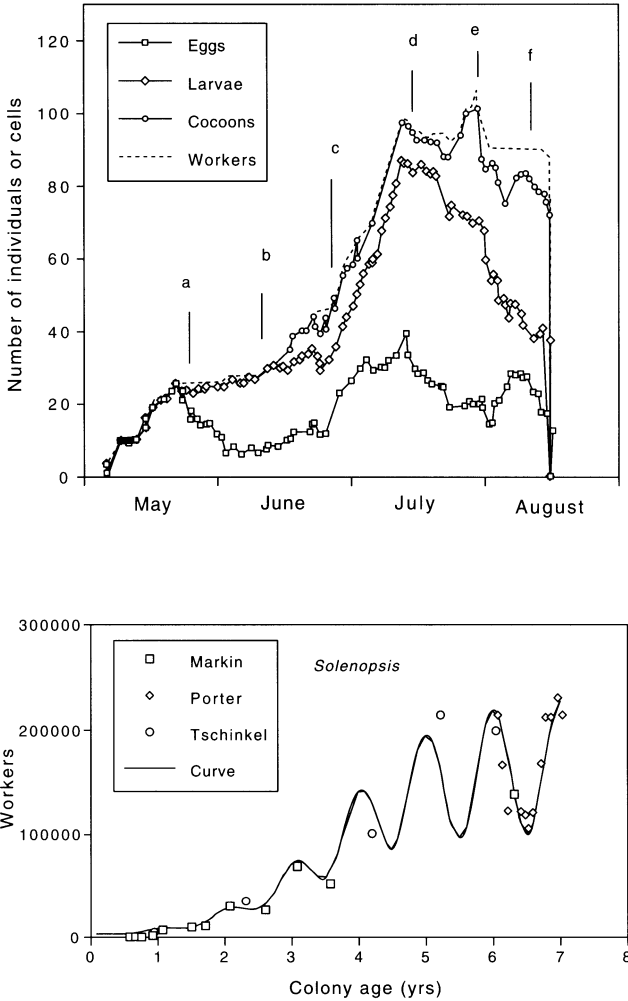


Figure 1.5 Colony development of (a) an annual social insect, the wasp *Parapolybia indica*. The letters indicate first larva hatched (=a), first cell capped (b), first adult emerged (c), a critical number of workers died (d), first male emerged (e), and foundress dies (f). (Reproduced from Gadagkar 1991. Used by permission of Cornell University Press.) (b) Development in a perennial species, the fire ant *Solenopsis invicta*. The single data points refer to counts in three different studies (Markin, Porter, and Tschinkel, as indicated in the graph). The curve is a fit to the data. (Reproduced from Tschinkel 1993 by permission of Ecological Society of America.)

Table 1.5
Colony Sizes of Social Insects

| <i>Species</i> | <i>Colony Size (Number of Workers)</i> | <i>References</i> |
|----------------------------------|--|----------------------------|
| ANTS | | |
| <i>Anomma wilverthi</i> | 20,000,000 | Wilson 1971, tab. 4.6 |
| <i>Aphaenogaster rudis</i> | 303 | Hölldobler and Wilson 1990 |
| <i>Atta colombica</i> | 2,500,000 | Wilson 1971 |
| <i>Cataglyphis albicans</i> | 700 | Schmid-Hempel 1983 |
| <i>Cataglyphis bicolor</i> | 2600 | Schmid-Hempel 1983 |
| <i>Eciton burchelli</i> | 425,000 | Wilson 1971, tab. 4.6 |
| <i>Formica fusca</i> | 500 | Brian 1965 |
| <i>Formica rufa</i> | 30,000 | Brian 1965 |
| <i>Lasius flavus</i> | 10,000 | Brian 1965 |
| <i>Monomorium pharaonis</i> | 2500 | Hölldobler and Wilson 1990 |
| <i>Myrmecia nigrocincta</i> | 821 | Haskins and Haskins 1980 |
| <i>Solenopsis invicta</i> | 50,000 | Porter and Tschinkel 1985 |
| BEES | | |
| <i>Apis mellifera</i> | 50,000 | Seeley 1985 |
| <i>Bombus terrestris</i> | 200 | Pers. obs. |
| <i>Bombus morio</i> | 2000 | Brian 1983 |
| WASPS | | |
| <i>Dolichovespula sylvestris</i> | 95 | Brian 1965 |
| <i>Paravespula germanica</i> | 1613 | Brian 1965 |
| <i>Paravespula vulgaris</i> | 1000 | Brian 1965 |
| <i>Protopolybia pumila</i> | 7000 | Brian 1965 |
| <i>Vespa crabro</i> | 100 | Brian 1965 |
| <i>Vespa tropica</i> | 313 | Ross and Matthews 1990 |
| TERMITES | | |
| <i>Coptotermes formosanus</i> | 395,800 | Gu-Xiang and Zi-Vong 1990 |
| <i>Incisitermes minor</i> | 9200 | Nutting 1969 |
| <i>Macrotermes</i> sp. | Ca. 2,000,000 | Lüscher 1955 |
| <i>Trinervitermes geminatus</i> | 19,000–52,000 | Sands 1965 |
| <i>Zootermopsis laticeps</i> | 2400 | Nutting 1969 |

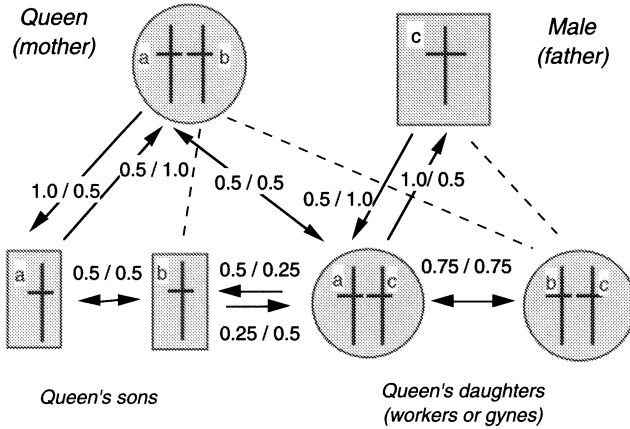


Figure 1.6 A simple pedigree of relatedness for a colony of social Hymenoptera, assuming one queen per colony, singly mated, and with no male production by the workers. Arrows indicate transmission of genes, symbolized by one locus with alleles *a*, *b*, and *c*, and as applicable to the class of individuals represented by the circles (females) or rectangles (males). Small figures give the respective values for regression relatedness and for life-for-life relatedness, respectively, for the corresponding pairs of individuals. For definitions of these terms, see box 5.1. The graph illustrates several asymmetries in the relatedness between pairs of individuals (classes), depending on who is the actor and the recipient of an interaction (direction of arrow). Individuals homozygous at the sex locus will develop into diploid males (not shown).

SEX AND CASTE DETERMINATION

In almost every case studied so far, sex of offspring in social insects is genetically determined. In the social Hymenoptera, sex follows the haplo-diploid mechanism where unfertilized, haploid eggs develop into males and fertilized, diploid eggs into females. In almost all cases, sex is furthermore determined by the alleles at a single locus, or at least this is strongly suspected. Hemi- or homozygous individuals are male, heterozygous individuals are female (Crozier and Pamilo 1996). When there are few sex alleles, or when the effective population size is small, the sex locus may become homozygous; these individuals develop into diploid males. Diploid males are known from a number of species in various hymenopteran taxa (see Crozier and Pamilo 1996, their table 1.4). For some partly social groups, such as the Euglossinae (the orchid bees), diploid males may impose limitations on the evolutionary path to sociality (Roubik et al. 1996). More importantly still, the mode of sex determination in the social Hymenoptera creates high values as well as asymmetries in the genetic relatedness among colony members that has important consequences for cooperation and conflict within the society—visible, for example, as biases in the sex ratio of offspring (Trivers and Hare 1976; Boomsma and Grafen 1991; Sundström 1994) (fig. 1.6).

On the other hand, the development of a female larva into different worker morphs or into a reproductive form (a daughter queen, here called gyne) is environmentally determined. It depends on the amount and quality of food given to the larva. Well-fed larvae or those given special nutrition (such as “royal jelly” in the honeybee) develop into large workers or into reproductives. Only a few exceptions from this pattern are known. In the stingless bees, genus *Melipona*, queens appear to be full heterozygotes of an independently segregating two-locus system (Kerr 1950, 1969). Food shortage will nevertheless cause such heterozygous larvae to develop into workers (Kerr and Nielsen 1966), thus demonstrating the important role of environmental effects on the worker/female determination. Genetic determination has also been suggested for the European slave-making ant *Harpagoxenus sublaevis*, where worker-like reproductive females (the ergatomorphs) differ from the typical winged queens by a single recessive allele (Winter and Buschinger 1986).

1.2 Populations of Colonies

The macroscopic population biology of social insects—the demography and dynamics of populations of colonies—is not as well known as the behavior of individual workers or the internal dynamics of colonies. Nevertheless, a number of studies in different taxa have shown that colony mortality is quite substantial, especially early in their life cycle (table 1.4, fig. 6.1). The study of the life cycles of ants and termites is naturally more difficult to carry out, because the cycles may last many years and often unfold in difficult-to-access underground nests. Long-term studies, such as the one carried out in 1931–1941 on the ant *Formica ulkei* (Scherba 1958), are consequently rare. Scherba estimated the annual birthrate of new colonies to be around 9.1% and the mortality rate to be 16%. Colonies probably lived for 20–25 years. These data match those reported by Talbot (1961) for the same species (table 1.5) and Porter and Jorgensen (1988) for harvester ants. Detailed studies on how important characteristics, such as the colony’s foraging range or interactions with neighbors, develop over the life cycle of the colony are unfortunately also very rare (Gordon 1992, 1995). Although the data are far from complete, the general pattern is that colony mortality early in life is quite high, while established colonies have a good chance to persist for a long time. The survival rate for entire colonies is therefore close to what ecologists call Type I survival, i.e., a rapid early decline followed by a low mortality rate afterwards. Enemies, adverse weather conditions, or food shortages are the selective events that are usually thought to lead to colony death.

Only a few studies so far have asked what may limit the population size of social insects. Physical conditions are of course limiting for the distribution of many species. For example, in the ant *Myrmica rubra*, the number of sunny days

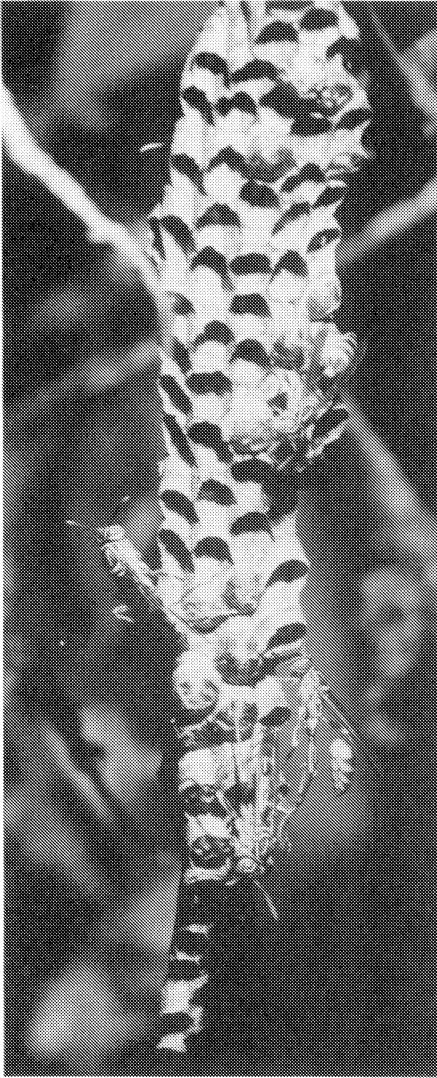
per year is a good predictor for its occurrence (Elmes and Wardlaw 1982). Summer temperatures may often limit colony growth, whereas winter temperatures limit overwinter colony survival (e.g., as in the meat ant *Iridomyrmex purpureus*: Greenslade 1975a,b). Besides these factors, nest sites are limited in some species (Pickles 1940). This has been demonstrated by Herbers (1986): the population density of the ant *Leptothorax* increased when additional nest sites were experimentally added.

1.3 Nesting

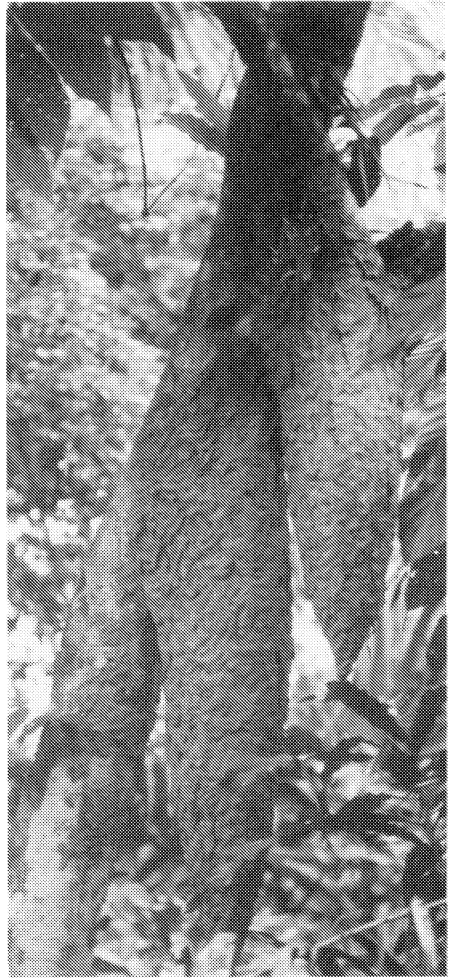
Nesting habits of social insects vary widely (fig. 1.7). Some nests are in the open, as found in army ants or Asian honeybees; other nests are protected by especially constructed envelopes (some wasps), and still others are ground nests in preexisting burrows (e.g., bumblebees) or nest cavities dug out by the colony's workers (e.g., desert ants such as the appropriately named *Cataglyphis*). Many species are cavity dwellers in trees (e.g., the tropical stingless bees, *Meliponini*). The sophistication of nest organization varies in similar ways. In ants, the brood is typically arranged in loose piles. Eggs, larvae, and pupae are scattered on the floor of the nest chamber. In the more advanced bees and in the wasps, the brood is placed singly in cells that are regularly spaced, as in the brood comb of the honeybee with its hexagonal cells. Sometimes a single colony occupies more than one nest ("polydomy" leading to a "polycalic" society). Contact among nests is maintained by the workers that transport the brood from one nest to another. Limitation in available nest sites is the most frequently cited explanation as to why social insect colonies are mono- or polydomous (Herbers 1986).

Colonies move to a new site much more frequently than previously thought. Herbers (1985) observed in North America that nests of fourteen ant species are regularly moved over the duration of a season. Usually, the colony expands during the summer and uses several nests, then contracts to a few hibernation sites in winter. In some species a typical nest lasts only for 2–3 weeks. It is likely that the causes for nest relocations are often associated with a change in microclimatic conditions, predation, food supplies, and, indeed, parasites (see chap. 4).

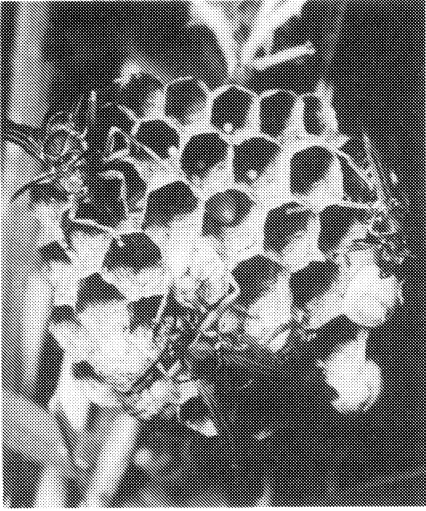
The spatial activity of colonies also includes the maintenance of territories. Colonies in most populations of social insects are in fact overdispersed. For example, ants possess a variety of behavioral repertoires to defend territories, including a rich array of pheromones to mark their boundaries or to alarm nestmates to defense (Hölldobler and Wilson 1990). In termites, the avoidance of other colonies' feeding galleries may separate neighbors. Territories are typically absent in the flying social insects, i.e., in bees and wasps. Territorial conflicts sometimes lead to the killing of adversaries. In some groups, e.g., the ant *Formica polyctena* (Mabelis 1979), the killed enemies are taken home as prey.



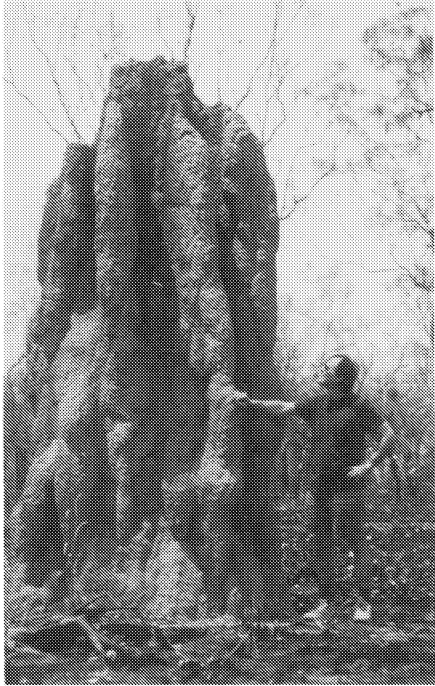
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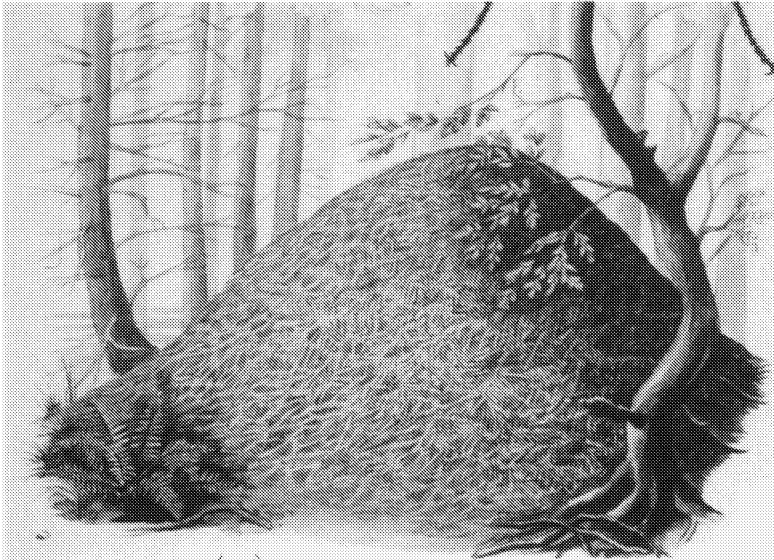
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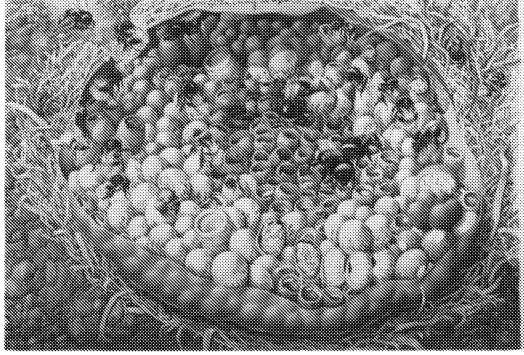
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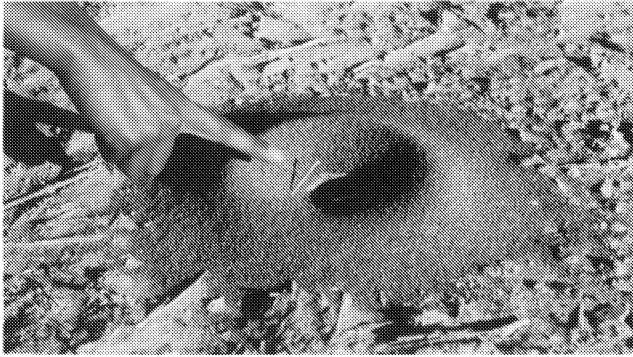
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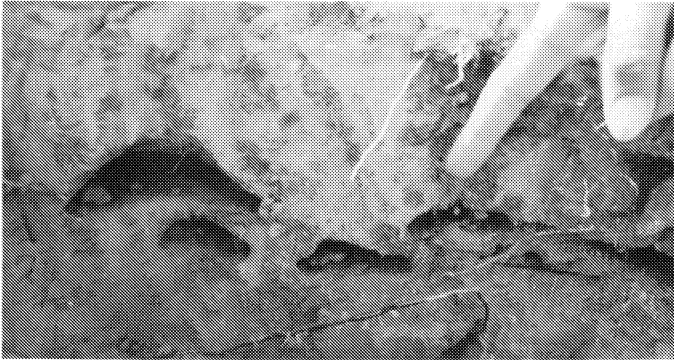
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Figure 1.7 Nests of social insects. (a) An open nest of the wasp *Mischocyttarus*, elongated cells pending from support structure; (b) an arboreal nest of the ant *Azteca*, with cover; (c) an open nest of the wasp *Polistes*, cells in a cluster; (d) massive mound of the termite *Nasutitermes* with solid outer walls; (e) mound of the wood ant *Formica*; (f) subterranean nest of a bumblebee, *Bombus* (original drawing provided by M. Pirker, reproduced by permission); (g) and (h) subterranean nests of the desert ant *Cataglyphis*, with entrance and brood chambers.

This pattern is more generally found in aggressive disputes between species rather than within species (Hölldobler and Wilson 1990, p. 414). In addition, ants, bees, and wasps regularly engage in robbery, i.e., they attack neighboring nests and steal food or brood.

Finally, spatial activities also include the observation that the reproductives are dispersing either before or after mating. Some of the phenomena associated with this process are quite spectacular. For example, the mating swarms of the seed-harvester ants *Pogonomyrmex* in the southwestern deserts of North America consist of thousands of winged males and females, whirling and diving in the air. After mating, queens will take off and disperse to found a new colony (Hölldobler and Wilson 1990). Similarly, termite sexuals leave the colony in the thousands and are harvested because they are considered to be a delicacy by local people. More subtle, but no less spectacular, are long-range dispersals such as reported for bumblebee queens that migrate for hundreds of kilometers along the Scandinavian coast (Mikkola 1984).

1.4 Summary

Social insects comprise about 20,000 species from several orders. Their mode of life, colony organization, reproductive pattern, and nesting habits differ widely. In many ants, bees, and wasps, typically, a queen founds a colony which then grows in worker numbers and eventually reproduces daughters (the gynes) and sons (the drones). Many bees and wasps are annual, while ants and termites are perennial. In termites, colonies are founded by a male-female pair. Deviations from the simple scheme include, for example, polygyny (more than one functional queen per colony) and dependent colony founding (in a host nest). Individual development in ants, bees, and wasps follows the holometabolous path with several larval instars that metamorphose into the adult form. Termites are hemimetabolous, where individuals develop through several nymphal stages that are part of the workforce of the colony. Queens can potentially be very long lived, while workers are replaced as the colony grows and eventually reproduces. While the behavior and turnover of workers within the colony is reasonably well studied, the dynamics of populations of colonies is often unknown. Sex in hymenopteran social insects is determined by a haplo-diploid mechanism that generates close and asymmetric genetic relationships among colony members.

2

The Parasites and Their Biology

In the ancient Greek world, a *Parasitos* was a person who received free meals from a rich patron in exchange for amusements and conversations (Brooks and McLennan 1993). Unfortunately, the term is not as easy to define in biology. Webster's International Dictionary defines it as "an organism living in or on another living organism, obtaining from it part or all of its organic nutriment, commonly exhibiting some degree of adaptive structural modifications, and causing some real damage to its host." Obviously, this definition leaves out phenomena such as social parasitism and leaves open problems such as defining real damage. However, it seems almost impossible to give a universal definition, and, since social parasitism is not discussed in this book, we may just as well stick to such vague descriptions.

In this chapter, an overview over the different parasite groups and their biology is given. The main emphasis is on those associated with social insects. A summary of the known parasites of social insects by taxonomic group is given in the lists in Appendixes 2.1 to 2.11. Not surprisingly, the number of parasite species (here called "parasite richness") described from the different social insect taxa is related to how well they are studied in general, i.e., the sampling effort (fig. 2.1). In the subsequent analyses, sampling effort will be controlled for by analyzing the residuals from the regression shown in figure 2.1 (the "standardized parasite richness") rather than the raw values themselves (Walther et al. 1995). Using the raw data, however, would not alter the major conclusions. The number of recorded parasite species per social insect host species is approximately Poisson-distributed, with an average of 2.63 ± 0.19 (S. E.; $N=488$) recorded parasites (1.31 ± 0.14 pathogens, 1.32 ± 0.10 parasitoids) per species (fig. 2.2). The record holder is the honeybee, *Apis mellifera*, with over seventy recorded parasite species in the database, but also with some 170 studies that are published and registered in *Biological Abstracts* each year. Another major reason why the European honeybee is so well known is that it is a managed species in most parts of the world. Beekeepers often spread diseases by exchanging frames and hive bodies that contain parasites. These are later noticed and thus become known to science.

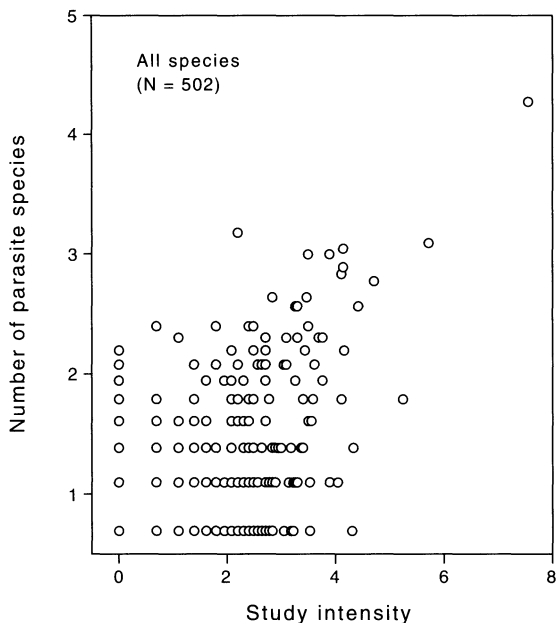


Figure 2.1 The number of parasites recorded per host species (parasite richness) in social insects. The abscissa is the number of published studies on the host species during 1985–1995 from a survey in *Biological Abstracts*. This quantity is used as a measure of sampling effort for the species. Only hosts where at least one parasite has been reported are included. Data ln-transformed to normalize variances. Parasite data are taken from the lists in appendix 2, except for socially parasitic host species, mites, and sphecid hosts (*Microstigmus*). The point on the upper right hand is the honeybee with 71 recorded parasites and 1899 published studies. The regression is: $Y=0.762+0.252 X$, $r^2=0.331$, $N=502$ species; $F=249.06$, $P < 0.0001$; with $Y=\ln(\text{parasite richness}+1)$, $X=\ln(\text{studies}+1)$. The residuals from this regression are used in subsequent analyses of this book ("standardized parasite richness").

2.1 Viruses

A common problem with investigating viral diseases of insects is the custom to name a virus after its host and thus to ignore possible multihost relationships. The methodological and conceptual progress of molecular epidemiology should reduce this problem in the future. Currently, more than twenty groups of viruses are known to be insect pathogens (Tanada and Kaya 1993). Among them, DNA viruses are prominent and include, among other groups, the nuclear polyhedrosis viruses, granulosis viruses, Polydnviridae (multipartite, double stranded), Poxviridae (Entomo-poxvirinae), Iridoviridae (nonenveloped,

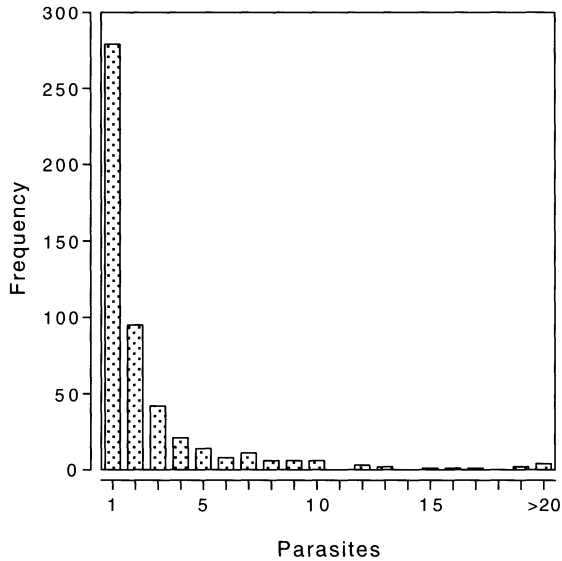


Figure 2.2 Distribution of the reported parasite species per social insect host species, where at least one parasite species has been reported. Data are taken from the records listed in appendix 2, except mites. The mean parasite richness is $\bar{x}=2.63 \pm 4.3$ (S.D., $N=502$ host species; range 1–71).

double-stranded viruses), and Parvoviridae (nonenveloped, single stranded). In the group, the Baculoviridae (BV) have received most of the attention because of their ease of detection and potential as microbial control agents. They account for some 90% of the reported cases in the Hymenoptera outside *Apis mellifera* (Evans and Entwistle 1987, their table 10.11). Baculoviruses are only found in arthropods. Known RNA viruses include the cytoplasmic polyhedrosis viruses, the Picornoviridae, and many others. Unfortunately, among the major social insect groups, next to nothing is known for the Isoptera (termites) and their relation to viruses.

The infective cycle of viruses always involves the attachment of the infective particles to the host cells, uptake into the cell, and uncoating of the virus, followed by expression and replication of the viral genome that leads to the production of progeny. Enzymes both from the virus and the host cell are involved in this process. In insects in general, the primary route of viral infection is the alimentary tract, i.e., when the animal feeds on infected material. Also, larvae are in general more affected by viruses than adults. The parasite usually can penetrate the gut wall only in the midgut section, because the other parts of the alimentary tract are of ectodermal origin and provide an effective barrier against

infections. Apparently the pH value of the intestinal tract is important for the establishment of the parasites. Under the appropriate conditions, the virions or infective stages degrade (e.g., virions of Baculoviridae are susceptible to alkaline conditions: Evans and Entwistle 1987, p. 302). Typically, guts of phytophagous insects have alkaline conditions while those of predatory or scavenging species have low pH values (Evans and Entwistle 1987). Another important element is the presence of the peritrophic membrane that is secreted by and lines the cells of the midgut and that can act as a shield to infections. Viruses are also transmitted transovarially, i.e., via the eggs or reproductive tract to offspring.

Iridescent viruses (IV, Iridoviridae) are known from the honeybee but have not been reported in other Hymenoptera. The name alludes to the typical iridescence observed in infected tissue in many of these viral infections (Tanada and Kaya 1993). Not much is known about the routes of infection. The virus typically resides in the alimentary tract, fat body, hypopharyngeal gland, and ovaries. Thus, it is reasonable to conclude that transmission and infection occur via food, feces, and gland secretions, and the virus can be passed on transovarially to offspring. In contrast to many other honeybee viruses, though, mites seem not to be involved as vectors. The honeybee IV is associated with “clustering disease” of the honeybee (and known to occur naturally only in *Apis cerana*), characterized by unusual inactivity and formation of small clusters of workers (Bailey and Ball 1978). High temperatures usually impede replication of iridoviruses (Tanada and Kaya 1993, p. 258).

Cytoplasmic polyhedrosis RNA viruses have been reported from a wide range of insect hosts (but only 3% of these in Hymenoptera; none in Isoptera: Tanada and Kaya 1993, p. 277). They seem to play no role in social insects. Other small RNA viruses, e.g., Birnaviridae or Picornaviridae, have broad host ranges and often cause inapparent infections. In the honeybee, almost twenty different RNA viruses have been identified (Ball and Bailey 1991).

Picornaviridae that attack insects are well known, e.g., the cricket paralysis virus (CrPV). This virus replicates in the cytoplasm of epidermal cells of the alimentary canal and also in nerve cells of ganglia (Tanada and Kaya 1993, p. 301). Picornaviridae are related to the mammalian polio virus. In social insects, acute and slow bee paralysis virus (APV, SPV), bee virus X (BVX), and sacbrood virus (SBV) are known in the honeybee. The normal pathway of infection is by oral ingestion or through the integument. Symptoms of bee paralysis virus infections are trembling movements combined with sprawled legs and wings, symptoms commonly called paralysis. Sometimes, hairs are lost and the animals get a shiny, black appearance. The disease is actually caused by chronic bee-paralysis virus (CBPV, not a Picornavirus), while APV persists only as an inapparent infection. APV may thus be rather common but often remains undetected because of few visible effects. For example, figure 2.3 shows how the occurrence of APV is revealed by infecting test bees with the extract of seemingly

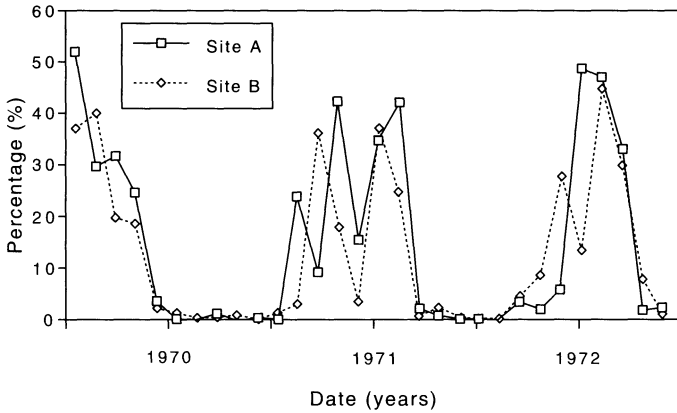


Figure 2.3 Percentage of test honeybee workers killed by acute bee paralysis virus (ABPV) when injected with extracts from seemingly healthy adult bees. Sources of extracts were colonies from two sites (site A, site B) in Rothamsted, England. (Reproduced from Bailey and Ball 1991, by permission of Academic Press.)

healthy bees. The mite *Varroa jacobsoni* acts as a vector and activator of the virus (Bailey and Ball 1991; chap. 3.2). *Varroa* can induce APV and SPV to multiply to lethal levels. Both viruses, however, do not normally cause mortality under natural conditions (B. Ball, pers. comm.). CBPV generates two different classes of syndromes: trembling-crawling bees, or those that are unable to fly and become hairless-black. It is thus thought that diseases like “Waldtrachtkrankheit” (type 1 syndrome) and “hairless-black syndrome” (“Schwarzsucht”) (the type 2 syndrome) are caused by the same agent. Diseased individuals die within a few days, and the affected colonies may collapse within a week (Bailey and Ball 1991, p. 11). The viral particles can be found in the ganglia cells of the thorax and abdomen, in the alimentary tract, and in mandibular and hypopharyngeal glands (Bailey and Ball 1991; Tanada and Kaya 1993). CBPV also has an associated small RNA virus (“chronic bee paralysis virus associate”: CBPVA). It is a satellite virus that interferes with the replication of CPBV (Bailey and Ball 1991, p. 16).

Sacbrood virus (SBV) is well known from the European *Apis mellifera* and Asian *A. cerana* and affects larvae. They become unable to pupate, since the endocuticle of the last instar cannot be shed, perhaps because the formation of chitinase is prevented. SBV is widely distributed and, for example, is the most common virus in parts of Australia (up to 90%; Hornitzky 1987). It can be found in up to 30% of the colonies in Britain. A slightly different strain from Thailand seems to have recently spread over much of the region in the Himalayas (Burma to India). It possibly exhibits a four-year cycle (Verma et al. 1990).

Deformed wing virus in the honeybee leads to deformed emerging adults; it is related to Egypt bee virus. The virus multiplies slowly and is vectored by *Varroa jacobsoni* (Bailey and Ball 1991). Several viruses are associated with the microsporidian honeybee parasite *Nosema apis*. These include black queen cell virus (BQCV), causing dark walls in queen cells. BQCV is also common in workers. Bailey et al. (1981), for example, found an average of 30% infection in workers in twenty-five investigated colonies at Rothamsted. It does not readily infect larvae and adults, even after experimental inoculations (Bailey and Woods 1977). Filamentous virus (FV) multiplies in fat bodies and ovarian tissue of adult honeybees. FV and also bee virus Y (BVY) are loosely associated with *N. apis*, although BVY can exist on its own. They produce no serious symptoms. Bailey and Ball (1991) suggest that infection by *Nosema* reduces host resistance to a point where the viruses are able to infect via the alimentary tract. As *Nosema* develops in the epithelial cells of the midgut, this is conceivable. Both BQCV and BVY have been claimed to add to the pathogenic effect of *Nosema apis*.

Bee virus X (BVX), distantly related to BVY, is another established honeybee virus. It has no relationship to infections by *Nosema* but is associated in a loose way with infections by the amoeba *Malpighamoeba mellifica*, since both the amoeba and the virus are transmitted in the same way—via fecal contamination. BVX develops winter epizootics that take a heavy toll. Cloudy wing virus, Kashmir bee virus, slow paralysis virus, Arkansas virus, and Egypt bee virus should also be added to the list of known honeybee viruses. Some 15% of colonies have been found infected by the cloudy wing virus in Britain. Its prevalence is presumably dependent on the occurrence of (unknown) chance events that affect the rate of spread (Bailey et al. 1981). Kashmir bee virus is remarkably virulent since it kills a bee within three days of infection. It does not only occur on the Indian subcontinent, where it can overlap with its other host *Apis cerana*, but also in New Zealand and Australia. The latter strains are also found to be highly pathogenic. Anderson and Gibbs (1982, cited in Bailey and Ball 1991) suggested that the virus was acquired in Australasia from a natural reservoir of stingless bees, but this has not been substantiated and is now considered unlikely (B. Ball, pers. comm.).

Varis et al. (1992) sampled dead honeybees from England and Finland and checked them for the presence of different viruses. Thirty bees from each sample location were screened by immunodiffusion tests for black queen cell virus (BQCV), bee viruses X (BVX) and Y (BVY), chronic paralysis virus (CBPV), acute paralysis virus (APV), Kashmir bee virus, sacbrood virus (SBV), cloudy wing virus (CWV), and deformed wing virus (DWV), while filamentous virus (FV) was identified with electron microscopy. Hence, their procedure could only reveal the fraction of the viruses found in dead but not live bees, and therefore does not give a true estimate of parasite prevalence. Interestingly, the

viruses occurred in similar proportions in both areas, except for FV. In Britain, FV is one of the most common and least harmful viruses (Bailey 1982). It usually decreases in summer (similar to *N. apis*). BVY was found in about 5% of the samples. It seems remarkable that the prevalence of FV is higher at northern latitudes (Finland: ca. 25%; Britain: 5%) (see also fig. 2.5 for *Crithidia*)—in particular, as winter mortality of hives in Finland (15%) is generally higher than in Britain. CWV was observed in approximately 25% of the samples. In Britain it is thought to increase colony mortality (e.g., Bailey et al. 1983a). Only CPV and BQCV (ca. 1% of cases) were found as additional viruses.

Although only the honeybee and to some extent the fire ant are reasonably well screened for the occurrence of viruses, the few available reports from other species cover distant taxa (Appendix 2.1). For example, Wigley and Dhana (1988, cited in Glare et al. 1993) identified cricket paralysis virus and Kashmir bee virus in the social wasp *Vespula germanica* (Vespidae). Entomopox-like viruses were found in bumblebees (Clark 1982), and acute bee paralysis virus has also been identified in their pollen loads (Bailey and Gibbs 1964). Clark (1982) collected bumblebees from flowers between April and September in Maryland in eastern North America. Of a total of 592 workers examined (*Bombus pennsylvanicus*, *B. fervidus*), 29 contained entomopox-like viruses (4.9%). A further 49 workers from *B. bimaculatus* and *B. vagans* were negative. Clark extracted small amounts of infected hemolymph with microcapillaries through the intersegmental membrane of the abdomen to test for infectivity on healthy hosts. Unfortunately this procedure gave no conclusive result because the workers soon died in the laboratory. All infected bees behaved normally when collected in the field and survived as well as healthy ones in the laboratory. In addition to hemolymph, the hypodermis and the salivary glands also contained viruses. This is somewhat unusual since in other insect families the viruses are more likely to be found in the fat body. The host range of entomopoxviruses seems to be relatively narrow, with little cross-infection between insect families.

The fire ants have been found to be infected by a nonoccluded baculovirus. Infection occurs in the cells of the fat tissue (Tanada and Kaya 1993). Avery et al. (1977; see also Jouvenaz 1986) reported viruslike particles in a species of the *Solenopsis saevissima* complex in Brazil (corresponding to *S. invicta* or *S. richteri* in North America) and also in *S. geminata* in Florida. They were not similar to those seen by Steiger et al. (1969) but more close morphologically and developmentally to those reported from the Rhinoceros Beetle *Oryctes* and the Whirligig Beetle *Gyrinus*. The effects on host mortality could not be reliably determined. An association of these viruslike particles with the microsporidian *Thelohania* that also infects the ants was observed (Avery et al. 1977). Steiger et al. (1969) observed virus-like particles in the cytoplasm of nerve and glia cells as well as in fat bodies of wood ants (*Formica lugubris*).

From these reports, it is safe to assume that the apparent lack of viruses in