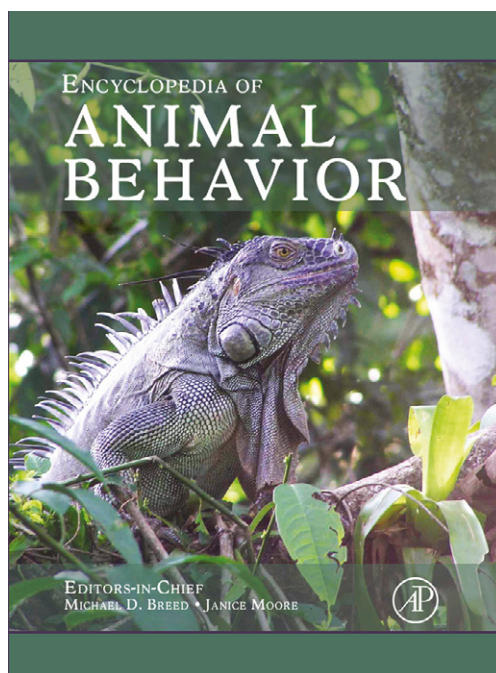


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Subsociality and the Evolution of Eusociality

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Introduction and Definitions

Social interactions are ubiquitous in animals. In some species, social interactions are confined to interactions between the sexes during mating. Species at the other extreme have complex societies in which individuals live in intimate association with nestmates, and social interactions are fundamental to all aspects of life. An array of terms has been used to categorize types of animal sociality. For example, the following categories were developed by Charles Michener and Edward O. Wilson to describe degrees of sociality in the social insects, particularly the insect order Hymenoptera (wasps, bees, and ants): communal, sub-, quasi-, semi-, para-, pre-, and eu-social (see [Table 1](#)).

Subsocial animals live in family groups consisting of parents and immature offspring, and are characterized by brood defense or brood provisioning by parents. Such parental care is taxonomically widespread and found in some crustaceans, spiders, mites, scorpions, millipedes, insects, and vertebrates. Besides parental care, alloparental care, in which adults provide protection or provisioning to nonoffspring is found in some insects, birds, and mammals. Semisocial animals live together in same-generation groups, have cooperative brood care (i.e., alloparental care occurs), and have a reproductive division of labor such that some individuals mainly reproduce, while others mainly perform other tasks such as foraging and brood-care. Finally, eusocial, or truly social groups contain multiple adult generations, have cooperative brood care, and have a reproductive division of labor such that nonreproductive helpers remain so more or less permanently.

Determining the animal societies that qualify for the eusocial label has been at the center of a lot of attention. In the older literature, only the ants, some bees and wasps (all in Hymenoptera), and the termites were recognized as being eusocial. More recent studies show that a wide variety of animals such as naked mole rats, aphids, an ambrosia beetle, thrips, and snapping shrimp fit the strict definition of eusociality. Several authors have suggested amending the categories in [Table 1](#), in particular, broadening the definition of eusociality to include taxa having only temporary helpers that provide alloparental care, and also removing the focus of the current classification system on characteristics found in the Hymenoptera.

In this article, I discuss the evolution of eusociality, in particular, how eusociality evolves from subsociality. I focus mainly on the well-studied Hymenoptera. The question of how eusociality evolves has occupied the

attention of many evolutionary biologists since Darwin. The evolution of permanently sterile individuals, as found in many insect societies, is paradoxical because alleles reducing fertility should be disfavored by natural selection. The ecological and evolutionary success of the eusocial insects makes this evolutionary enigma even more compelling. There have been a range of complementary hypotheses that attempt to explain various aspects of the evolution of eusociality: evolutionary mechanisms that have enabled the evolution of eusociality; selection pressures that have favored the evolution of eusociality; factors that facilitate or enable the evolution of eusociality; the general pathways and specific scenarios by which eusociality can evolve; and the genetic and developmental mechanisms underlying traits involved in the evolution of eusociality ([Table 2](#)).

Whenever possible, empirical studies of these hypotheses are described. In many cases, studying these hypotheses empirically has proven difficult because of the absence of an obvious study system for elucidating the evolutionary origin of eusociality. Eusocial lineages with sterile workers and large societies are highly derived and have been eusocial for millions of years. The selection pressures and traits of these taxa are likely to be very different than those at the origin of eusociality. Other lineages such as xylocopine bees, halictid bees, and vespidae wasps, contain species or populations that range from subsocial to eusocial. The traits and selective pressures found in these lineages may be more relevant to understanding the origin of eusociality. However, in most cases, these lineages likely have also had the same degree of sociality for millions of years.

Evolutionary Mechanisms for the Evolution of Eusociality

Kin Selection and Multilevel Selection

The question of the evolutionary mechanism by which eusociality can evolve has been asked more broadly as: How can reproductive altruism evolve? Darwin suggested that selection at the family-level could result in the evolution of sterile helpers, as found in eusocial insects. That is, even though sterile helpers do not reproduce, their close relatives, who are also likely to carry genes underlying conditionally expressed helper traits, do reproduce and pass on the conditional helper genes. William D. Hamilton formalized these ideas in his theory of inclusive

Table 1 Levels of social organization in insects, after Michener and Wilson

	<i>Parental care</i>	<i>Alloparental care</i>	<i>Reproductive division of labor</i>	<i>Overlapping adult generations</i>
<i>Presocial</i>				
Subsocial	+	–	–	–
<i>Parasocial</i>				
Communal	+	–	–	–
Quasisocial	+	+	–	–
Semisocial	+	+	+	–
Eusocial	+	+	+	+

Table 2 Summary of hypothesis providing different levels of explanation for the evolution of eusociality

<i>Level of explanation</i>	<i>List of relevant theories, hypotheses, scenarios, and factors</i>
Ultimate selective pressures	Increased productivity, nest defense, assured fitness returns
Evolutionary mechanism	Kin selection/multilevel selection
Preconditions and facilitating factors	Haplodiploid hypothesis, subsociality, demographic factors, strict lifetime monogamy
Pathways	Subsocial route, semisocial route
Behavioral and physiological mechanisms	Parental manipulation, subfertility hypothesis, nutritional hypothesis
Genetic and developmental mechanisms	Reproductive groundplan hypothesis, heterochrony hypothesis

*See text for further explanation of the placement of various hypotheses.

fitness and showed that altruistic behaviors evolve when the fitness benefits (b) to recipients of altruistic acts times the relatedness between social partners (r) is greater than the fitness costs to the performer of altruistic acts: $rb - c > 0$. This relationship is called Hamilton's rule and is the foundation of inclusive fitness or kin selection theory.

Kin selection can also be described in the mathematically equivalent levels of selection framework (sometimes referred to simply as group selection, although this is less correct because multiple levels of selection, e.g., within- and among-groups are always simultaneously considered). In this case, whether altruistic behaviors evolve depend on the balance between selection within social groups and selection among social groups. In fact, kin selection is a special type of multilevel selection, involving between- and within-kin-group selection. Selection among social groups (i.e., colonies) in social insects is clearly important, and can arise due to direct competition between colonies for resources, or any other factor that causes some colonies to survive better and produce more reproductive individuals relative to other colonies. As a result, some authors have suggested that selection among colonies could be important for the evolutionary origin of eusociality, irrespective of kin selection. This is theoretically possible, but it seems likely that social groups at the origin of eusociality are actually always composed of relatives, so that, in this case, kin selection can be said to be the ultimate evolutionary mechanism for how eusociality evolves. Supporting this supposition, phylogenetic analysis of extant eusocial lineages indicates that the ancestral condition is always closely related kin groups with a

single, singly mated reproductive (i.e., there is strict lifetime monogamy).

Parental Manipulation and Mutualism as Alternatives to Kin Selection?

Parental manipulation and mutualism are often presented as alternative hypotheses to kin selection for the evolution of eusociality. The mutualism hypothesis proposes that eusociality can evolve through mutualistic benefits to groups of individuals that live together and reciprocally assist one another. However, many authors argue that mutualism alone cannot lead to eusociality. The parental manipulation hypothesis suggests that mothers restrict the reproductive options of some offspring so that they assist in the rearing of additional fully fertile offspring. However, parental manipulation is not a mutually exclusive alternative to kin selection, and each may operate sequentially or in concert. Furthermore, parental manipulation involves parent–offspring interactions and need not be considered distinct from kin selection theory.

The genetic underpinnings of parental manipulation by mothers and kin selected expression of altruistic behavior by workers differ, and as a result there are expected differences in the evolutionary dynamics of these genes for these two routes to eusociality. In most kin selection models, genes causing altruistic behaviors are located and expressed in the genomes of helpers that provide care to relatives. These behaviors can be considered to be under 'offspring control,' because whether an offspring expresses the altruistic helping behaviors depends directly on its own genotype. In contrast, under

parental manipulation models, whether an offspring expresses helping behavior to its sibs depends on its mother's genotype. While both alleles causing parental manipulation and worker altruism alleles must satisfy Hamilton's rule, the differences in the genetic basis of these traits means that the benefit to cost ratio necessary for parental manipulation alleles to spread is often less than for worker altruism alleles.

Michener and Brothers observed the behavior of mother-offspring groups of halictid bees to determine whether offspring became helpers as a result of parental manipulation or offspring control. Mother bees were observed to frequently nudge their most fertile offspring back into the nest where brood care behaviors occurs, suggesting that behavioral parental manipulation may play an important role in the evolution of eusociality.

Selective Factors Favoring the Evolution of Eusociality

Ultimately, whether alleles influencing eusocial traits, such as sib-care behavior, spread in a population depends on the specific benefits of helping and group-living relative to independently reproducing; that is the underlying ecological factors that influence the magnitude of the 'b' and 'c' terms in Hamilton's rule. These selective benefits explain *why* eusociality evolves, whereas the other hypotheses and factors summarized in **Table 2** explain at various levels *how* eusociality evolves. Possible advantages of joining a group and helping versus attempting independent reproduction include increased per capita productivity, increased nest defense against predators or parasites, and the potential to inherit proven nest sites. Furthermore, helping has higher assurance of fitness returns because even if a helper dies before its immature nestmates reach adulthood, other helpers can potentially finish rearing the immature, whereas if an independently nesting parent dies before its offspring reach adulthood, there is no chance the parent will achieve any fitness returns for its investment. Similarly, if partially grown immatures are available to receive help, individuals that remain and help may have a 'reproductive head start' relative to individuals that disperse and reproduce on their own. Empirical studies with various social lineages suggest that all of these factors are important in the evolution of eusociality, and often these factors may be lineage-specific.

Factors Promoting the Evolution of Eusociality: Haplodiploidy and Subsociality

For much of the twentieth century, biologists believed that eusociality originated more than ten times within the insect order Hymenoptera and only once in a non-hymenopteran insect (termites). Hamilton's haplodiploid

hypothesis suggests that eusociality has evolved more frequently in the haplodiploid Hymenoptera because of the asymmetry in relatedness between haplodiploid females and their relatives. Specifically, full-sibling haplodiploid females are more closely related to one another on average ($r=0.75$) than they are to their brothers ($r=0.25$) or to their offspring ($r=0.5$), while full-sibling diploid males and females are equally related to one another and their own offspring ($r=0.5$). As a result of this relatedness asymmetry, alleles causing haplodiploid females to help care for their sisters instead of their own offspring should spread more readily in haplodiploids relative to in diploids.

The haplodiploid hypothesis is pleasingly simple and was initially widely embraced. However, its importance in explaining the taxonomic distribution of eusociality has now been long doubted for several reasons. Averaged across both male and female siblings, haplodiploid females are equally related to their full sibs or offspring ($r=0.5$), just as diploids. In order to capitalize on the high relatedness of haplodiploid females to their brothers, female helpers must invest relatively more resources in rearing sisters, and this female-biased investment must be associated with helping behavior. Factors such as multiple queens and multiple mating that decrease relatedness are commonly found in the eusocial Hymenoptera, so that the theoretical benefit of haplodiploidy disappears or is greatly mitigated. While low observed relatedness values have been taken as evidence refuting the haplodiploid hypothesis, conditions found in highly eusocial populations likely do not reflect conditions at the evolutionary origin of eusociality. Indeed, as described above, monogamy seems to be the ancestral condition in eusocial lineages. Finally, the phylogenetic association between haplodiploidy and eusociality may not be as strong as was once perceived. Several large taxonomic groups are haplodiploid but do not have eusocial members (e.g., some mites, scale insects, whiteflies, and beetles), and eusociality occurs in several diploid groups, including termites, naked mole rats, aphids, snapping shrimp, and an ambrosia beetle.

Traits besides the relatedness asymmetry caused by haplodiploidy may help to explain the apparent prevalence of eusociality in the Hymenoptera. For example, maternal care (i.e., subsociality), nest-building, mandibulate mouthparts, the female sting, above average chromosome numbers, short lifespan of adults relative to juvenile development time, strict lifetime monogamy, and protogyny enabled by haplodiploidy have all been proposed to facilitate the evolution of eusociality. These traits are sometimes termed 'preadaptations' for colonial life. In contradiction, some authors suggest that there are unlikely to be a small number of factors important in the evolutionary origin of eusociality across all eusocial lineages.

Nevertheless, one factor, subsociality, does seem to be a universal and necessary precondition for the evolution

of eusociality. Indeed, it is widely accepted that alloparental care, one of the defining characteristics of eusociality, is derived from parental care, which defines subsociality. Interestingly, maternal care (i.e., subsociality) is found more commonly in the Hymenoptera than in any other arthropod group. Population genetic models demonstrate that maternal care evolves more readily in haplodiploids relative to diploids. Some authors have pointed out that haplodiploidy is likely more closely associated with subsociality than eusociality. For example, subsociality is only found in those mites and ticks (subclass Acari) that are haplodiploid. Haplodiploidy and subsociality also co-occur in some thrips (Thysanoptera), bees and wasps (aculeate Hymenoptera), and ambrosia beetles (Coleoptera: Xyleborini). If haplodiploidy facilitates the evolution of subsociality, and subsociality is a necessary precondition for eusociality, then eusociality should also be more likely in haplodiploids. Thus, there are still strong reasons to expect an association between haplodiploidy and eusociality.

Evolutionary Pathways to Eusociality: Subsocial Versus Semisocial

Two primary evolutionary routes to eusociality have been proposed: the subsocial route and the semisocial route. In the subsocial route, some offspring do not disperse and reproduce, but instead remain at the nest and help rear siblings. In this route, the mother survives, so her reproduction continues after the emergence of her first offspring. The nondispersal of some offspring together with alloparental care leads to overlap of adult generations and cooperative brood care that occurs by definition in eusociality. Because the subsocial route starts with a single family unit, helpers provide care to close relatives (siblings), and kin selection can act efficiently.

In the semisocial route, individuals from the same generation form aggregations. Some of these individuals become helpers that rear the offspring of their nestmates, and if some of these offspring remain to also become helpers, and individuals from both generations coexist, eusociality can evolve. In this semisocial route, helpers potentially provide care to offspring of unrelated adults, or if founding members are sisters, helpers provide care to nieces. Semisocial colonies sometimes form when the mother dies prior to the emergence of her offspring; the resulting group of sibs lives in a semisocial colony. The benefit to cost ratio must be higher for the semisocial route to work relative to the subsocial route, as prescribed by Hamilton's rule, because the relatedness between non-reproductives in the colony and the next generation is lower than in a subsocial colony. Since phylogenetic analysis identifies the ancestral condition of eusocial lineages to be a monogamous family unit, it seems that eusociality has evolved via the subsocial route.

Proximate Hypotheses for the Evolution of Eusociality

Because kin selection theory provides an ultimate evolutionary explanation for how eusociality can evolve, but does not provide insight into the more proximate developmental, physiological, or genetic basis of eusociality, several authors have sought additional levels of explanation. For example, parental manipulation provides a specific behavioral mechanism for the evolution of eusociality, namely, 'mom made me do it.' According to the subfertility hypothesis, some offspring have reduced fertility and are incapable of nesting alone, but can still provide help at their natal nest. If helping behavior is only expressed when offspring are in poor condition, subfertility provides a scenario by which helping behavior can spread. Indeed, in all cases, helping behavior must be conditionally expressed for it to evolve. Hunt's nutritional scenario, based on observations and experiments with social wasps, provides further explicit ecological and behavioral mechanistic details for the evolution of eusociality in wasps. Specifically, in this scenario, the exchange of protein-rich saliva between larvae and adults underlies a reproductive division of labor between well-nourished reproductive individuals and undernourished helpers.

The Genetic and Developmental Basis of Eusociality

West-Eberhard's ovarian groundplan scenario, and the related reproductive groundplan hypothesis, elaborated by James Hunt and Gro Amdan, have a developmental focus and describe how queen and worker phenotypes diverge based on an ancestral developmental program. Specifically, solitary insects all have more or less similar reproductive cycles with corresponding behavioral cycles, involving foraging and reproducing components. Under the groundplan hypothesis, these components of the ancestral reproductive groundplan can be separated during the course of social evolution and used to build societies composed of reproductive and nonreproductive individuals, that is, queens and workers. Studies with honeybees support the link between reproductive state and behavior in workers, suggesting that evolutionarily conserved genetic and physiological mechanisms may contribute to division of labor in eusocial lineages. Similarly, studies with *Polistes* wasps suggest that simple modification of conserved life history traits associated with diapause cycles may underlie the origin of queen and worker castes in these wasps.

The heterochrony hypothesis proposes that prereproductive alloparental care of offspring towards their sibs (i.e., sib care) is caused by the early expression of maternal

care genes, so that just like the groundplan hypotheses, complex social traits characterizing eusociality can arise from simple changes in preexisting genetic and developmental machinery. It is widely accepted that alloparental care behaviors are developmentally homologous with and evolutionarily derived from parental care behaviors. Ancestrally, maternal care genes are expressed only after mating. The heterochrony hypothesis proposes that in the derived condition, genes for maternal care are conditionally expressed prereproductively in female helpers towards siblings instead of offspring. In this view, sib care behavior is a derived trait and the evolution of the capacity for females to provide care prereproductively towards their sibs is a first step in the evolutionary origin of eusociality from subsociality. There may often be a small number of genes underlying this behavioral heterochrony, permitting rapid social evolution given the appropriate genetic variation. In some cases, conditionally expressed sib care, a first step from subsociality to eusociality, may occur without the subsequent evolution of any other eusocial traits.

The heterochrony hypothesis also makes explicit predictions about the genetic basis of sib care behavior. Many of the same genes should be expressed in adults performing sib care behaviors as in adults performing maternal care behaviors. This will especially be true in populations of incipiently eusocial species but less so in those with an advanced degree of eusociality, where more genes are expected to have caste-limited expression due to selection for the elaboration of queen–worker divergence. However, because the evolutionary elaboration of sib care behaviors and queen–worker phenotypic differences is likely based upon simple modification of preexisting physiological, behavioral, and genetic machinery, queen and worker traits even in highly eusocial species are expected to have a common molecular basis. Recent studies of patterns of gene expression in *Polistes* wasps and honeybees support these predictions.

Conclusions

The evolution of sociality is considered to be one of the major transitions of evolution. A range of hypotheses explain why sociality evolves, the evolutionary mechanism for how it can evolve, as well as novel, more proximate developmental, genetic, and behavioral details

for how it can evolve. Currently, empirical study of the evolution of eusociality largely lags behind theory. Observational and experimental studies of the selective benefits of social living, together with emerging studies of the developmental, genetic, and behavioral underpinnings of social traits will change this, and will increase our understanding of the evolution of sociality.

See also: Ant, Bee and Wasp Social Evolution; Cooperation and Sociality; Crustacean Social Evolution; Kin Selection and Relatedness; Levels of Selection; Sex and Social Evolution; Social Evolution in 'Other' Insects and Arachnids; Social Insects: Behavioral Genetics; Spiders: Social Evolution; Termites: Social Evolution; William Donald Hamilton.

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