

In Richard D. Alexander, Paul W. Sherman, Jennifer U.M. Jarvis (Eds.), *The Biology of the Naked Mole-Rat: (Monographs in Behavior and Ecology)*, Princeton University Press, 1991; pp. 3-44

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The Evolution of Eusociality

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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 helpers 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 also 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 (subsociability) 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 (subsociable 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 Subsociety

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 diplodiploid 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. Subsocality 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 Goodard 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 diploid 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 matrifilial 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

situation would occur when the mother and daughter team of baby-producer and worker is twice as good as the mother and daughter operating separately or with their roles reversed. The limits on divergence between queen or worker phenotypes will be set by the point at which optimal helping and optimal queenship are achieved, given particular extrinsic conditions and the relationship of queenship and helping to one another in the particular kind of social life involved.

Under complete metamorphosis, the hymenopteran mother, in contrast to termite and naked mole-rat mothers, appears to be able initially to give to her helping daughter only a small timing advantage, since the daughter cannot help until she has emerged in adult form. Even if reproductive female hymenopterans were always monogamous so that their incipient worker offspring were more closely related to sisters than to their own offspring, how could the hymenopteran mother evolve a lifetime long enough to use all of any of her offsprings' reproductive effort? All social Hymenoptera forage for their food and the food of their offspring outside the safety of the nest. Many fly during this foraging, and many have stings and aggressively defend the (often exposed) nest. Hymenopteran helpers thus tend not to be soldiers and workers but foraging soldier-workers. Soldiering is presumably the most dangerous task of all.

Naked mole-rats and termites, in contrast, protect themselves by living underground or inside their food (wood), which itself presents a barrier to predators, and all have relatively nonaggressive workers (and, in termites, separate soldier castes). Some termites that dwell and forage underground lack a soldier caste (Sands 1972), although young termite colonies tend to invest earlier and more heavily in soldiers than do ant colonies (Krishna and Weesner 1969; Haverty 1977).

Both long-distance foraging and aggressive nest defense are high-risk tasks, and specializations for their efficient execution should lead to rapid senescence in worker phenotypes because of the effect of high mortality rates on reproductive value (see also Oster and Wilson 1978). At the same time, the relief of the hymenopteran parent from these same high-risk duties would lower mortality and select for long life in the reproductive phenotype. The same divergence has obviously occurred in termites, but it involved replacing the adult stage in evolving workers by extending juvenile stages, including stationary molts in lower termites; reducing the numbers of juvenile instars in higher termites; and "workerizing" effects of juvenile hormone, in contrast to effects of juvenile hormone that bias morphology and physiology toward the reproductive stage in hymenopterans (Luscher 1977).

The above discussion still leaves bothersome questions. If the exposed nests of Hymenoptera tended to cause shortening of worker-soldier lifetimes, and the protected nests of termites and naked mole-rats tended to inhibit divergences of lifetimes in reproductives and workers because of lowered risk to

workers, then how have the astonishing differences in life spans of termite workers and queens come about, and why is there as yet no evidence of divergences of life spans in naked mole-rats?

It seems necessary to postulate that, even though termite nests are relatively safe from many or most kinds of predators, certain threats have allowed highly reproductive heroic acts by helpers. Perhaps such acts involve primarily arthropod predators and include soldiers placing their heads in openings in the nest (as with nasutes) or workers repairing a nest break. Single individuals or small numbers might thereby save the entire colony from arthropod invaders. Perhaps naked mole-rats have indeed evolved divergent life spans between breeding females and workers. We still do not have enough data to show this effect, although the continual monitoring behavior and high levels of activity and aggression of the breeding female (Reeve and Sherman, chap. 11) suggest otherwise. More likely, perhaps, naked mole-rats have consistently lacked the kinds of predators that caused situations in which dramatic heroism could be repeated, yielding dramatically shortened life spans in workers. It is important that heroism here be understood as involving a high likelihood of mortality in members of one caste as a result of acts that have a high likelihood of protecting members of another caste.

If the above arguments concerning the importance of early reproductive effort and senescence in the evolution of workers are correct, then certain general predictions about queen and worker life spans are possible. Hymenopteran females undertake considerable risks in hunting and subduing prey. The evolution of eusociality in such forms should involve increased risk of extrinsic mortality to helpers and decreased risk to reproductives, leading to a reduction in worker life span and an increase in the life span of the queen compared with those of solitary relatives. Maximum life spans of eusocial hymenopteran queens (determined in the laboratory) are much greater than those of solitary relatives (Wilson 1971), whereas those of workers are generally similar (in ants) or shorter. Termites invading sound wood from habitats under bark filled with competitors and predators (Hamilton 1978) probably experienced a reduction in extrinsic mortality rates of both helpers and reproductives. As would be predicted, the life spans of termite kings and queens are much longer than the adult life spans of cockroach species, the longest known of which is that of the semelparous subsocial American woodroach, *Cryptocercus punctulatus*, which seems to tend its brood somewhat longer than 3 yr (see Nalepa 1988). Life spans of termite workers and pseudergates (so-called false workers) are probably slightly longer than those of most cockroaches.

The longest-lived workers among termites should be found in the wood-eaters inhabiting large logs, the shortest in grass-eating forms with foraging workers (cf. wood-dwelling *Kaloterme*s, *Neoterme*s, and *Reticuliterme*s with *Mastoterme*s and other species that have open-foraging workers; see Oster and Wilson 1978). A problem with this comparison is that the species with open-

foraging workers generally inhabit large, complex colonies that are notoriously difficult to maintain in the laboratory. Therefore, the recorded maximum life spans for these species are more likely to be underestimates than are those for the wood-dwelling species. Among eusocial hymenopterans, the workers of flying wasps and bees should have the shortest life spans, especially when nests are exposed and the workers are highly specialized for defense (e.g., honey bees, which have barbed stings). Comparisons among different ant species should parallel those predicted for termites. It might be expected that the least aggressive, most helpless, most protected reproductives (e.g., those that found new colonies by fission or are otherwise "claustral" as opposed to foraging ant queens) should be the longest-lived reproductives. In fact, claustral lone foundresses are not longer-lived than foraging lone foundresses. Foraging by ant queens, usually confined to the period when the first workers are raised, may have little effect on their senescence rates because the initial workers have come to represent the queen's somatic rather than reproductive effort (Lin and Michener 1972; West-Eberhard 1975) and senescence begins only after the onset of exerting reproductive effort (Williams 1957; Hamilton 1966). The same problem applies to a comparison of claustral queens founding colonies with swarms founding colonies.

SENESCENCE AND DEVELOPMENTAL PATHWAYS IN TERMITES

Schedules of extrinsic mortality associated with different tasks, through their effects on life patterns of reproductive effort, should influence developmental pathways in termites in which flexibility is possible through larval, stationary, and nymphal molts (castes often vary with instars in termites; Wheeler 1928; Oster and Wilson 1978). Thus, among termites, workers in wood-dwelling species should be most capable of becoming soldiers because they are more apt than open-foraging workers to have long, somewhat indefinite life spans (Miller 1969). Soldiers in all termite species should be less apt to become workers than vice versa (Hewitt et al. 1969; Miller 1969; Noirot 1969; Wilson 1971; Watson and Abbey 1977). According to Gay (1968), soldier-nymph intercastes are more common than worker-nymph intercastes, but both are aberrations and exceedingly rare. Similarly, the ability of workers (or pseudergates) to molt into reproductives (neotenic or imagos) after functioning as workers should be reduced or suppressed in species whose foragers experience high extrinsic mortality. In fact, workers (pseudergates) have the capability of molting into reproductives only in lower termites, which do not forage openly, and soldiers in these species apparently lack the capability of becoming reproductives (Wilson 1971). A parallel in ants occurs in some species in which workers have rudimentary spermathecae and soldiers do not (Wheeler 1910). Recent views suggest that determinate workers may be associated with exposed foraging in both lower and higher termites (Hewitt et al. 1969; Noirot

1969; Watson et al. 1977), and indeterminate neuter castes may be restricted to the wood-dwelling *Kalotermitidae* (Watson et al. 1977).

REASON FOR AGGRESSION BETWEEN MOTHER AND HELPERS IN SMALL-COLONY EUSOCIAL FORMS

Eusocial species may be divided into small-colony forms (up to ca. 1,000 individuals) and large-colony forms (from ca. 1,000 individuals to several million). In small-colony forms (e.g., sweat bees, allodapine carpenter bees, bumblebees, some paper wasps, and naked mole-rats), the queen is the most active and aggressive individual in the colony; we believe she is continually monitoring the reproductive status of others and defending her right to produce offspring. (Reeve and Sherman [chap. 11] believe that queen aggression in small-colony forms may also incite workers to greater activity.) In large-colony forms (e.g., termites, honey bees, stingless bees, most ants), the queen may be passive, or even helpless, with workers not only tending her but coming to her for the pheromones that determine their nature as sterile helpers. In small-colony forms, castes are typically undifferentiated in morphology, physiology, or life span; in large-colony forms, there is typically dramatic differentiation in all these regards. In small-colony forms, the queen appears to control production of offspring, including sex ratios; in large-colony forms, workers sometimes control the proportion of males produced and may even produce the males. Because this division into two main categories does not appear to have been made previously, we do not know how many colonies lie between these extremes, nor have we yet attempted to describe the combinations of the above conditions expected in colonies of intermediate sizes. Wilson (1971) divided eusocial colonies into four sizes and discussed primarily degrees of caste differentiation and queen dominance.

From the outset, it is important to a daughter that the mother remain reproductive and healthy. If the mother is failing in these regards, then the daughter gains from assuming the role of reproductive female herself, without a delay that reduces her overall reproduction. Moreover, when more than one daughter is present, it is important to each daughter that she, rather than one of her sisters, be the replacement for her mother when and if the mother's reproductive powers wane. Accordingly, one expects daughters to monitor their mother more or less continually and retain the ability to shift rapidly into a reproductive mode, because the juveniles produced and reared by the new reproductive are twice as much like her as the offspring she would have reared if her sister had assumed the reproductive role.

So long as the colony remains small and the life spans of reproductive individuals and helpers are not very different, then helpers may be expected to resist evolutionary specialization as workers that significantly reduces or eliminates their ability to replace their mother rapidly. In small colonies, each

helper has a relatively high chance of being the replacing reproductive if the mother dies, and if life spans are more or less the same between reproductive and helpers, the likelihood of a replacement of the reproductive during each helper's lifetime remains high.

As a corollary of the above, in small-colony eusocial forms, reproductive individuals (mothers) may be expected both to monitor their daughter-helpers' reproductive condition more or less continually and to demonstrate repeatedly their likelihood of remaining healthy and reproductive. In other words, one expects evidence of aggression, but not all-out or damaging aggression, between mothers and their helper or worker-soldier daughters in an incipiently eusocial colony from the start. This appears to be a good description of interactions between the breeding female and other individuals in a naked mole-rat colony (e.g., Isil 1983; Reeve and Sherman, chap. 11; Jarvis, chap. 13). Sisters, however, may be expected to fight, even until one is killed, for control of a nest in which the mother has died (e.g., Lacey and Sherman, chap. 10).

REASON FOR ABSENCE OF AGGRESSION BETWEEN MOTHER AND HELPER, AND CONTINUED DIVERGENCE OF PHENOTYPES, IN LARGE-COLONY EUSOCIAL FORMS

As eusocial colonies become large and long-lasting, mothers become increasingly specialized as producers of young, and offspring as workers and soldiers. Mothers become increasingly capable of providing larger numbers of helpers with sufficient numbers of close relatives to tend and of doing so for longer periods. As this happens, daughters have fewer opportunities to become replacement reproductives, both because their mother lives longer and because so many other individuals are available to replace her; the identity of a queen's replacement thus becomes a sweepstakes, with each individual having a chance of, say, one in a million, or even less.

The changes with colony size can reduce or eventually eliminate the monitoring of helpers by reproductives and cause the reproductive female to specialize so thoroughly in offspring production that she becomes increasingly dependent upon her helper offspring. One result is that the nonreproductive castes in large-colony forms, far from making any effort to escape the pheromones and other influences that cause them to remain nonreproductive, now exert effort to obtain the pheromone that causes them to take the worker or soldier route of development. This is true in part because an offspring with little likelihood of becoming a reproductive when changeovers occur gains from causing or enabling its mother to continue as the reproductive rather than being replaced by a sister of the offspring. Eusocial castes specializing extensively or irreversibly as workers or soldiers are therefore expected to occur only in large-colony eusocial forms.

REASON FOR WORKER CONTROL WHEN INTERESTS OF QUEEN AND WORKER CONFLICT IN LARGE-COLONY EUSOCIAL FORMS

In large-colony forms following the specialization of workers and soldiers and the corresponding relaxation of aggressive control over the reproductive states of workers and soldiers, workers can gain control of sex ratios and other features of colony life in which their interests differ from those of the queen. Some reproductive abilities will be retained by workers during the evolution to large-colony status because they are valuable to the queen. Thus, in Hymenoptera, the ability of workers to make males parthenogenetically is valuable to the queen if she dies and cannot be replaced. In termites, the ability of workers to become supplementary reproductives in parts of the tunnel system distant from the royal pair can be useful to the royal pair itself. Reproductives maintain relaxed control over the activities of workers because, in general, workers in large colonies do not gain by competing with reproductives. This lack of control can, however, also lead to easy and simple ways for nonreproductive castes to act in their own interests contrary to the interests of the reproductives. This argument predicts that worker-queen conflict will be restricted to certain activities, such as producing males in Hymenoptera (Bourke 1988) and establishing peripheral colonies by fission in termites.

Because first helper castes may, in evolutionary terms, have become the somatic effort of the queen, the queen has evolved to grow and increase in reproductive value, sometimes dramatically (in termites and ants), after adulthood and after colony foundation. Such changes in the queen can be considered one of the ways in which a parent colony can be improved as a reproductive resource from the viewpoint of offspring that are deciding whether to emigrate or to become helpers.

Summary

Darwin solved the general problem of worker sterility in eusocial forms by noting that if the trait of sterility can be carried without being expressed, and if those who express it sufficiently help those who carry it but do not express it, then the trait can spread by natural selection. W. D. Hamilton developed the idea of reproduction via collateral relatives and noted a relationship among haplodiploidy, closer relationships between full-sisters than between mothers and daughters, workers being restricted to females, and multiple origins of eusociality in the Hymenoptera.

We believe that the favorable combination of traits and circumstances that enabled (or caused) termites and naked mole-rats to evolve eusociality in-

cluded gradual metamorphosis, subsociality (extensive parental care), and life in long-lasting, expansible niches (nests or microhabitats) safe from predation and rich with food that does not require exiting the safety of the niche to obtain it. In Hymenoptera haplodiploidy complements the preadaptations of widespread subsociality, powerful flight, and the presence of stings in females. It may have helped to overcome the disadvantages of complete metamorphosis for the evolution of eusociality: juveniles (larvae) are poor worker prospects, and the intervening pupal stage and the extensiveness of morphological and physiological transformation prevent gradual improvement in juvenile ability to help during development toward adulthood. Except for eusocial clones (e.g., aphids), eusociality is apparently always preceded evolutionarily by subsociality (extensive parental care); subsociality is at least as concentrated in the Hymenoptera as are independent origins of eusociality.

The sting is also regarded as instrumental in enabling Hymenoptera to evolve eusociality repeatedly in exposed locations (vulnerable to predators). Hymenoptera nesting in the open were able to create expanding and more or less permanent (usually paper) nests. Termites and naked mole-rats depended on locating abundant food in the vicinity of hidden or fortresslike, long-lasting, and expansible nest sites (fallen trees, patches of underground tubers).

Also contributing to hymenopteran eusociality were the powerful flight capabilities of the order Apocrita, derived from a history of carrying food to ensconced juveniles and useful for bringing food to young and for building and defending nests. Eusocial Hymenoptera that moved into niches resembling those of termites and naked-mole rats (except that Hymenoptera usually forage externally) have in some cases (ants and a few bees) lost both flight and the sting.

High risks associated with external foraging and defending exposed nest sites (probably from vertebrate predators) may have contributed to the evolution of eusociality in some Hymenoptera by causing disruptive selection on life-effort patterns in reproductives and workers (actually worker-soldiers), leading to life-span differences that permitted irreversible worker specialization. Incipient queens thus became long-lived enough to supply dependent juvenile relatives throughout the lives of their incipient worker offspring (seasonality can permit such ability without life-span differences). Other dangers (probably arthropodan), reducible through parental care and helping, must also have occurred in the microhabitats of termites (and probably ants) to bring about divergence in life lengths and the evolution of soldiers. Consistent with expectations from senescence theory, life spans of workers and soldiers in most eusocial Hymenoptera, under relatively high rates of mortality, have probably shortened, compared with noneusocial members of related groups; conversely, life spans of all castes of termites, naked mole-rats, and some ants have probably lengthened.

Birds and mammals are like termites in metamorphosis and parental care but less like them in ability to locate safe or defensible, expansible, permanent nest sites with ample food for large colonies. Apparently as a result, cooperatively breeding vertebrates have been halted evolutionarily in relatively small groups, usually with temporary helpers, and evidently always before divergence of phenotypes between reproductives and helpers.

Cooperatively breeding vertebrates resemble small-colony eusocial forms (those with up to several hundred individuals, e.g., *Polistes* wasps, halictine bees, naked mole-rats), in which the breeding female and male (female only, in the Hymenoptera) are the most active and aggressive members of the colony. Reproductives in such colonies seem required to defend their positions by monitoring the reproductive states of offspring and demonstrating their own reproductive health (through vigor and dominance), presumably because in small colonies it is profitable for each worker to retain the ability to replace swiftly an inadequate reproductive individual. In colonies with thousands or millions of individuals, replacement of reproductives becomes a sweepstakes, with the evident correlate that worker castes tend to specialize completely as helpers and reproductives become passive and dependent. Phenotypic divergence of reproductives and other castes, especially in life spans, is virtually restricted to large-colony forms. Divergence of life spans, in particular, would appear to exaggerate and perpetuate the differences in selective regimes between small-colony and large-colony eusocial forms because long-lived queens are unlikely to be replaced within the life span of any individual short-lived worker or soldier.

Acknowledgments

This paper was begun about 1975; the arguments on subsociality and gradual metamorphosis were developed by early 1976, when R.D.A.'s construction of a hypothetical eusocial mammal as a subterranean tropical rodent feeding on underground tubers caused T. A. Vaughan of Northern Arizona University to tell him that this hypothetical species was "a perfect description" of naked mole-rats. That conversation led to subsequent correspondence between J.U.M. Jarvis and R.D.A. and initiated the cooperation leading to the current volume (see the Preface).

Arguments about nest sites and their significance in relation to senescence and heroism were initiated in 1975 and developed considerably during a graduate seminar on eusociality held at Michigan in 1983. Materials on naked mole-rats, and the comparisons of small- and large-colony eusociality, were added in 1984–1985. Some of the arguments in the early part of the paper appear in the excellent review article of Andersson (1984). We have attempted

to avoid repetition yet retain enough of the general arguments to provide overall coherence.

For criticisms of the manuscript, we are grateful to S. H. Braude, G. C. Eickwort, J. Herbers, P. Pamilo, D. Queller, T. D. Seeley, P. W. Sherman, J. E. Strassmann, and, especially, M. J. West-Eberhard.

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Systematics and Evolution of the Family Bathyergidae

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The mole-rat family Bathyergidae has an exclusively African history dating to the early Miocene. Taxa in this family are endemic to sub-Saharan Africa with at least three species in two genera (*Georychus* and *Bathyergus*) restricted to South Africa, two monotypic genera (*Heterocephalus* and *Heliophobius*) restricted to eastern Africa, and one genus (*Cryptomys*) comprising seven species having a broader distribution in western, eastern, and southern Africa. The Bathyergidae is not to be confused with the Spalacidae; this latter family of mole-rats, comprising a single genus (*Spalax*), occurs in the eastern Mediterranean region, eastern Europe, and southern Russia (see Jarvis and Bennett, chap. 3). The systematics and evolutionary biology of the Bathyergidae relative to other rodent families has been debated for more than 80 years, resulting in many different classification schemes. Even within the family, information pertaining to the relationships among genera and the overall taxonomy is incomplete.

From an evolutionary standpoint, the Bathyergidae is an interesting group in several respects. First, the family represents an early rodent radiation in Africa, and its distribution and endemism suggest that this radiation was complex. Second, as discussed in detail in the following chapter, population structure within the family ranges from solitary to the highly structured social system of the naked mole-rat (Jarvis and Bennett, chap. 3). Third, the family is unique among the Rodentia in exhibiting several combinations of traits that confuse their placement within the order. Systematic and evolutionary studies on this family should therefore prove enlightening with respect to the historical biogeography of Africa, the evolution of eusociality, and the classification and patterns of morphological evolution in rodents.

Here we provide an overview of bathyergid systematics and evolution by discussing (1) the relationship of the Bathyergidae to other rodent families, (2) bathyergid taxonomy, (3) the relationships of genera and species within the family, and (4) the zoogeography and paleontological history of the family. In the next chapter, Jarvis and Bennett provide an overview of the behavior and ecology of the Bathyergidae.