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The Biology of the Naked Mole-Rat



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The Biology of the Naked Mole-Rat

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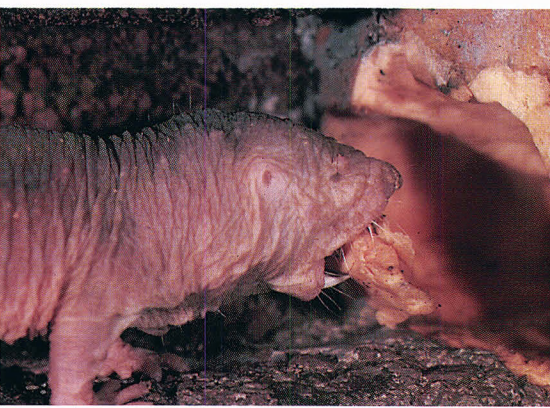
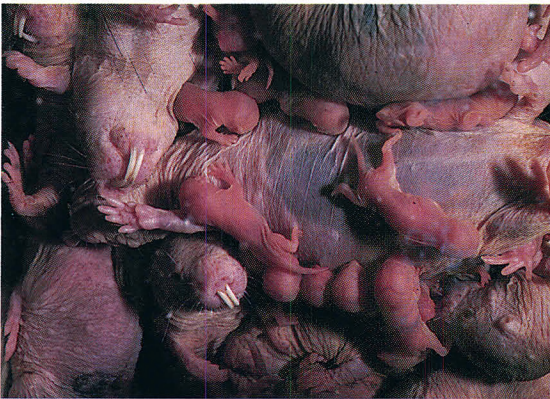
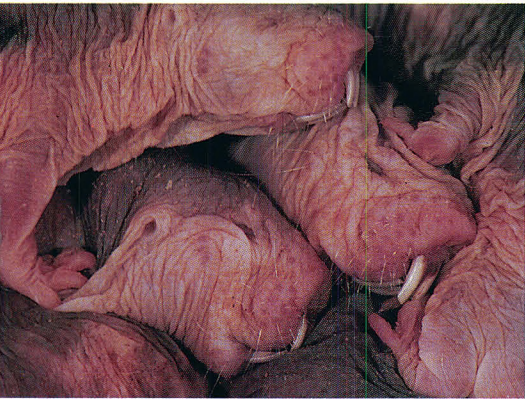
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Preface

This book summarizes our current knowledge of the biology of the naked mole-rat (*Heterocephalus glaber*). The genesis of the book occurred at a meeting in August 1985, at Ann Arbor, Michigan, among R. D. Alexander, R. A. Brett, J.U.M. Jarvis, E. A. Lacey, and P. W. Sherman (plate P-1). At that gathering an outline was tentatively agreed upon and writing assignments were made. Since then the book has grown and changed, partly because of the evolving interests of the participants and also because of our having solicited contributions from everyone active in naked mole-rat research. The resulting volume covers a broad range of topics, including systematics, evolution, ecology, behavior, genetics, reproductive biology, and husbandry; continuity is provided by the common focus on a single species, the use of common terminology, and by frequent cross-referencing among chapters.

This is truly a collaborative book: most chapters have more than one author, and even those that do not have benefited from the input of ideas and often data from several individuals. However, authors have not attempted to reach consensus, and indeed some important disagreements remain. This is to be expected, since the biology of *H. glaber* has been studied quantitatively for only about 20 years. We believe that the differing opinions presented will ultimately enhance rather than detract from the book's value. By highlighting controversies as well as agreements, we hope to point the way for future research on these unusual and fascinating little rodents.

History of Recent Naked Mole-Rat Research

In 1967, J.U.M. Jarvis, who was a graduate student at the University of Nairobi in Kenya, began studying *Heterocephalus glaber* as a part of her dissertation on the mole-rats of eastern Africa. The animals were known to be colonial, and she observed that they apparently cooperated in excavating extensive systems of subterranean burrows. She found no pregnant females in monthly field samples, suggesting that breeding was opportunistic, perhaps depending on rainfall.

By 1974, Jarvis had joined the faculty at the University of Cape Town in South Africa. She returned to Kenya to collect naked mole-rats for physiological studies and attempted to establish breeding groups in the laboratory at Cape Town. Because she was unable to collect entire colonies in the field, Jarvis combined individuals from several different wild-caught colonies. Initially there was considerable aggression, especially among females, in these



Plate P-1 The group that gathered in August 1985 at Ann Arbor, Michigan to discuss naked mole-rat biology, the genesis of this volume occurred at the meeting. From left: R. A. Brett, P. W. Sherman, J. U. M. Jarvis, E. A. Lacey, and R. D. Alexander

mixed colonies. The conflicts gradually tapered off once a female began breeding; thereafter, breeding was usually restricted to one female in each colony. Whether or not the results from these mixed laboratory colonies reflected the situation in nature was at that point unclear.

In the mid-1970s, R. D. Alexander, a professor at the University of Michigan, lectured on the evolution of eusociality at several universities in the western United States. In an effort to explain why vertebrates had apparently not evolved eusociality, he hypothesized a fictitious mammal that, if it existed, would be eusocial. This hypothetical creature had certain features that patterned its social evolution after that of termites (e.g., the potential for heroic acts that assisted collateral relatives, the existence of an ultrasafe but expansible nest, and an ample supply of food requiring minimal risk to obtain it). Alexander hypothesized that this mythical beast would probably be a completely subterranean rodent that fed on large tubers and lived in burrows inaccessible to most but not all predators, in a xeric tropical region with heavy clay soil.

When Alexander presented his lecture at Northern Arizona University in May 1976, T. L. Vaughan was in the audience. After the lecture, Vaughan astonished Alexander by saying “Your hypothetical eusocial mammal is a perfect description of the naked mole-rat of Africa.” Vaughan showed Alexander some preserved specimens of *H. glaber*, and provided him with Jarvis’s address.

Alexander wrote to Jarvis, posing a series of questions about naked mole-rats designed to test whether or not they were indeed eusocial. Jarvis responded to Alexander’s letter in detail, and all her answers tantalizingly seemed to be in the appropriate direction to suggest eusociality. Jarvis later commented to L. Gamlin of *New Scientist* magazine (July 30, 1987, no. 1571, p. 41) “I realized eventually that there was always only one breeding female per colony, and I knew there was division of labor—the penny was beginning to drop. But it was only when I received a letter from Dick Alexander in 1976 that the significance of it really became clear.”

P. W. Sherman had been a doctoral student with Alexander and had studied ground squirrel social behavior for his dissertation; in 1976 he began a post-doctoral fellowship at the University of California (Berkeley). In June 1977, he attended the annual meeting of the American Society of Mammalogists at Michigan State University and heard a lecture by M. W. Hildebrand on adaptations for fossorial life. The behavior of the naked mole-rat featured prominently in this lecture, and a freeze-dried specimen was exhibited. The telephone lines between Berkeley and Ann Arbor buzzed. Sherman and Alexander decided to look at naked mole-rats in the field, and together with their wives, C. Kagarise Sherman and L. K. Alexander, they organized an expedition to Kenya. Jarvis invited them to visit Cape Town on the way.

Alexander and Sherman met Jarvis for the first time in late November 1979. Upon their arrival, Jarvis presented the two Americans with a rough draft of her (now famous) paper on the question of eusociality in *H. glaber* (eventually published in *Science* magazine in 1981). Alexander and Sherman commented extensively on the manuscript and invited Jarvis to join them in Kenya. The five expedition members got together in Nairobi a week later and drove 200 km southeast to the town of Mtito Andei, the site where much of the field research and collecting described in this volume have taken place. In three weeks at Mtito Andei, the researchers gathered basic ecological information (including colony distributions and food plants) and captured individuals from six *H. glaber* colonies, which were returned alive to the United States. These animals and their descendants have been studied at Michigan and Cornell University (where Sherman moved in 1980) ever since.

Over the years, Alexander has been particularly interested in what naked mole-rats can tell us about the evolution of eusociality (chap. 1), hairlessness, and altriciality (chap. 15). From 1980 to 1989 he sponsored four postgraduate students who studied the Michigan colonies. S. Finger and S. Isil investigated

division of labor within colonies, with Isil receiving a master's degree for this work. S. H. Braude completed an undergraduate honors thesis on burrowing behavior in the lab (see Chapter 8) and subsequently began a study of behavioral ecology in the field (chap. 6) for his doctoral dissertation. More recently, J. W. Pepper has studied mole-rat vocalizations in the lab at Michigan (see Chapter 9).

Sherman has worked with numerous undergraduates and three postgraduate students in studying the social behavior, colony structure, and genetics of the Cornell colonies. In particular, E. A. Lacey completed an undergraduate honors thesis on the animals (chap. 10), and S. F. Payne received a Master's degree for her similar behavioral studies. Recently, H. K. Reeve has studied the genetic structure of colonies and the role of the breeding female in colony organization (chap. 11). Given the common focus of Alexander's and Sherman's groups on behavior, they joined forces to develop ethograms of vocal (chap. 9) and nonvocal (chap. 8) behaviors.

In 1980, Jarvis spent 6 weeks in the field, accompanied by R. Buffenstein, K. C. Davies, and M. Griffin. This expedition gathered information on the distribution of naked mole-rats in Kenya, mapped burrows, and explored food abundance and distribution. Three complete colonies and individuals from three others were collected and returned alive to Cape Town. Techniques for maintenance and husbandry were developed (Appendix), and these colonies have thrived and reproduced. Their reproductive biology has been studied by Jarvis (chap. 13) and by four postgraduate students: B. Broll, who is interested in chemical control of reproduction and age polyethism, and R. Buffenstein, E. McDaid, and M. J. O'Riain, who together with P. Ross (University of Witwatersrand) are collaborating to study the factors affecting growth and body size (chap. 12). Jarvis has also sponsored three other postgraduate students, K. C. Davies, N. C. Bennett, and B. G. Lovegrove, who have investigated the ecology, behavior, and physiology of other less social genera and species in the family Bathyergidae (chap. 3).

R. A. Brett came on the mole-rat scene in 1982. Until then, most behavioral data had been obtained from captive animals. For his dissertation, Brett studied the population structure, food distribution, burrowing patterns, and demography of *H. glaber* near Mito Andei, and radio-tracked individuals to investigate activity patterns and to map a complete burrow system. Key portions of his Ph.D. dissertation are presented as chapters 4 and 5 in this volume. In the course of his studies, Brett took four incomplete colonies to the Institute of Zoology in London. The reproductive physiology and the social and hormonal correlates of reproductive suppression in these animals and their descendants have been investigated by D. H. Abbott, L. M. George, and two postgraduate students, C. H. Liddell and C. G. Faulkes (chap. 14).

In 1983, R. L. Honeycutt (then at Harvard) began studying the systematics and phylogeny of the rodent family Bathyergidae in collaboration with D. A.

Schlitter and several postgraduate students. During four expeditions to Kenya, they collected specimens and tissue samples from several hundred naked mole-rats in six localities for genetic studies. These have been analyzed using DNA sequencing technology, mitochondrial DNA (chap. 2), and, in collaboration with K. Nelson and Sherman, using starch-gel electrophoresis (chap. 7).

Taken together, the results presented in this volume thus summarize the first two decades of concentrated research on naked mole-rats. This book is intended to provide a working base of empirical information and a common terminology for future studies of these remarkable creatures and for discussions of the intriguing theoretical issues raised by various facets of their social and reproductive biology.

Organization of the Book

The chapters in this volume fall, roughly, into four sections. The first section (chap. 1–3) introduces readers to the study animals and the many reasons for our interest in them. Chapter 1 is a theoretical treatise on the evolution of eusociality and a discussion of the pivotal position occupied by the naked mole-rat in evolutionary hypotheses for its existence. Chapters 2 and 3 are more empirical, deal specifically with mole-rats, and introduce readers to the systematics and evolution of the rodent family Bathyergidae and to the behavior and ecology of the 5 genera and 12 species in the family. These three opening chapters set the stage for a closer look at *Heterocephalus glaber*.

The second section (chap. 4–7) comprises field studies. These are intended to give readers an understanding of what naked mole-rats are like in nature and to serve as a basis of comparison with the laboratory studies that make up the latter half of this volume. Chapters 4 and 5 present information about colony sizes and compositions, spacing between colonies, the extent and layout of burrow systems, the timing of breeding, colony expansion and fissioning, the types and distributions of food sources, and predation. The following chapter (chap. 6) is a detailed look at participation in “volcanoing” (kicking out excavated soil from within the burrow system onto the surface), which is one of the most important and (apparently) dangerous of mole-rat behaviors. The second section of the book ends with chapter 7, a discussion of the population genetics of *H. glaber*, focusing on inter- and intracolony comparisons based on data from nuclear and mitochondrial genomes.

Chapters 8–11, the book’s third section, describe naked mole-rat behavior and the social organization of colonies. Qualitative descriptions of the animals’ social and nonsocial behaviors (chap. 8) and vocalizations (chap. 9) are presented, along with hypotheses about the functional significance of each. Using these descriptions as a starting point, chapter 10 investigates whether *H. glaber* colonies are collections of individuals that do approximately the same

things or instead are organized into subgroups with specialized functions. In Chapter 11, the behavior of the breeding female, the central figure in the colony, is investigated and her role in maintaining reproductive suppression and in colony dynamics is addressed.

In chapters 12–14, the book's final section, the reproductive biology of captive naked mole-rats is considered. In chapter 12, interindividual variability in growth and behavior is explored, and in chapter 13, various reproductive parameters are described, including the process by which breeding females and males are "chosen," breeding behavior, litter sizes, sex ratios, inter-litter intervals, the development of pups, and reproductive maturity and longevity. Finally, some of the hormonal correlates underlying divisions of labor in reproduction and colony maintenance tasks are explored in chapter 14.

Obviously, questions about the functioning of naked mole-rat societies would best be answered with field data. However, this is impossible because the animals rarely come aboveground, and they abscond if their burrows are tampered with. Thus, chapters in the third and fourth sections are based on laboratory studies. In all cases, the colonies were housed in transparent artificial burrow systems and maintained in quiet, warm, humid, and dimly illuminated rooms. Despite efforts to mimic natural conditions, however, our laboratory set-ups have at least three important differences: (1) artificial tunnel systems are 0.1%–3.0% as long as those dug by wild *H. glaber* colonies; (2) lab tunnels are not earthen, and the mole-rats cannot disperse, expand, or otherwise modify their structure (all attempts at "ant farm" arrangements to house naked mole-rats have failed); and (3) no predators harass lab colonies, no rainstorms afflict them, and they are constantly supplied with large quantities of fresh, succulent foods at predictable locations. Mindful of these differences between the laboratory and nature, authors of chapters in the third and fourth sections of this volume have attempted to relate their findings to field data whenever possible. Nonetheless, their results should be viewed as hypotheses to be tested, eventually, in wild colonies.

The volume concludes with a coda (chap. 15) discussing some of the most intriguing evolutionary questions about naked mole-rats that have not been adequately addressed. This chapter points the way to exciting future research possibilities. To facilitate such endeavors, we have included an Appendix explaining how to capture and transport naked mole-rats and how to maintain them in captivity. The husbandry of this mammal is a bit tricky, and we felt that a summary of our experiences would encourage readers and help them get started on their own field and laboratory studies.

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The Biology of the Naked Mole-Rat

1

The Evolution of Eusociality

Richard D. Alexander, Katharine M. Noonan,
and Bernard J. Crespi

Eusociality is a remarkable topic in evolutionary biology. The term, introduced by Michener (1969), refers to species that live in colonies of overlapping generations in which one or a few individuals produce all the offspring and the rest serve as functionally sterile helpers (workers, soldiers) in rearing juveniles and protecting the colony. The wasps, bees, ants, and termites known to live this way had previously been called the “social” insects.

The recent discovery of eusociality in aphids (Aoki 1977, 1979, 1982) and naked mole-rats (Jarvis 1981, this volume) has provided biologists with new impetus to understand more fully the origins and selective background of this phenomenon, which has already played a central role in the analyses of sociality in all animals (Hamilton 1964) and, indeed, of evolution itself (Darwin 1859). These two new instances both broaden the search for correlates of eusociality in the widely different groups in which it has evolved independently and stimulate comparative study of related species of insects and vertebrates with homologous behaviors verging on eusociality (Eickwort 1981; J. L. Brown 1987; Lacey and Sherman, chap. 10).

An unusual and complicated form of sociality has thus evolved independently in four different groups, and in one, the Hymenoptera, has persisted from perhaps a dozen independent origins (F. M. Carpenter 1953; Evans 1958; Michener 1958; Wilson 1971). Explaining this phenomenon requires attention to a number of different questions. Darwin (1859) answered the basic one, How can natural selection produce forms that would give up the opportunity to reproduce, instead using their lives to contribute to the success of the offspring of another individual?

Darwin’s Question: How Can Sterility Evolve?

Darwin used the origin of sterile castes as a potential falsifying proposition for his theory of evolution by natural selection. He referred to “the neuters or sterile castes in insect-communities . . . [which] from being sterile . . . cannot propagate their kind” as “the one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory” (1859, p. 236). To solve the problem of how the sterile castes could evolve, he generated the magnificent hypothesis, which still stands, that if sterility (or any trait of a

sterile form) can be carried without being expressed, then if those who express it contribute enough to the reproduction of others who carry the trait but do not express it, the trait itself can be “advanced by natural selection” (p. 236). In other words, if functionally sterile individuals help relatives produce offspring and thereby cause enough copies of the helping tendency to be created, then the tendency (ability, potential) can spread. Darwin was particularly concerned with how the sterile castes could evolve their own sets of attributes; his statements indicate that when he spoke of selection at the level of the “family” and “community” in eusocial insects, he was referring to the spread and preservation of traits that exist among the members of groups of related individuals. Thus, in the same context, he noted that “A breed of cattle always yielding oxen [castrates] with extraordinarily long horns could be slowly formed by carefully watching which individual bulls and cows, when matched, produced oxen with the longest horns; and yet no one ox could ever have propagated its kind” (p. 238). Similarly, he remarked that tasty vegetables could be produced by saving seeds from relatives of the vegetables already tasted or eaten and therefore unable to produce seeds. He also noted that cattle with “the flesh and fat . . . well marbled together” could be bred although “the animal has been slaughtered” if “the breeder goes . . . to the same family” (p. 238).

Darwin’s hypothesis could scarcely be improved on today, even though, not knowing about genes, he had to rely on the concept of trait survival, and he had no way of being quantitative. His various remarks taken together are quite close to what modern investigators such as Hamilton (1964) and D. S. Wilson (1980) mean when they refer, respectively, to “inclusive-fitness maximizing” and “trait-group selection.” Darwin’s “family” method of selection to preserve traits is one of those long advocated by agricultural scientists (e.g., Lush 1947). His remarks cited here demonstrate the error of assertions either that Darwin invoked (a simplistic and unsupportable kind of) group selection to explain eusociality or that he did not discuss selection above or below the level of the individual. Darwin also showed in these statements that he understood how organisms can carry the potential (which we now know to be genetic) for varying their phenotypes between profoundly different states, depending on environmental circumstances.

Fisher (1930, p. 177) began the quantification of Darwin’s idea of reproduction via collateral relatives (although he gave no evidence of being aware of Darwin’s discussion when he did so) by developing a hypothesis to explain how bright coloration that attracted (and taught) predators could evolve in distasteful or poisonous caterpillars. He noted that if bright coloration were to spread among distasteful or poisonous caterpillars traveling in sibling groups, then a caterpillar with a new allele making it slightly more noticeable and thus more likely to give its life being tested could thereby teach a predator to avoid the entire sibling group. But, that caterpillar would have to save more than two full siblings, since each would have only a 50% chance of carrying the same

allele for brighter color. (Using phylogenetic inference, Sillén-Tullberg [1988] argued that distastefulness and bright coloration often preceded gregariousness in lepidopterous larvae, but this argument does not negate the possibility of continued exaggeration of these traits among gregarious forms.) Fisher (1930, p. 181) also remarked that tendencies of humans to risk their lives in heroic acts are most likely to have spread and become exaggerated because of the beneficial effects on copies of the genes responsible located in the collection of the hero's relatives.

Haldane (1932) carried the arguments about reproduction via collateral relatives further and also related them to the eusocial insects. (Haldane is reported to have commented [Maynard Smith 1975; pers. comm.] that we should expect individuals in species like our own to have evolved to give their lives only for more than two brothers or more than eight cousins, since brothers have a one in two chance of carrying alleles for such bravery and cousins a one in eight chance. This comment is said by Maynard Smith to have been made sometime in the early 1950s in a pub with only Maynard Smith and Helen Spurway Haldane present [see also Haldane 1955]. The close resemblance of this reported statement to Hamilton's [1964] statement has aroused some attention [see also Hamilton 1976]. In any case, the original idea of reproduction via collateral relatives was Darwin's, its initial quantification was by Fisher, and, as discussed later, Hamilton [1964] first developed it extensively.) Williams and Williams (1957) discussed the evolution of eusocial insects, approximately in Darwin's terms, but they were unaware of Fisher's discussions (G. C. Williams, pers. comm.) and added no new arguments.

Hamilton (1964) not only developed the ideas of Darwin, Fisher, and Haldane extensively, but he also showed that maximization of what he called *inclusive fitness* (a process some others have called *kin selection*, following Maynard Smith 1964) really applies to all social species. The general principle, familiar now to nearly all biologists, is that one can reproduce not only by creating and assisting descendants but also by assisting nondescendant or collateral relatives, and, other things being equal, it pays more to help closer relatives than to help more distant ones.

The Taxonomic Distribution of Eusociality

While these discussions of the process or the mechanics of the evolution of eusociality were going on, another virtually independent discussion of the patterns (phylogeny) of evolutionary change in eusocial forms and their relatives was taking place (Wheeler 1923, 1928; F. M. Carpenter 1930, 1953; Evans, 1958; Michener 1958; Wilson 1971; West-Eberhard 1978a,b; J. M. Carpenter, in press). This series of studies proceeded primarily by description and comparison of eusocial forms with their closest noneusocial relatives and by the

techniques of phylogenetic reconstruction. Thus, Evans (1958) and Michener (1958) provided excellent reviews of the probable phylogenies of social behavior in bees and wasps, respectively. These various comparative and phylogenetic studies revealed that eusociality has persisted from at least 12 or 13 independent evolutionary origins in the Hymenoptera and from only 1 (or possibly 2 or 3; see Noirot and Pasteels 1987) origin in all other arthropods. (An exception is the clonal forms in aphids [Aoki 1977, 1979, 1982], which, according to Hamilton [1987] may have originated many times but suffered frequent extinctions because of diseases and parasites.) This finding shows that Darwin's theoretical answer to the general question of how sterility can evolve is only a beginning. It does not tell us why eusociality appeared or succeeded in the particular taxonomic groups in which it occurs today, and why it either did not evolve or did not persist in any other organisms.

Hymenoptera: The Haplodiploidy Argument

As Hamilton (1964) pointed out, special genetic systems can increase the reproductive benefit from tending collateral rather than descendant relatives. Hamilton showed that the Hymenoptera have a peculiar genetic asymmetry because of their haplodiploid method of sex determination. Because males are haploid, all of a male's sperm are genetically identical. Thus, when a female is monogamous, her daughters share all the genes from their father and half the genes from their mother. In respect to genes identical by immediate descent, daughters share an average of three-fourths rather than the usual half, even though they still share only half the genes of their own daughters. Hamilton offered the reasonable suggestion that this genetic asymmetry may have contributed to the tendency of the Hymenoptera to become eusocial. He added that it might also help explain why hymenopteran workers are essentially all females, since, on the average, one-fourth of a male's genes are identical to those of his sisters.

Hamilton's (1964) papers caused a surge of attention to the question of how and why eusociality evolved, and especially why it evolved more times in the Hymenoptera than in all other animals combined. His cautious and conservative suggestions about the effects of haplodiploidy on relatedness between helpers and their siblings and offspring, and about the prevalence of females among workers in the Hymenoptera, were widely accepted, turned into dogma, and "came to dominate many textbook and popular accounts" (Andersson 1984, p. 166). Indeed, for a while it seemed that most biologists believed that to explain sterile castes one had to locate a genetic asymmetry like that in the Hymenoptera, in which siblings are genetically more similar to each other than to parents and offspring. Bartz for example, writing on the evolution of termites, stated that unless parents are related, their (inbreeding) offsprings' off-

spring will not be more closely related to their sibs than to their offspring, so that “the selection pressure to remain and raise siblings disappears in a single generation” (1979, p. 5765).

This argument has been doubted on several different grounds (Hamilton 1964; Lin and Michener 1972; Alexander 1974; Ghiselin 1974; West-Eberhard 1975, 1978a; Trivers and Hare 1976; Evans 1977; Craig 1979, 1980, 1982; Eickwort 1981; Andersson 1984). Thus, (1) multiple matings by females reduce the closeness of relationship between sisters, (2) males, which also must be tended as juveniles, are not as closely related to females as their sisters, and (3) early in the development of each colony, queen control of sex ratios causes her interests in this regard, rather than those of daughters, to be served. All of these effects (and others that may or may not be relevant to the origins of eusociality, such as multiple reproductive females or short-lived reproductive females, either of which may produce workers that assist reproductives other than their mothers; see, e.g., West-Eberhard 1978a) tend to erode the advantage to potential helpers from haplodiploidy. Moreover, social interactions cannot be predicted from genetic relationships (Hamilton's r) alone (including those caused by sex-ratio biases within broods in haplodiploid forms); to suppose that they can is to ignore variables of age, life stage, and environment that also adjust reproductive costs and benefits ($b + c$ in Hamilton's expression $rb - c > 0$). If nepotism toward collateral relatives required that individuals be more closely related to those relatives than to their own offspring, then nepotism would not be expected to extend beyond the nuclear family except for sisters in haplodiploid, monogamous species.

Following Hamilton's (1964) development of the concept of inclusive fitness, models to help account for the restricted distribution of eusociality were almost invariably developed explicitly either to help explain eusociality in the Hymenoptera or to account for its existence in the Isoptera by incorporating some mechanism that gives an effect paralleling that of haplodiploidy. But haplodiploidy does not occur in two of the three major groups that evolved eusociality (Isoptera and Rodentia). Moreover, haplodiploidy occurs in all Hymenoptera and several other groups of arthropods (Hamilton 1964, 1967; Borgia 1980; Andersson 1984), not merely in the Hymenoptera that became eusocial. Finally, some individuals among the progeny of a eusocial colony do not help rear siblings but become reproductive adults that found new colonies. Unless such individuals are, for some reason, less closely related to their siblings than to their offspring, we need to know about something other than genetic relatedness to explain even haplodiploid eusocial systems.

Haplodiploidy, then, is neither necessary nor sufficient to account for the appearance and maintenance of eusociality. As many authors have recently suggested (as did Hamilton 1964), we are required to search for additional contributing factors. Did the ancestors of termites and naked mole-rats possess traits that have the same genetic effect as haplodiploidy (see, e.g., Hamilton

1972; Bartz 1979; Lacy 1980)? Do some members of these groups possess other distinctive traits, or live in some special circumstances, that contributed to eusociality, as a result of effects different from those of haplodiploidy? Are there relevant features, or combinations of features, common to all eusocial forms or their ancestors and not exclusive to the Hymenoptera? Why was it profitable for the ancestors of eusocial forms to begin to live in groups, and in what kinds of groups did they live? What causes some offspring to remain in the parents' nest? Why do they begin helping? What happened within the social groups in which the ancestors of eusocial forms lived to cause them to continue to evolve along the route to eusociality, and what particular steps occurred along the evolutionary routes leading to the current diversity of eusocial forms? We consider these various questions in order.

Do Termites and Naked Mole-Rats Mimic Haplodiploidy?

As Hamilton (1964) realized, the termites, which have diploid sex determination, represented an embarrassment to the haplodiploid aspect of his argument. Hamilton (1964, 1972), Taylor (1978), Bartz (1979), and Lacy (1980) tried to solve this problem by postulating situations in termites that would mimic the consequences of haplodiploidy. Bartz (1979), for example, argued that if male and female mates in termites are each highly homozygous but unrelated, then their offspring may be more closely related to each other than to their parents because the different gametes of each sex will be very similar genetically. The offspring will also be extremely heterozygous. To re-create high levels of homozygosity, Bartz postulated that within each colony the original parents typically die and are replaced by secondary reproductives from their brood, which inbreed as brother and sister. He argued that, through successive inbreeding, genetic drift (the result of reproduction by only a few individuals) would re-create homozygous genotypes in the eventual reproductives that would found new colonies through outbreeding.

Even if Bartz's (1979) theoretical argument accurately describes life in modern termites, the requirement that nests last several generations to re-create homozygosity suggests that it has little bearing on how helpship and eusociality originated in the orthopteroid (or rodent) line, because we might expect nests to have lasted but a single generation in their noneusocial ancestors, as, for example, in their distant relative, the subsocial wood cockroach *Cryptocercus* (Nalepa 1988). Before dismissing the argument too quickly, however, we must consider the possibility that termites (and naked mole-rats) did indeed live in long-lasting, multigenerational inbreeding groups before they were eusocial and that they later evolved to form new groupings or new colonies at intervals through outbreeding. This could have occurred because of the kinds of places in which they lived. In other words, underground tunnels (naked

mole-rats) or the interior of logs (termites) could provide abundant local food supplies and unusual safety and be long-lasting and expansible, thereby meeting the needs of an enlarging social group (see later arguments). Thus, they could represent niches that would lead to just the situation postulated by Bartz (1979). Naked mole-rats, at least, are apparently extremely inbred (Reeve et al. 1990; see also Honeycutt et al., chap. 7). If Bartz's hypothesis were correct, however, we would predict that naked mole-rats establish colonies by extreme outbreeding. If they do not (there is no evidence of it yet, and Reeve et al. believe that their data indicate continuous rather than cyclic inbreeding), their ability to achieve and maintain eusociality diminishes the significance of Bartz's hypothesis.

Lacy (1980) proposed that if a large part of the primitive termite genome were sex-linked, a significant asymmetry in the coefficients of relationship would have resulted, causing early termites, like haplodiploid forms, to be more closely related to same-sex siblings than to their own offspring. But termite workers are both male and female, and there is no indication as yet that workers of either sex favor siblings of their own sex (see discussion and references in Andersson 1984; Crozier and Luykx 1985). It appears that the evolution of termite eusociality is unlikely to have been based on a male haploid analogy.

Are There Other Traits Relevant to Eusociality?

Although it may seem doubtful that the repeated evolution (or persistence) of eusociality in the Hymenoptera occurred solely because of their haplodiploidy, we still must ask why it happened there so many times and only once in the other 90% of the insects. In the arguments that follow, we are in no way doubting that genetic relatedness (kin selection, maximizing inclusive fitness) is central in explaining cooperation, helping behavior, and the evolution of eusociality. The genetic question addressed is the narrower one of whether the closer relatedness of full sisters, as compared with parents and offspring, in monogamous, haplodiploid forms is sufficient to account for 12 or more separate origins of hymenopteran eusociality, as compared to 2 origins representing all other animals.

Testing the connection between haplodiploidy and the prevalence of eusociality in the Hymenoptera involves determining the relative chances that the Hymenoptera and the rest of the insects, or the entire animal kingdom, would become eusocial, independent of the genetic asymmetry of haplodiploidy. Hamilton's (1964) arguments implied that without the effect of haplodiploidy the hymenopteran and orthopteroid lines would have been equally likely to produce eusocial forms, or at least that the Hymenoptera would not have been 12 times as likely to do so. If we doubt that haplodiploidy accounts

for the greater number of origins (or retentions) of eusociality in Hymenoptera, then we must ask if there are other correlates of eusociality that would have given the Hymenoptera an advantage. Or, is there a correlate of eusociality in the Hymenoptera that is more important than haplodiploidy? The answer to both questions, we believe, is yes.

Subsociality as a Universal Precursor of Eusociality

An old argument in the eusocial insect literature about whether eusociality evolved through a semisocial or a subsocial precursor (see, e.g., Michener 1958) has recently been revived in a slightly different form (Lin and Michener 1972; West-Eberhard 1975, 1978a). In Wheeler's (1923) usage, *subsocial* meant parental, referring to social groups made up of parents and offspring. Wheeler (1928, p. 12), however, restricted the term to forms in which the parent "continuously feeds the . . . [offspring] with prepared food (progressive provisioning)." The offspring of subsocial forms are thus tended or provisioned, though not necessarily all the way to adulthood, and they do not become sterile helpers. *Semisocial*, also an old term in entomology, meant that individuals of the same stage and age aggregate or herd together with (in the usage of Michener 1958) "division of labor (often weak or temporal) or cooperative activity" and (also Michener's usage) "without parent-offspring relationship" (p. 441). Michener (1969) introduced the term *parasocial* to include *semisocial*, *communal*, and *quasi-social*, all of which refer to particular kinds of social activity in bees, involving individuals of the same general age and stage, sometimes sisters. He used *semisocial* to refer to small colonies showing "cooperative activity and division of labor among adult bees as in true social groups" and *subsocial* as "family groups each consisting of one adult female and a number of her immature offspring which are protected and progressively fed by the adult" (p. 304). Here we argue for slightly less specific meanings of subsocial (any species with parental care), thus including Wheeler's (1928, p. 13) "infrasocial stages" 4, 5, and 6, rather than 6 alone, which requires continuous feeding with prepared food (progressive provisioning) and semisocial (aggregations of individuals of approximately the same age and stage) (note that parasociality can be substituted for semisociality in the statements that follow with little change of meaning).

In terms of the origins of eusociality, the contrasting of subsociality and semisociality may have been misleading, because, as Michener (1958) pointed out, all of the so-called semisocial bees that can be used as examples are already subsocial (so, it appears, are the semisocial wasps). Female Hymenoptera that group or share nests are thus already parental. Michener believed that species that preprovision and seal the cells of their offspring could not have been subsocial before they were semisocial because they never associate with

any but their adult offspring, but this point only bears on the question of whether social interactions between juveniles and their parents preceded social interactions between adult siblings or vice versa. The question that Wheeler (1923) first raised must be rephrased to ask, not whether semisociality or subsociality leads to eusociality, but rather whether subsociality (parental care, whether it is progressive provisioning involving social interactions or not) leads to eusociality directly or through semisociality. In other words, to what extent did interactions among adults, taking place in species with adults that were already parental, affect the likelihood that eusociality would evolve? Has cooperative group-nesting among adult bees and wasps facilitated the evolution of eusociality? Did helpers initially aid younger siblings in growing up in nests founded by their mother (or both parents), or did helping first occur among sisters after the mother was dead, so that helpers in fact aided primarily nieces and nephews? Or did both patterns exist during the evolution of eusociality in different forms?

In some modern social wasps, inseminated females found nests together, with only one producing the eggs and the others serving as workers (West-Eberhard 1969; Noonan 1981); in others, nests are founded by multiple queens, which are at least sometimes sisters (West-Eberhard 1978a, pers. comm.), and swarms of workers. In honey bees (*Apis*) and stingless bees (Meliponinae), nests are founded by single queens and swarms of workers. In army ants, which do not have subterranean nests, colonies form by fission. Fission also occurs in "polydomous" ants, and sometimes in termites when colony tunnels become very long, so that the first workers are siblings of the (new) reproductives. In ground-nesting bees, females (sometimes sisters) may cooperate in digging tunnels and guarding communally used nest entrances; some associations seem to involve reproductive division of labor. In some bees, subterranean nests are founded by lone females, which die, leaving their adult daughters functioning in a group in much the same way as multiple foundresses (Michener 1969, 1974, 1985).

These various examples of cooperation among (sometimes) sister reproductives and helpers—without the mother present and sometimes without evidence of age or size differences—raise the question of whether worker castes may not have evolved from helping other individuals (sometimes, at least, sisters) of about the same age, as in nest founding (Lin and Michener 1972; West-Eberhard 1978a). At first this may seem particularly likely, given that, to specialize as workers, helpers require juveniles that need helping *throughout their reproductive lives*. (Specialized workers differ from workers that help briefly but retain a strong capacity to become an independent reproductive, therefore retaining a phenotype virtually indistinguishable from that of individuals that never help.) This condition is facilitated by queens evolving to live longer than their helper daughters. To take the most favorable case, if a female and her worker sisters mature at the same time, she does not need to outlive

them to provide sufficient eggs to use all of their reproductive effort, as would their mother, who would be much older than they.

However, evolution of phenotypic divergence into worker and queen castes (i.e., evolutionary inception of eusociality) in these circumstances would seem unlikely for four reasons. First, as cooperative foundresses, incipient workers would not realize the savings in time possible to matrifilial workers because, upon their emergence as adults, they would not be given the headstart of being provided with eggs, ready to be helped (see also Queller 1989). Second, taking up workership after joint nest founding (as opposed to laying one's own eggs) usually would not circumvent the added time and risks of mating and colony founding (benefits to helpers that simply stayed in the mother's nest), though it may reduce them. Some of these problems are circumvented in groups of cooperative sisters using their deceased mother's nest, but in such cases one has to ask if helping began in the context of aiding the mother's younger offspring (as in the usual lone-foundress matrifilial model) and was later transferred to the sisters' offspring or to even more distant relatives. Third, various unavoidable uncertainties, such as mortality during dispersal and nest founding or in overwintering, would presumably cause facultative helping to be favored over obligate workership. That is, it would appear more difficult, or more indirect, to evolve profound caste differences and to drive the initiation of caste divergence back into the early stages of development, as is the case in highly eusocial modern species (see below). Finally, incipient workers helping nieces and nephews or cousins would have to be able to give much help inexpensively, or else have little chance of reproducing by independent nesting, to make helping pay genetically.

In summary, in group-nesting species with parental females, such as halictine bees (Michener 1969), sisters (or even nonrelatives) may cooperate and show extensive parental care, but most modern eusocial forms tend to have single queens. Group founding of nests in ants and social wasps is often followed by severe aggression, eliminating all but one queen (West-Eberhard 1978b; Rissing and Pollock 1986). Because founding by swarms is derived, helping of nonsiblings by tropical polistine workers (West-Eberhard, pers. comm.) is probably not relevant to the origins of helping. In such forms, presumably, all effort is devoted to developing a colony large enough to resist predation before any reorganization that could result in workers' tending only relatives can take place.

Helpers in eusocial forms typically contribute to the success of younger siblings, not same-age or older siblings and not nieces and nephews. Generally speaking, parental care (subsociality) preadapts species for the evolution of forms of eusociality in which older individuals help younger ones. West-Eberhard (1978a) believed that the first workers in polygynous wasp societies evolved in forms in which the lone founding mother died, leaving groups of sisters (or sisters and granddaughters), some of which lay eggs while others

work. Such forms would seem likely to have preceded others in which the offspring in such a nest formed a group comprising workers and one breeding female. However, they may also be regarded as derived forms (derived from a matrifilial society in which adult females reared or protected juvenile sisters), exhibiting a particular form of group nesting in response to predation or other difficulties of independent nest founding.

Group founding of nests in eusocial forms, it would seem, occurs for one or more of three reasons: (1) new single-queen nests are sometimes vulnerable to predators and parasites, especially when foraging away from the nest is mandatory; (2) subordinate females may be able to replace a queen either by helping or simply by lurking on or near her nest during its early stages (Noonan 1981); and (3) subterranean cavities suitable for nests may be expensive to locate or excavate. All three situations could contribute to cooperation among founding sisters. The question is, did helping among potential queens (sisters or not) contribute to eusociality, or did eusociality actually stem from parental care, where group and swarm nesting involving multiple reproductives are secondary, and cooperation among parental sisters rarely if ever leads to worker specialization.

The implication of these combined considerations is that some small-colony multiple-foundress social wasps and ground-nesting bees have remained in an apparently primitive social (subsocial or small-colony eusocial) condition partly because the selective situations that would lead them to phenotypic divergences paralleling other (small- and large-colony) eusocial insects are less likely to occur among sister foundresses or same-age sisters in their dead mother's nest. In other cases (e.g., honey bees, stingless bees, some tropical wasps that use swarms to found nests), nests initiated by single foundresses have become too vulnerable to predation. These types of nests are especially vulnerable, probably because of the food value of a large colony of juveniles and stored food. Obviously, nest founding by swarms cannot be a primitive trait in the evolution of eusociality. There seems to be no particular evidence that group founding by sisters has simply persisted as a primitive trait, gradually evolving into swarm founding. Neither are there cases of univoltine eusocial species with multiple foundresses. Such cases might be expected from the "semisocial" hypothesis, but they could not occur in species with matrifilial origins of eusociality. It seems to us, therefore, that the paltry evidence available tends to return us to the matrifilial family, founded by lone females or monogamous pairs, as the likely primitive condition preceding the evolution of eusociality in both Hymenoptera and Isoptera (primitively, the founding female need live only long enough to provide her first generation of offspring with eggs or dependent offspring).

In other words, excluding aphids (Aoki 1977, 1979, 1982) and other clone-forming species (e.g., polyembryonic forms), sterile castes may always have evolved in forms that were already extensively parental, whether or not they

have always been preceded in evolution by helpers at the nest that were tending younger siblings. The original social groupings from which eusociality evolved in the Hymenoptera, Isoptera, and Rodentia, according to this hypothesis, would have been composed of parents and their offspring, whether or not groupings of nesting females also occurred.

Parent-Offspring Groups as Ancestral to Eusocial Forms

Parental care can be viewed as a kind of social grouping between parents and offspring. Reasons for group living have been discussed by several authors (Alexander 1974, 1977, 1979, 1987, 1989; Wilson 1975; Hoogland and Sherman 1976; Gamboa 1978; Rubenstein and Wrangham 1987). Alexander and Hoogland and Sherman argued that there are few primary reasons for group living (i.e., selective situations that could account for the origins of group living, as opposed to secondary effects deriving from it or involved only in maintaining or furthering it): (1) clumping on clumped resources (initially involving competitive effects, rather than cooperation, unless cooperative group living had already evolved for other reasons); (2) “selfish” herds (Hamilton 1971) in which individuals use others to facilitate their own safety from predators (also not initially cooperative); or (3) cooperative efforts to secure elusive or powerful prey or to combat some other extrinsic threat, such as predators (or a cooperative effort such as huddling together during winter by flying squirrels; Alexander 1977, 1989). There seem to be no other likely reasons for expecting parent-offspring groups to form. Because parents and offspring are closely related, however, and because such groups presumably form as a part of parental care, some kind of cooperative or helpful effect in respect to either predators or food seems likely always to be the primary reason for the grouping, as is assumed in the above arguments.

Presumably, parents of any species evolve temporary groupings with their offspring because the offspring are thereby protected from predators or can be fed, or both, since feeding offspring is itself likely to be a direct or indirect protection against predators, and protection from predators may facilitate feeding. Thus, a parent that protects its offspring by placing it in a safe place, such as a nest (e.g., monotremes, reptiles, and birds), is likely to create a situation in which feeding the offspring is beneficial because food is probably not maximally available at safe nest sites. Similarly, any parent that simply keeps its offspring nearby (e.g., mammals, many parental insects) also may benefit from providing food, since food suitable for the offspring is often not optimal at locations where it is optimal for the parent. Finally, a parent that places its offspring where food is optimal for the offspring may be constrained to protect the offspring as it feeds (including providing protective nests or other struc-

tures, as in some wasps), since it is unlikely that food resources and predator protection for the offspring are optimal in the same places and times; when they are, parental care presumably does not evolve. Once juveniles are concentrated in locations with abundant food, however, predators are likely to concentrate on the locality, and adding parental care may sufficiently alleviate predator effects so as to enhance the parents' reproduction.

Expanding these considerations may help explain the evolution of parental care in diverse groups such as nesting birds for example, in comparing nesting birds with altricial and precocial young, or mammals that hide their offspring with those that take them along from birth. It may also bear directly on the evolution of eusociality. We argue below that some forms evolved eusociality partly because parent-offspring groups happened to begin living in those rare microhabitats where both food and protection from predators were enhanced by parental care for multigenerational periods.

Taxonomic Distribution and Antiquity of Subsociality

As already suggested, subsociality (parental care involving direct interaction between parent and offspring) may be a universal (and perhaps obligate) precursor of eusociality in sexually reproducing forms. To consider the significance of this argument for the taxonomic distribution of eusociality, we must address some additional, difficult questions. What is the distribution of subsociality in the Hymenoptera compared with the rest of the insects, arthropods, or animals in general? What is the relationship between the distribution of haplodiploidy and the distribution of subsociality outside the Hymenoptera? How many species, in other words, possess each of these two apparent preadaptations for the evolution of eusociality, and how many possess both? We assume that the more widespread a supposed evolutionary precursor of any derived condition in a taxonomic group, the more chances for the appearance of the derived condition.

Far more subsociality is known in the Hymenoptera than in all the rest of the insects (or arthropods) combined, indeed, probably more than in all other animal species. Spradbery (1973) indicated that there are around 35,000–40,000 species of aculeate Hymenoptera exclusive of the 10,000–15,000 eusocial ants. Fewer than 5,000 species of wasps and bees are eusocial (Wilson 1971), and most of the remaining forms are parental; about 10,000–20,000 species carry enough food to their young to take them all the way to adulthood. Not all parents in these subsocial groups interact with their offspring, but at least the stage is set for that possibility (Wilson 1971).

In contrast, fewer than 300 orthopteroids and a handful of other diplo-diploid insects (Wilson 1971; Eickwort 1981) are known or thought to be extensively

parental. The relatives of termites (cockroaches and webspinners) include fewer than 8,000 estimated species, subsocial or not, of which 3,700 have been described (Roth and Willis 1960; Borror and DeLong 1964).

On the basis of numbers of extant species, eusociality evolved once for perhaps every 2,500 modern species of subsocial Hymenoptera and once for every 300 modern species of subsocial orthopteroids. Even without the presumed advantage of haplodiploidy, then, on the basis of frequency of subsociality we might have expected the Hymenoptera to produce eusocial forms almost 100 times as often as the orthopteroids. Roughly speaking, the Hymenoptera include up to 99% (all but 300 of 30,000–40,000) of the modern subsocial species and account for 92%–93% of the origins of eusociality. These figures are approximately what would be expected if subsociality were an essential prerequisite of eusociality, and haplodiploidy (or something else correlated with it, which we argue below is, for the Hymenoptera, complete metamorphosis) had a somewhat negative effect on its likelihood of appearance.

These comparisons, however, involve only the relative numbers of extant species and the supposed numbers of independent origins of eusociality necessary to account for extant forms. It would be more accurate, but obviously impossible, to take into accurate account the relative numbers of subsocial species in hymenopteran and orthopteroid lines throughout geological history, their relative antiquities, and the total number of origins of eusociality. We can state, however, that orthopteroids are considerably older than hymenopterans, the fossil record of cockroaches extending to the Carboniferous (ca. 300 million years before the present [M.Y.B.P.]; F. M. Carpenter 1930) and that of the wholly subsocial order Embioptera (not thought, however, to be ancestral to termites) to the Permian (ca. 260 M.Y.B.P.; Reik 1970). The oldest Hymenoptera are from the Triassic (ca. 220 M.Y.B.P.; Burnham 1978).

Orthopteroids were probably also relatively much more abundant in earlier geological periods, the situation reversing itself at some unknown time (F. M. Carpenter 1930). According to Carpenter, cockroaches made up 80% of the Upper Carboniferous insect fauna, and Burnham (1978) regarded ants as the most abundant insects in Tertiary deposits. The earliest ant and termite fossils are of similar age (ca. 135 M.Y.B.P.; Reik 1970; Burnham 1978). The oldest hymenopteran fossil of the suborder Apocrita (parasitic and parental forms) is from the Jurassic (ca. 180 M.Y.B.P.; Reik 1970; Rasnitsyn 1975, 1977), whereas the oldest bee fossils appear now to date not from the Oligocene (ca. 34 M.Y.B.P.; Burnham 1978), as long believed, but from 100 M.Y.B.P. (a worker of the genus *Trigona*; Michener and Grimaldi 1988). The oldest evidence of eusociality in wasps is from the Oligocene (ca. 34 M.Y.B.P.; Burnham 1978). The antiquity of subsociality in orthopteroids is unknown. There are no fossilized hymenopterans or orthopteroids suggesting origins of eusociality additional to those suggested by extant species (Burnham 1978). As Evans (1977) pointed out, many eusocial lines could have been lost without

a trace, but there is no reason to expect such losses to have been biased by taxonomic group.

Finally, one must also take into account that once eusociality has evolved in a particular form, additional origins may be less likely. The abundance and diversity of ants, for example, surely affects the likelihood that eusocial forms resembling them, either in taxonomy or in life-style, will evolve today; moreover, ants represent a fearsome source of predation for any incipiently eusocial arthropods that begin accumulating food and vulnerable juvenile stages in stationary locations.

Thus, in something less than 180 million yr, subsocial Hymenoptera gave rise to at least 12 different eusocial lines, and in something less than 280 million yr, subsocial orthopteroids gave rise to at least 1 eusocial line. Subsociality may be one and a half to two times older in orthopteroids than in hymenopterans, whereas eusociality may be of equal age in the two groups, though probably younger in bees and wasps than in ants and termites. These figures do not tell us how many subsocial species actually existed in each group across geologic history. For subsociality to account for a 12:1 ratio in appearance of eusocial forms, assuming a 2:1 advantage in time for orthopteroids and no advantage from haplodiploidy for hymenopterans, the Hymenoptera would be expected to have at least 24 times as many subsocial species as orthopteroids. This figure may be accurate for all of geologic time, or even low, but today the Hymenoptera probably have about 100 times as many subsocial species.

Except for not requiring interactions between parents and offspring in defining subsociality, we have not biased the figures against Hamilton's (1964) suggestion; in fact, the opposite is more likely. If, for example, we followed Hamilton (1978; 1980 lecture delivered to the Animal Behaviour Society in Seattle, Washington) and included the parasitic Hymenoptera as possible direct precursors of eusocial forms, we might have expected the Hymenoptera to have evolved eusociality several hundred times as often as the orthopteroids did. Moreover, if we limit our search for subsociality outside the Hymenoptera to the groups that are likely ancestral to termites, we find not 300 cases of subsociality but fewer than 50 actual reported cases.

These calculations are obviously too crude and approximate to be very useful, and no one would have thought to attempt them if the dogma had not been generated that haplodiploidy is sufficient to explain the apparently disproportionate number of origins of eusociality in Hymenoptera. The comparisons just made merely show that there is no empirical evidence that haplodiploidy gave a net advantage to the Hymenoptera in the likelihood of evolving sterile castes and that simply comparing numbers of independent origins of sterile castes does not constitute such evidence. Indeed, the figures just reviewed imply that, to whatever extent haplodiploidy favored the evolution of eusociality in the Hymenoptera, some as yet unknown preadaptations favored the evolution of

eusociality in the ancestors of termites. We believe that such preadaptations did exist in the ancestors of termites, and we develop the argument below. First, however, we comment further on haplodiploidy.

Haplodiploidy and Subsociality Outside the Hymenoptera

Because of widespread association of haplodiploidy and subsociality (Borgia 1980), if all haplodiploid and diploid arthropods were considered, haplodiploidy would probably appear to have promoted eusociality even less readily than is implied above. As Hamilton (1967) first pointed out, haplodiploidy occurs in many subsocial mites, beetles, thrips, and other arthropods outside the Hymenoptera (see Andersson 1984, table 1). Indeed, in arthropods, haplodiploidy seems more closely correlated with subsociality than with eusociality. There is a likely reason for this correlation. If siblings live in groups by themselves, as occurs in many parental organisms (one correlate being that otherwise parents are required to evolve ways of avoiding tending someone else's young), they sometimes may have no one to mate with but one another. Again, as Hamilton (1967) showed, when brother-sister matings are the rule (and males are not parental), it pays a female to make only enough males to inseminate her daughters. The haplodiploid female can accomplish this because she controls the sex of each offspring by controlling the fertilization of each egg as it is laid.

As Borgia (1980) noted, the first time a haploid male was produced, it would have been a macromutation, and we might wonder how such a novelty competed initially. In a sibling group (e.g., of a subsocial form), however, such a male would not have to compete with unrelated, normal, diploid males in the population at large, and, as concerns sexual competition, it would tend to have its sisters all to itself.

Therefore, in all animals, subsociality may frequently have led to local mate competition, and vice versa; and local mate competition, whether preceded by subsociality or not, may have facilitated the preserving of haploid males (e.g., in ancestral Hymenoptera). We hypothesize that while such transitions were occurring, subsociality was here and there giving way to eusociality. Haplodiploidy, when present, almost surely contributed to this situation, especially in species with monogamous females.

Why Are Hymenopteran Workers Female, Those of Termites and Naked Mole-Rats of Both Sexes?

By denying that an advantage from closer relatedness among sisters was the principal reason for the evolution of helpers and workers in Hymenoptera, the

above arguments leave unanswered why hymenopteran workers are female, whereas those of other eusocial forms are approximately equally divided between the sexes. Hamilton (1964, 1972) suggested an answer for the Hymenoptera (see also Lin and Michener 1972; Alexander 1974; West-Eberhard 1975; Andersson 1984). Throughout the Hymenoptera, with rare exceptions (e.g., Cowan 1978; Eickwort 1981), only females show parental behavior. Only the females, in other words, are subsocial. The first helping at the nest in Hymenoptera was probably done by recently emerged adult females. It would seem that natural selection would have favored females that increased the proportion of females in their broods when such early helping was useful or likely (e.g., in first broods). If, in this manner, males were eliminated by their manipulative mothers from the situation in which helping was reproductive, then they would have had little or no opportunity to evolve the ability to become workers.

Female helping in Hymenoptera must have been promoted by the female hymenopteran's powerful flight and her sting (Alexander 1974; West-Eberhard 1975; Andersson 1984; Starr 1985). Evolutionarily, stings were initially ovipositors, then prey paralyzers, then defensive (and less often prey-carrying) devices (Snodgrass 1935; Evans and West-Eberhard 1970). As special aspects of parental care, they are possessed only by females. Because of the widespread divergence in life spans (senescence patterns) between reproductives and workers in many eusocial forms (see below), we believe that nest defense was a central aspect of early helping behavior. Females of the suborder Apocrita possessed the sting and powerful flight abilities—both presumably evolved in the context of parental behavior, primarily as means of finding, subduing, and transporting food to offspring in safe locations—as well as other parental tendencies and abilities. From the start, females of Apocrita were uniquely equipped to be helpers at the nest, and their mothers were preadapted to perpetuate the sex difference in helping by adjusting the sex ratios of their offspring appropriately.

Kukuk et al. (1989) denied the significance of the sting in the evolution of eusociality, but they accomplished this largely by denying it a function except repulsion of vertebrate predation on eusocial nests, which they argue would have been restricted to large-colony derived forms. If stings were used against arthropods, or against small vertebrates such as mice and shrews, however, then even small-colony forms may have benefited. In any case, one must find an adaptive reason for the maintenance of the female sting as a weapon through whatever stages and times were necessary for the evolution of large-colony eusocial forms, assuming that the initial eusocial forms lived in small colonies (see also Starr 1985, 1989).

Why are the workers of both termites and naked mole-rats composed of both sexes? In ancestral termites and naked mole-rats, the female may have been somewhat more parental than the male or even the sole tending parent. Unlike

the larvae and pupae of Hymenoptera, which are tended directly or indirectly until adulthood, the juveniles of termites and naked mole-rats are not helpless for long. They quickly become active and relatively independent (naked mole-rats begin working as small juveniles, about 30 days of age; Jarvis 1981; Lacey and Sherman, chap. 10; Jarvis et al., chap. 12). Moreover, parental care in modern eusocial termites and naked mole-rats, except for nursing and grooming in the latter, is carried out mainly by small (young) animals (see Lacey and Sherman, chap. 10; Jarvis, chap. 13); this surely was not the case in the sub-social ancestors of termites and naked mole-rats. Unlike adult hymenopteran workers, which must have evolved sterility through redirection of already evolved parental abilities, the parental abilities of juvenile termites and naked mole-rats must have evolved concomitantly with the evolution of eusociality or as a part of it. Even if one sex of juvenile termites or naked mole-rats was initially more amenable to the evolution of quasi-parental care, the ancestral termite and naked mole-rat females were not preadapted to adjust the sexes of their offspring easily and quickly to meet changes in the immediate situation, as do hymenopteran females. All of these facts would tend to favor the evolution of more or less equal helper abilities in the two sexes of termites and naked mole-rats.

Why Are Helper Sex Ratios Male-Biased Outside the Hymenoptera?

In diploid species, at least three factors are important in considering likely patterns of altruism between same-sex siblings and between different-sex siblings: (1) sexual (mate) competition, (2) avoidance of deleterious inbreeding, and (3) degree of relationship between the altruist and the assisted offspring relative to the degree of relationship between the altruist and its own offspring (or those of its mate).

Two helper situations are possible in family groups (with one mother): assistance to offspring of siblings or assistance directly to siblings. Sexual competition is greater between siblings (or between parent and adult offspring) when they are of like sex, but deleterious inbreeding can occur only between individuals of different sexes. Thus sexual competition reduces the likelihood of cooperative breeding involving individuals of the same sex, and the risk of inbreeding reduces the likelihood of cooperative breeding involving relatives of different sexes. Because sexual competition is more intense among males, a greater tendency to disperse may be characteristic of females in situations involving a high risk of inbreeding, whereas lowered success in breeding may characterize young adult males. Both factors will tend to produce a male bias among helpers at the nest.

Female vertebrates and insects alike are generally more confident of their parenthood than are males, because a female can usually be more certain that an offspring or an egg came from her body than a male can be that it came from his sperm. (The exceptions are certain externally fertilizing fish and amphibians in which the male is involved more directly than the female in the act of fertilization, and in which, as expected, the male is also more parental than the female [Williams 1966; Alexander 1974].) Therefore, both males and females are, on the average, more closely related to their sister's offspring than to their brother's. Helpers of siblings are most likely to be brothers or sisters of the mother. This bias is most trivial in the case of the ensconced termite king and queen, where the male's confidence of parenthood very likely approaches that of the female; this supposition is reinforced by the presence of nonmotile sperm (Sivinski 1980) and simplified genitalia (Eberhard 1985) in at least some termites. It is difficult, on this basis, to find any reason from kin selection for expecting a bias in the sex ratio of sterile termites.

Let us apply these considerations to the data available for vertebrates, chiefly birds and pack-living canids. The probability of constant association of bird or canine siblings in family groups from hatching or birth to adulthood implies that mechanisms reducing deleterious inbreeding can easily evolve (i.e., individuals ought to be able to recognize siblings as such, if it is important, and to behave appropriately). If so, then sexual competition between sisters might become more important than inbreeding between brothers and sisters in inhibiting helping and close interaction among adults. Moreover, a female's brother should be more willing to invest in her offspring than her sister will be, since, on the average, the brother is less closely related to his mate's offspring than the sister is to her own offspring. The effect is increased whenever a male's ability to sequester a mate and prevent other males' access to her is reduced. This situation is in turn likely whenever the male involved is not a clear dominant or must mate within a group (e.g., a canine pack) in which sexual monopolization of females is difficult or impossible. These facts play a role in the quasi-parental attention shown in some human societies by the mother's brother (Alexander 1974, 1977, 1979; see also Greene 1978; Kurland 1979; Flinn 1981).

Female offspring are also less satisfactory than male offspring as auxiliaries to the reproduction of the original parents. The average relationship of females to their own offspring is greater than their relationship to their mother's offspring because of the possibility of multiple mating and different fathers. This possibility might lead to selection that favors or reinforces monogamy in parents that are evolving to secure an increasing amount of auxiliary parental care from their broods.

All arguments appear to support the notion that in vertebrate families increased parental investment involving nonbreeding adults behaving parentally

most often involves a male's rearing of the offspring of his sister or mother. This is true only if one does not include situations in which one of the conditions of a male's becoming a helper is access (even if secondary) to the reproducing female, as in some human families (Berreman 1962) and in Tasmanian native hens (Maynard Smith and Ridpath 1972).

Once a reproductive pattern involving auxiliary parents has been established, plasticity in reproductive rates matching fluctuations in environmental resources may be accomplished in part through variations in clutch and litter sizes without restricting parental care to the actual parents, especially if only groups are able to capture an abundance of game (as in canines) or to defend a territory (as in birds). Apparently, these conditions could lead to gain from the frequent production of broods containing single females (or a small number, depending on the likelihood of mortality and of beneficial pack fission) and several (more) males. This situation has been recorded rather frequently in wild pack-living canines (Estes and Goodard 1967; Lawick-Goodall and Lawick-Goodall 1970; Lawick-Goodall 1971; Mech 1970; Schaller 1972). Males in such circumstances may more often move between packs singly, though females also do so, apparently as a result of being ostracized by other females; and the presence of two or more females in the pack may often be responsible for large packs splitting into two or more smaller packs. Furthermore, the above situation may account for reports that males other than dominants are sometimes the sole breeders in canine packs containing one female and several males (in this hypothesis her brothers) (Murie 1944). Such a male may be an unrelated joiner of the pack, and the other males may benefit by allowing him to father the offspring of their sister as an alternative to inbreeding.

Occasionally sex ratios favoring females might occur if environmental resources fluctuate such that, after a period favoring auxiliary parents and male-biased sex ratios, monogamous breeding is favored. In a male-biased population in which two parents are sufficient, parents should gain by producing female-biased broods. Maturation would have to occur within a season, or predictability of the quality of seasons would have to extend beyond a year.

The model proposed here to explain sex ratios in temporary helpers at the nest among vertebrates does not incorporate the possibility of sex ratios' being affected by local mate competition or direct differential parental investment in the two sexes. Neither does it deal with the difficult question of the effects of parental investment extending beyond the onset of the offspring's reproduction, a virtual certainty in many mammals. Nevertheless, it appears to account for several observations on vertebrates: (1) a preponderance of males serving as auxiliary parents to the offspring of relatives (several birds and canines); (2) male-biased sex ratios (e.g., several birds and canines; also naked mole-rats; see Brett, chap. 4; Jarvis, chap. 13); (3) a high frequency of litters containing

one or two females and several males (African hunting dogs; Estes and Goddard 1967; Lawick-Goodall and Lawick-Goodall 1970; Lawick-Goodall 1971; Schaller 1972); (4) increases in male biases in the sex ratio during poor seasons or in dense populations (wolves; Mech 1970); (5) significant female biases in the sex ratio during good times (wolves; Mech 1970); (6) movement of lone females as well as males between packs, even though all males are not breeding (wolves; Mech 1970); and (7) occasional nondominant males siring the offspring of single females in packs containing other more dominant males (wolves; Mech 1970).

If all juveniles passed through a period during which they acted as helpers to their parents, dimorphism between helpers and independent breeders would not necessarily be expected, and such dimorphism may be absent in most or even all cooperatively breeding vertebrates. Dimorphism may yet be discovered among some facultatively cofounding or lone-founding *Polistes* queens, in which smaller individuals might be likely to serve as workers to larger ones except during unusually good years or following unusually high winter mortality, when the number of superior nest sites exceeds the number of surviving queens (West-Eberhard 1969; Gibo 1974; Noonan, unpubl. data). To our knowledge, no one has examined the possibility that vertebrates may have consistently different phenotypes correlating with tendencies to produce their own offspring or to assist other relatives in breeding.

Do Orthopteroids and Vertebrates Have Special Advantages?

Two new questions arise out of our arguments concerning the importance of subsociality to the evolution of eusociality. First, what still undiscovered traits or situations enabled or caused the ancestors of termites to evolve eusociality, given that their prospects appear so poor on the basis of their diplodiploid sex determination, the absence of powerful defensive devices, and the relative rarity of subsociality (compared with Hymenoptera) in their ancestors? Except for the efforts to invoke some parallel to the effects of haplodiploidy (above), this topic has been little discussed. The higher vertebrates are nearly all subsocial; birds and mammals are all parental. The second question, then, is: If special genetic asymmetries are not required, why haven't birds and mammals evolved eusociality repeatedly?

We believe that termites and naked mole-rats had two remarkable advantages over the Hymenoptera in evolving eusociality: (1) their gradual metamorphosis; and (2) the distinctively safe, long-lasting, expansible, and food-rich locations that they began to inhabit. To explain this, we must use still another theory to which Hamilton has been a major contributor (Hamilton 1966), Williams's (1957) pleiotropic theory for the evolution of senescence (for a general review, see Alexander 1987).

GRADUAL METAMORPHOSIS

It may be supposed that the evolution of eusociality requires merely an overlap between the reproductive life of the mother and the helping ability of the oldest offspring. For extensive or irreversible worker specialization to be advantageous, however, the parent must live long enough to provide opportunities for the helper to use all of its reproductive effort, its whole lifetime, in helping its siblings. If helpers cannot use their whole lifetimes in helping, they should not evolve to be extensively or irreversibly specialized as helpers, but they should retain the ability to become reproductive (adults) quickly and elaborate the tendency to test continually the existing reproductives and their potential replacements. The alternative is that opportunities for some kind of truly remarkable heroism permit the saving of large numbers of more distant relatives; such a situation may have been involved in wasps that have large numbers of outbreeding queens and highly specialized and irreversible worker-soldiers (West-Eberhard, pers. comm.). However, these wasps may merely illustrate the importance of predators in shaping founding by swarms and avoidance of small-sized funnels in colony formation. Predators also affected the specialization of worker-soldiers, which originally evolved as a result of the care of closer relatives.

One possible solution to the dilemma posed above is for a female to produce a large single brood of offspring that could benefit from assistance across a period approximately equivalent to the helping lifetime of the older sibling. This is roughly what happens each season with the north-temperate-zone paper wasp, *Polistes fuscatus* (West-Eberhard 1969; Noonan 1981). Another solution is that the mother could produce successive, smaller broods of offspring that could be helped, as occurs in most modern large-colony eusocial forms (e.g., termites, ants, honey bees); obviously, this possibility has been enhanced by the evolution of relatively longer lifetimes in reproductive individuals. When mothers do not consistently provide siblings throughout the lifetimes of helping offspring, and helpers retain their ability and tendency to reproduce on their own at some point, situations like those existing in cooperatively breeding birds and mammals prevail.

These considerations lead us to hypothesize that organisms with gradual metamorphosis, such as termites, birds, and mammals, have an inherent advantage in evolving eusociality over organisms with complete metamorphosis, such as the Hymenoptera. Gradual metamorphosis means that juveniles more or less resemble adults and change more gradually into the adult form and function. For example, juvenile termites and naked mole-rats, unlike juveniles of the subsocial Hymenoptera, become self-sufficient at early ages. Because they are more nearly active miniatures of the adults, they could start helping younger siblings while they themselves were still immature and improve steadily in helping ability as they matured. They might also need less help than

juvenile hymenopterans, although this assumption depends on the kind of help needed (e.g., defending the nest as compared to supplying food) and on the manner and extent of change during the juvenile life (i.e., as sociality advanced, very young termites and naked mole-rats could have evolved to use more assistance, and older juveniles could have evolved to become more independent). The overlap of lifetimes required to favor evolution of functional sterility in helpers is more likely if helping begins in juveniles.

Williams (1957), Medawar (1957), and Hamilton (1966) all argued that senescence in all organisms, including ourselves, occurs because of the accumulation of deleterious gene effects late in life and that this accumulation occurs because selection is less potent later in life. Genes acting later in life affect less of each living individual's reproduction and do not affect at all the reproduction of individuals that have died as a result of accidents, predators, or parasites. Either genes with good early effects and bad later ones, alleles with good early effects and no later ones, or genes with the same phenotypic effects but different reproductive effects across adult life, then, would lead to senescence. Despite such deleterious effects, these sorts of genes would persist unless there were alternative alleles whose effects were sufficiently beneficial throughout adult life for them to outcompete genes beneficial early in life and deleterious later. This is an unlikely possibility, especially in long-lived organisms with complex and sequentially patterned adult lives (for a review of the topic of senescence, including much of the recent literature, see Alexander 1987).

Reproductive effort in the form of helping by juveniles would lower the residual reproductive value of helpers and tend to raise mortality, causing the onset of senescence in the juveniles themselves. The result would be a ballooning of the importance of modified juvenile attributes and an even earlier onset of senescence. This process could continue until the juvenile termite or naked mole-rat had evolved never to reach adulthood under ordinary circumstances. It is significant for this argument that termite workers have frequently been described as permanent juveniles (Kennedy 1947; Wilson 1971) and that juvenile hormone promotes worker differentiation in termites (Luscher 1972, 1977; Wanyonyi 1974).

In contrast, hymenopterans, with complete metamorphosis involving a maggotlike larva followed by an inactive pupal stage, cannot begin helping on a large scale until they have emerged in the adult form. Moreover, even if the larva evolves some helping ability (such as silk production in some ants; Wilson and Hölldobler 1980), it cannot gradually improve such workership during development toward the adult stage as can the nymphal termite juvenile. This means that, compared with termites or naked mole-rats and barring differences in opportunities for heroic nest defense, young hymenopterans gain primarily a slight timing advantage from the early onset of reproductive effort by helping younger siblings rather than by reproducing themselves; even this effect can be significant, emphasizing the importance of the ecological

correlates of eusociality (Queller 1989). Although hymenopteran siblings may be needier than termite or naked mole-rat siblings with respect to worker help, a longer period of sustained “parental” effort on the part of helpers would be required for the help to pay off. Thus, in Hymenoptera, selection for the early exertion of reproductive effort (directed toward siblings rather than offspring) would be much less effective than in ancestors of termites in accomplishing intraspecific divergence of life lengths. The divergence is necessary to provide adult offspring with alternatives to independent reproduction that would consistently use all the offspring’s reproductive effort.

Sterility is not an all-or-nothing phenomenon. Differing proportions of helpers without offspring may die because they helped; and most individuals in eusocial castes actually have some ability to make their own offspring in special circumstances. For a reproductive to live long enough to enable a helper to use all of its reproductive effort in helping, reproductive phenotypes must evolve to senesce more slowly than worker and soldier phenotypes, leading to an overlap of the reproductives’ lives with the helper stages of at least the first individuals to undertake workerlike activities (Wheeler 1928; Evans 1958; Alexander 1974; Breed 1975, 1976). In modern eusocial insects this overlap is often extensive. Short-lived helpers and long-lived reproductives characterize all Isoptera and most modern Hymenoptera. This generality links processes of senescence fundamentally to the evolution of eusociality and helps explain why helpers become more resigned to workership in some social species than in others (see below). It also explains the longstanding observation that when mothers and their offspring occur together in the same nest they do not both produce offspring; instead, the situation evidently always involves matrilineal eusociality (Wheeler 1928; Evans 1958, 1977; Alexander 1974).

In some eusocial forms, queens do not live much (or any) longer than the workers. In some temperate forms, such as *Polistes fuscatus*, queens evidently have not evolved to live through a second winter, and they can make all the eggs for new reproductives by middle or late summer without living much (or any) longer than their first-generation offspring (workers). The workers are left with no option but to assist their mother’s reproductive offspring, because they emerge too late to produce adult offspring of their own in time to mate and overwinter (West-Eberhard 1969; Noonan 1981). Why founding females have not evolved to live longer in the bees in which groups of sisters compete (and cooperate) in connection with reproduction in the same nest (Michener 1969, 1974, 1985; Lin and Michener 1972; West-Eberhard 1978a) appears moot.

According to the present model, disruptive selection in effort patterns occurs when parents are able to provide certain of their offspring (at least the firstborn) with opportunities to spend some of their reproductive effort on siblings before they would be able to reproduce on their own without incurring the risks of mating and establishing a new nest. Inclusive-fitness savings in

time and a reduced risk of death before reproducing could even compensate for drops in relatedness to juveniles tended by offspring (such as the necessity of tending half siblings or even nieces or nephews). Both patterns of exerting reproductive effort (on offspring and collateral relatives) would persist in offspring (as facultative developmental alternatives), however, because they could be reproductively equivalent at any time, and the relative advantages of the two patterns usually fluctuate with some predictability during the life of the colony.

SAFE OR DEFENSIBLE, LONG-LASTING, INITIALLY SMALL,
EXPANSIBLE, FOOD-RICH NEST SITES

In addition to gradual metamorphosis, termites and naked mole-rats have the advantage of a safe niche (microhabitat, nest) from which there is no necessity to exit because food is abundant within the site and because the niche is both long-lasting and expansible to accommodate a growing social group. Thus, many termites live within log fortresses, which are also their food. The nest or niche expands as the termites excavate the log, and they may also locate additional logs by burrowing underground and enhance defensibility by thickening or reinforcing walls with mud. Many species have evolved the ability to construct mud tunnels to additional food sources; some also live underground and forage outside on grasses (evidently secondarily; Wilson 1971). Naked mole-rats live underground, feeding primarily on large tubers, which must be approached and located by digging but which provide continuing food sources that do not require exit from the relative safety of underground tunnels (see Brett, chap. 5). At least in termites, nests typically begin small and, in some cases, can be expanded to accommodate thousands or millions of individuals, with abundant food still available locally.

These conditions are unlike those of virtually all social and solitary (nest-building) Hymenoptera, which must locate and transport food back to the nest, often by flying. We suggest that the peculiar combination of nest-site attributes shared by termites and naked mole-rats represents an important contribution to the likelihood of their evolving eusociality, compared with the Hymenoptera and with cooperatively breeding birds and mammals. For the most part, subterranean mammals either do not have abundant food supplies that can be located and used without emerging from the safety of the underground tunnels, or their food is distributed such that, even if they forage underground, the formation and maintenance of groups larger than a parent and its offspring are inhibited (e.g., moles that feed on insects, earthworms, or small subterranean parts of dispersed plants). Similarly, most birds and nonsubterranean mammals live or nest in locations that either are not defensible across generations or cannot be expanded to accommodate large social groups and still be defensible. A few species, such as hunting dogs, beavers, dwarf mongooses, and hole-nesting

birds, produce offspring in relative safety and have evolved ways of moving significant amounts of food back to the den (transport, regurgitation, helper lactation). These are the vertebrate forms that most closely approach eusociality (see also Lacey and Sherman, chap. 10). Presumably, if their niches were expansible and their food supplies sufficiently abundant and localized around the nest site, some of them would have continued to evolve toward large-colony eusociality.

Four conditions can therefore be postulated that might lead to incipient eusociality. All depend on a safe, maintainable, or improvable (and costly or unlikely) nest site. (The third condition assumes monogamy and haplodiploidy; the others assume monogamy but do not require closer relatedness between siblings than between parent and offspring.)

1. Young are produced faster in the incipient eusocial colony even though all or virtually all emigrating nonsocial parents find suitable nest sites and produce viable young. In other words, expanding and improving a particular kind of nest site after it has been located and started is better (for the mother, as manipulator, or for the mother and all participating individual offspring) than distributing descendants among an adequate number of nest sites suitable for the raising of a single brood.

2. Young are produced faster in the incipient eusocial colony, but only because most emigrating nonsocial founders fail to reproduce. In other words, nest sites (or suitable nest sites) are severely limiting (Emlen 1981, 1984; Koenig and Pitelka 1981).

3. Young are not produced faster or saved in higher proportions in the incipiently eusocial colonies, but they are more closely related to helpers than are offspring. Thus, staying home and helping is genetically more profitable than starting a new family if the two alternatives produce the same number of descendants.

4. Young are not produced faster in the incipiently eusocial colony, but they are saved and helped enough to cause their producers to outreproduce noncolonial competitors. In other words, one must imagine that per capita reproduction becomes increasingly effective with three, four, or even up to hundreds of thousands of caretakers (parents and alloparents) as compared with one or two parents.

Nest sites meeting one or more of the above requirements must continue to be safe for multigenerational periods. If new colonies are initiated by individuals or pairs, as in most eusocial forms, nest sites may initially be hidden or inconspicuous or simply not valuable enough as food sources to attract certain kinds of predators. If eusocial colonies continue to increase in size, however, the nest must become physically or behaviorally more defensible because larger colonies of organisms with many juveniles are more attractive and detectable to parasites and predators. Structural defensibility can be enhanced by extending tunnels and making them more complex (enabling flight or delaying

predators), minimizing sizes and numbers of openings into the nest, and enhancing the strength of walls. Behavioral defensibility can be enhanced by evolving tendencies and abilities of helpers to ward off attackers and by increasing the numbers of such defenders. Structural and behavioral defensibility can evolve together as access to a nest is restricted to passages defensible by individuals or small numbers of individuals (e.g., the enclosed paper nests of bald-faced hornets) and as individuals evolve increasingly effective defenses (Wilson 1971) for the particular kinds of structures they defend (e.g., enlarged heads and jaws; expellers of toxic substances as in squirt-gun termites, *Nasutitermes*). There is a sense here in which eusociality is indeed a continuation of parental care of offspring hidden or otherwise made safe in a nest.

Most eusocial forms live in the soil. Underground nests can be relatively invulnerable and also difficult to locate. Aside from army ant colonies, (up to 700,000 individuals), the largest eusocial colonies (ants, termites; up to 10 million) either live primarily in the soil or extend their nests into it (Wilson 1971). Moreover, most eusocial forms that maintain nests in the open (primarily wasps) live in the smallest and least permanent colonies. Their relatives with large colonies (e.g., tropical wasps, honey bees, and stingless bees) invariably enclose the nest, either in a cavity or an enveloping structure (West-Eberhard, pers. comm.). In addition, they have evolved the ability to eliminate the small-colony vulnerable stages from their nesting cycle by swarming to found new colonies, and they are particularly aggressive and feared by humans (and probably other vertebrates). Army ants, which are nomadic and fearsome even to large vertebrates, also fission to start new colonies. Fallen tree trunks appear to rank next to soil as nesting sites meeting the above requirements.

Nesting sites that promote eusociality must also be places where a single female can monopolize the production of offspring and the use of helpers during the early stages in the evolution of eusociality. If our scenario emphasizing such origins is appropriate, these requirements appear to rule out locations, such as caves, where multiple safe and proximal sites for single-female or pair nesting prevent such monopolization.

It seems to follow from the argument thus far that small animals are more likely than large ones to evolve eusociality. We speculate that large animals, such as birds and mammals, may not be able to increase the value of logs and tree trunks sufficiently to allow them to evolve eusociality in such places and that nest-site limitations were thus crucial in such forms. Several predictions about vertebrate sociality follow. First, the most nearly eusocial vertebrates should be expected to live in the soil, in large hollow trees or logs, or in constructed dens with similar characteristics (as do beavers). Second, if, for example, giant hollow trees and, say, hole-nesting social woodpeckers or kingfishers coexisted long enough, our argument would predict the evolution of eusociality. Third, if caves typically had structures in them, such as hollow

spheres with small openings (spheres that could be expanded), then either birds or bats might have become eusocial.

Many small organisms live in apparently suitable sites yet have not evolved eusociality. Some may have failed to do so because parental care is of little or no value to them. Others, such as subsocial Embioptera, Gryllidae, Dermaptera, Hemiptera, Coleoptera, Scorpionida, and Arachnida that live subsocially in seemingly appropriate sites (but which, for one reason or another, may be too short-lived), may lack the ability to initiate evolution of adequate defense of a nest site or may not have been subsocial long enough. Many of these small forms are semelparous, and it seems obvious that the ancestors of all eusocial forms were iteroparous. Semelparous adults are not likely to improve nesting sites significantly or to create conditions leading their offspring to tarry at the nest. Moreover, even if some offspring did tarry, there would be no younger siblings to help unless the parents were iteroparous.

It may seem that eusociality should evolve much more easily in the tropics, because it is easier to establish there the kind of more or less continuous breeding that accompanies increasing colony size and continued nest defense. The life cycle of temperate insects may usually be so set by the seasons as to make it quite difficult to initiate continuous breeding as an aspect of the initiation of eusociality. This speculation seems to predict that persistent subsociality in the soil and in wood may be more prevalent in temperate regions than in the tropics (when it occurs in the tropics it is more likely to change to eusociality) and that eusocial insects evolved in the tropics. However, the possibility of seasonality yielding the selective situation that would lead to obligate workership in first broods without altering life spans in workers or queens, as described above for *Polistes fuscatus*, represents a counterargument.

Further Comments on Vertebrate Eusociality

It may be an oversimplification to assume that there are no eusocial vertebrates except naked mole-rats (see also Lacey and Sherman, chap. 10). African hunting dogs and wolves live in packs that hunt cooperatively. In some cases, one female and one male have pups, and their offspring from the last season or two help them rear the young, carrying back meat that they regurgitate for the pups and probably protecting them and their parents from some kinds of danger (Lawick-Goodall and Lawick-Goodall 1970; Mech 1970, 1988). Surely, helping in some of these species regularly causes helpers to produce no offspring. But the social groups are smaller than those of the eusocial insects, and there is no evidence yet of morphological divergence of parental and helper phenotypes.

Some cooperatively breeding birds behave like the social canines (Emlen 1984; J. L. Brown 1987) and, possibly, beavers (Wilson 1975), dwarf mon-

gooses (Rood 1978), and naked mole-rats (Jarvis 1981; Lacey and Sherman, chap. 10; Jarvis et al., chap. 12; Faulkes et al., chap. 14). Some of these mammals and birds are similar to some wasps and bees, in which groups are small, phenotypes have diverged little or not at all among castes, obvious competition occurs among potential breeders, and high proportions of helpers seem to be waiting and watching in case they get the chance to breed.

In contrast to mammals, birds would appear to be significantly hampered because they cannot simultaneously expand nest sites to accommodate large numbers of individuals and defend them in stationary locations on a multigenerational basis. They do not possess sting equivalents to deal with the kinds of predators that wasps and bees are able to deter, and, as a consequence, they are not able to construct and use expansible nests equivalent to the exposed paper and mud nests of Hymenoptera.

Helper and parental phenotypes may also have failed to diverge in vertebrates because the jobs of parents and helpers do are very similar. Vertebrate workers may not have the same opportunities as eusocial insects for magnificently reproductive (family-saving) suicidal acts (probably in defense against vertebrates) and the specializations improving the ability to do them (West-Eberhard 1975). Canines probably lack the kinds of predators that could guide such evolution. Birds may have the predators but nothing paralleling the venomous sting of female Hymenoptera. One hymenopteran worker can deter either a huge predator (like a human or a bear) that can destroy its whole family (of hundreds or thousands) in one swipe, or a bumbler that could do it only by accident. By plugging a break in the nest fortress, one termite can also deter a predator. It is more difficult for most vertebrates to be such heroes, though such opportunities may exist for naked mole-rats when predatory snakes enter their burrows (see Jarvis and Bennett chap. 3; Brett, chap. 4; Braude, chap. 6).

Mammalian and avian social groups (other than "selfish herds") never get as big as those of the eusocial insects, and this also restricts the opportunities for superreproductive heroism. The ultimate heroes among eusocial forms are the polistine wasp and honey bee soldier-workers whose barbed stings cannot be extracted, making their attacks on predators irreversibly suicidal. One predicts that barbed stings will be used for defense only in species that form new colonies in swarms, such as honey bees and some tropical wasps. In very small colonies, workers are too valuable for suicidal attacks to be beneficial. The only other barbed stings are those of some ants, which evidently use them to kill prey (A. Mintzer, pers. comm.), and those of the wasp genus *Oxybelus*, which uses them to carry prey (Evans and West-Eberhard 1970); the prediction thus seems to be met.

Another reason why the vertebrate reproductive and worker failed to diverge sufficiently could be the relatively great behavioral plasticity of vertebrates, which reduces the likelihood of the evolution of alternative phenotypes (separate and discontinuous; behavioral, physiological, and/or morphological).

(Environmentally determined alternative phenotypes have evolved thousands of times in insects, not merely in connection with social life, but much more frequently in regard to dispersal in species in short-lived habitats, e.g., the phases of migratory locusts, alary morphs in Orthoptera and Hemiptera, alternative phenotypes in successive generations or on different hosts in aphids.) Assuming that vertebrate helpers at the nest improve the reproduction of their parents or siblings, their failure to evolve sterile castes may result from the absence of long-term predictable fluctuations in the reproductive value of helping versus reproducing directly. Again, the reversible flexibility of the individual vertebrate phenotype may be partly responsible for damping the effective severity of such fluctuations, and the relatively long lives and the iteroparity of vertebrates may have reduced the number of such fluctuations.

Causes and Effects of Queenship: Tracing Probable Changes as Eusociality Evolves

WHY DO SOME OFFSPRING TARRY IN THE PARENTS' NEST?

The point at which offspring leave the parent's care is a dangerous one. It would not be surprising to find offspring sometimes remaining in a parent's proximity after parental care had diminished to virtually nothing, particularly if the parent locates or builds a nest that is somewhat safer than the rest of the world. In other words, if the parent owns a relatively safe nest or home site, then an offspring can prolong parental care merely by remaining there. Even if the parent no longer gives benefits directly to the offspring, merely tolerating its presence increases the offspring's safety from predators. As a result, adults temporarily unable to locate suitable nest sites or mates may profit by spending time at the natal nest.

An adult offspring tarrying in the parent's nest would thereby be in a position to aid the parent in tending younger siblings. Thus, one might expect that helpers at the nest would appear in species with relatively safe nest sites (or the ability to protect offspring that stay nearby), species for which it is often temporarily difficult or dangerous to begin new nests, and especially, species for which both conditions exist.

As many authors have suggested (e.g., Emlen 1981; Koenig and Pitelka 1981; Woolfenden and Fitzpatrick 1984), starting new nests may be difficult or expensive because the habitat is already "filled" with nesting pairs or families. This would be especially likely if safe new nest sites, such as hollow trees, decaying logs, or particular kinds of underground niches, were a scarce resource. For some species, new nests are always expensive because older nests become safer through the efforts of their owners. This alone could create

conditions in which helping might pay off genetically for some offspring, specifically those that mature at the opportune times. As argued earlier, improvements in parents' reproductive situations (nest safety, food supply) could make it profitable for older offspring to stay in the natal nest to feed or protect siblings, whether or not they were as closely related as their own offspring, rather than to attempt starting a new nest (Alexander 1974; Andersson 1984). Part of this advantage could come simply from the parents' being able to provide juveniles that can profit from assistance either more quickly or in greater numbers than the newly adult offspring can provide for itself.

HOW QUEENSHIP BEGINS: ASYMMETRY IN RELATEDNESS OF MOTHER AND DAUGHTER TO HELPED INDIVIDUALS

Let us try to reconstruct the sequence of steps by which queenship, and therefore eusociality, is initiated in matrilineal societies. When offspring initially start to help at the nest, they may be presumed to be unspecialized for helping and thus to have phenotypes similar to those of their parents. Females can either be inseminated or not. Assuming that at least sometimes they are inseminated and therefore can lay eggs (in Hymenoptera they could lay male-producing eggs even if unmated), what will happen if, say, a mother and daughter are both producing eggs? As Charnov (1978) has suggested, in matrilineal colonies, mothers that suppress their daughters' reproduction—for example, by eating their daughters' eggs (egg eating is a phenomenon commonly observed on wasp nests)—gain over those that do not, because daughters' eggs produce grandchildren that share only one-fourth of the mother's genes, whereas the mother's eggs produce daughters that share half the mother's genes. Therefore, eating of daughters' eggs by mothers is expected to spread.

Daughters that eat their mother's (female-producing) eggs do not gain genetically if their mothers are monogamous, because their mother's eggs produce sisters to the daughters, which, on the average, share half (termites) or three-fourths (Hymenoptera) of the daughters' genes and the daughter's own offspring also share only half of her genes. Sisters that lay eggs, however, produce nieces that share only one-fourth (or three-eighths) of the genes of a potential egg-eating daughter. Therefore, if they can make the distinction, daughters should be expected to eat their sisters' eggs but not their mother's (in haplodiploid forms, this argument applies only to the female-producing eggs of mothers; see Ratnieks 1988).

We can extend the egg-eating example or generalize from it: Mothers should evolve to prevent their daughters from attaining reproductive maturity or reproductive condition. Prevention could include a variety of activities, such as suppressing hormone production or interfering with the daughters' likelihood of being inseminated. Daughters, on the other hand, are expected to be passive about becoming reproductive, so long as their mothers have

throughout history been monogamous, their sisters are not likely to become reproductive, and their mother is providing them with all the siblings they are able to tend and is likely to do so for the daughters' entire adult lives (i.e., the mother gives evidence of being healthy and vigorous).

One expects, then, an asymmetry in the behavior of mother and daughter from the beginning. The mother is expected to prevent her daughter from producing offspring, and the daughter is not expected to resist. The same mother-daughter asymmetry prevails under both haplodiploidy and diplodiploidy, and with respect to fathers and sons under diplodiploidy.

The mother is also expected to resist taking on risky tasks that might cause her own death and leave her daughter in charge of the nest, because the daughter can only produce offspring half as much like the mother as her own offspring. Mothers thus gain from avoiding dangerous tasks that can be assumed by daughters, tasks like foraging and defending the nest. Before any specialization of mothers as offspring-producers (that do not defend the nest or forage) and of daughters as workers or soldiers (i.e., when daughters are potentially just as reproductive as their mothers), daughters (under diplodiploidy) presumably have the same interest in avoiding dangerous tasks as the mother. Once the slightest difference between mothers and daughters has appeared — even if it is only a matter of individual experience that makes the daughter slightly better at foraging or defense or the mother slightly better at egg production — the daughters are expected to be immediately more willing to undertake riskier tasks than the mother. They should explicitly be more willing to undertake such tasks when doing so decreases the risk to the mother. The first reason for risk taking is that the mother has now become a better producer of juveniles that share half (or more) of the daughter's genes than the daughter herself. She can even continue this activity after the daughter is dead, should the daughter lose her life protecting the mother. Second, the daughter does not gain from protecting some of her sisters if she and her mother both lose their lives as a result (as opposed to the daughter's losing her life protecting her mother while her sisters also lose theirs). This is true because if the daughter and mother both die and the colony lives on, from a nonreproductive daughter's viewpoint, its offspring will be nieces produced by sisters. The survival of a worker's mother is more important than that of her sisters. Although workers in a eusocial colony appear mainly to be tending siblings, their primary duty, other than defending the nest, is evidently to protect their mother, the queen.

The above asymmetry presumably begins because mother-daughter teams that assume the above relationships to one another reproduce more effectively than those assuming symmetrical or other relationships. Presumably, mother-daughter teams do not form except when the pair can outreproduce other mother-daughter pairs that breed independently of one another. The second general part of this model (below) attempts to identify situations in which this condition prevails.

REASONS FOR DIVERGENCE OF PHENOTYPES OF
MOTHER AND HELPER

Offspring taking up defensive or foraging activities on behalf of sibs in their parental nests before leaving to reproduce independently experience an earlier onset of reproduction (by helping sibs). They may also experience higher mortality from extrinsic causes immediately after the onset of reproduction than do their contemporary siblings that leave to reproduce independently as soon as they mature. These two important parameters help shape senescence by natural selection because mortality rates affect the potency of selection across lifetimes (Williams 1957; Hamilton 1966; Alexander 1987). The differences in the two parameters for helping and nonhelping offspring would tend to accelerate the senescence of helper phenotypes compared to reproductive ones and thereby diminish the importance of any direct reproduction that helpers achieve later after they leave their parental nests. The self-aggravating nature of senescence would cause the lifetimes of workers to continue to diverge through shortening of worker lifetimes. At the same time, the longevity of reproductives increases if workers consistently assume the riskier parental duties. The reproductives are then freed to use more completely durable, defensible nest sites, and the durability of these sites may even be extended as a result of worker labor and defense. In turn, the benefits to helpers of staying at the parental nest and exerting even more reproductive effort on behalf of siblings would be enhanced. The positive feedback just described potentially can cause divergence of helper and reproductive phenotypes to the point at which the reproductive lifetimes of the helper and its parent overlap completely, and direct reproduction later in life becomes so negligible that helpers gain reproductively by becoming effectively or even obligately sterile. This divergence can occur even if lifetimes of both helpers and reproductives are lengthened as a result of a shifting of colonies into safer locations (burrows, logs) as sociality evolves.

These arguments, and those given earlier regarding the evolution of senescence, mean that, in a cooperatively breeding species, even slight divergence between mother and daughter with respect to ability to lay eggs and help at the nest, respectively, will in many situations set into motion a continuing selection for divergence in their phenotypes. The higher mortalities of helpers and the correlative lower mortalities of mothers will lead to differences in their senescence patterns, and the greater the divergence between the two kinds of life patterns, the more effective will be the selection for divergence. For example, when the mother has evolved to be somewhat less than twice as good as her daughters at reproduction, leaving aside the daughters' ability to forage and defend as compared to the mother's, the daughters would be expected to be indifferent about replacing even a promiscuous mother (although they are not indifferent about whether or not she is promiscuous). More precisely, this