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Author: WILSON, EDWARD O.

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One Giant Leap: How Insects Achieved Altruism and Colonial Life

EDWARD O. WILSON

The advanced colonial state of eusociality has evolved in insects as a defense of nest sites within foraging distance of persistent food sources. In the Hymenoptera, the final step in the approach to eusociality is through a suite of preadaptations comprising simultaneous provisioning, fidelity to the nest, and a preexisting propensity toward dominance behavior and the selection of tasks according to opportunity. The only genetic change needed to cross the threshold to the eusocial grade is the foundress's possession of an allele that holds the foundress and her offspring to the nest. The preadaptations provide the phenotypic flexibility required for eusociality, as well as the key emergent traits arising from interactions of the group members. Group (colony-level) selection then immediately acts on both of these traits. The rarity of the origin of eusociality is evidently due to the rarity of the combination of progressive provisioning with environments of the kind that give an edge to group selection over individual direct selection, causing offspring to stay at the natal nest rather than disperse. Several lines of evidence, examined here, suggest that collateral kin selection does not play a significant role.

Keywords: sociobiology, altruism, social insects, evolution, kin selection

Eusociality, the care across generations of the offspring of a reproductive caste by a nonreproductive or less reproductive worker caste, is the most advanced level of social life in the insects. Although the condition is rare in evolution, once attained, it has often been spectacularly successful. Thus, while only 2% of known insect species are eusocial, these species compose most of the insect biomass; in one patch of rainforest assayed near Manaus in Amazonian Brazil, they made up over three-fourths of the insect biomass (Fittkau and Klinge 1973). The eusocial insects, and in particular the ants and termites, tend to dominate the more persistent and defensible parts of terrestrial environments (Wilson 1990).

Why has eusociality been so successful? The well-documented answer is that organized groups beat solitaires in competition for resources, and large organized groups beat smaller ones of the same species (Hölldobler and Wilson 1990, Tschinkel 2006). Why, then, has eusociality been so rare? The answer is that it requires collateral altruism, which is behavior benefiting others at the cost of the lifetime production of offspring by the altruist. The existence of collateral altruism is one of the perennial problems of evolutionary biology. Given its genetic consequences, how can programmed sacrifices to collaterally related group members arise by natural selection?

In this article I argue that the origin of altruism leading to eusociality cannot be deduced by aprioristic reasoning based on general models. It can, however, be revealed by reconstructing actual histories with empirical data. Partial reconstructions have been made in the past, for example, in the seminal contributions of Wheeler (1928, 1933), Evans (1958), and Michener (1958). Recently, and especially during the past decade, a flood of new information from diverse disciplines has permitted the construction of a much more coherent scenario than was conceivable in the past. Especially important in both its originality and completeness is the synthesis by Hunt (2007), culminating his own research and that of others, mostly on the social wasps.

The narrow evolutionary path to eusociality

In all the species that display the earliest stages of eusociality, behavior protects a persistent, defensible resource from predators, parasites, or competitors. The resource invariably consists of a nest and dependable food within foraging range of the nest. The females of many species of aculeate wasps, for

Edward O. Wilson (e-mail: ewilson@oeb.harvard.edu) is with the Museum of Comparative Zoology at Harvard University in Cambridge, Massachusetts.
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example, construct nests and then provision them with paralyzed prey for the larvae to consume. Among the 50,000 to 60,000 known aculeates, at least 7 independent lines have reached the eusocial condition (Wilson and Hölldobler 2005). In contrast, of the more than 70,000 parasitoid and other apocritan hymenopteran species, whose females travel from prey to prey to lay their eggs, none is known to be eusocial, nor is any one of the hugely diverse 5000 described species of sawflies and horntails. Larvae of some sawfly species form aggregations, but not eusocial colonies, and the adults lead solitary lives (Costa 2006).

Almost all of the thousands of known species of bark and ambrosia beetles, which compose the families Scolytidae and Platypodidae, depend on ephemeral deadwood for shelter and food. Many also dig burrows and care for their young in them. A very few of the latter are able to cut and sustain burrows in living wood, allowing the coexistence of numerous generations. Among these latter few, a single one, the Australian eucalyptus-boring beetle *Platypus (=Austroplatypus) incompertus,* is known to have developed eusociality. Because of the persistence of this species' habitat, tunnel systems are estimated to have survived, and presumably to have housed the same families, for up to 37 years (Kent and Simpson 1992).

In a parallel manner, the handful of known eusocial aphids and thrips are gall inducers, enjoying a rich food supply in a secure, defensible home of their own making (Crespi 1992, Stern and Foster 1996). The vast majority of other known aphid and adelgid species (roughly 4000 in number) and thrips species (about 5000 strong) often form aggregations, but do not form galls or divide labor. Similarly, several snapping shrimp species of the genus *Synalpheus,* out of roughly 10,000 known decapod crustacean species, have reached the eusocial level. *Synalpheus* is highly unusual among decapods in constructing and defending nests in sponges (Duffy et al. 2000).

A second preadaptation that favors the transition to eusociality is the propensity, documented in solitary bees, to behave like eusocial species when forced together experimentally. In *Ceratina* and *Lasioglossum,* the coerced partners proceed variously to divide labor in foraging, tunneling, and guarding (Sakagami and Maeta 1987, Wcislo 1997, Jeanson et al. 2005). Furthermore, in at least two species of *Lasioglossum,* females engage in leading by one bee and following by the other bee, which characterizes primitively eusocial bees. The division of labor appears to be the result of a preexisting behavioral ground plan, in which solitary individuals tend to move from one job to another after the first is completed. In eusocial species, the algorithm is transferred to the avoidance of a job already being filled by another nestmate. It is evident that progressively provisioning bees and wasps are "spring-loaded" (strongly predisposed, with a trigger) for a rapid shift to eusociality, once group selection favors the change.

The results of the forced-group experiments fit the fixed-threshold model of the origin of labor division proposed for the emergence of the phenomenon in established insect societies (Robinson and Page 1989, Bonabeau et al. 1996, Beshers and Fewell 2001). The model posits that variation, sometimes genetic in origin and sometimes purely phenotypic, exists in the response thresholds associated with various tasks. When two or more individuals interact, those with the lowest threshold are the first to begin the task. The activity inhibits their partners, who are then more likely to move on to whatever other tasks are available. Thus, once again, the group impact of a single phenotypically flexible allelic change that inhibits dispersal from the natal nest would seem to be enough to carry preadapted species across the eusocial threshold.

Crossing the eusocial threshold

The key preadaptation for eusociality in the social Hymenoptera is progressive provisioning, a behavior that in solitary species arises by individual direct selection. Although experimental field studies of the ecological pressures on pre-eusocial species have scarcely begun, one published example is especially instructive. Females of the sphecid wasp *Ammophila pubescens* provision their soil burrows with caterpillars, creating cells in succession, laying an egg in each cell with the caterpillar prey, and sealing it. (In the other method of mass provisioning practiced by wasps and bees, the larvae are continuously supplied with prey as they develop.) Because the *Ammophila* females are forced to open and close their nests to keep the larvae inside fed, they lose many of their eggs to cuckoo flies (Field and Brace 2004). It is entirely reasonable to suppose that if a second *Ammophila* female were available to serve as a guard, the loss of eggs would be considerably reduced.

Simultaneous progressive provisioning, by which multiple larvae are reared at the same time (Field 2005), is especially potent as a preadaptation in the Hymenoptera. From this wholly solitary adaptation, it is but one short step in evolution for adult offspring to remain at the nest and help their mother raise siblings, instead of dispersing to rear brood of their own (Wilson 1971, 1975, Michener 1974). In that generation the eusocial colony originates. Then and thereafter, group selection proceeds, uniquely targeting the emergent traits created by the interaction of the colony members. The different roles of the reproductive mother and her nonreproductive offspring are not genetically determined. Rather, as the evidence from primitively eusocial species has shown, they represent different phenotypes of the same recently modified genome.

Altruism and eusociality are thus evidently born from the appearance of a phenotypically flexible eusocial allele (or ensemble of such alleles) in a progressively provisioning mother, and from group selection acting on emergent group traits, which are socially binding and sufficiently powerful to overbalance the dissolutive effects of individual direct selection. One small step, so to speak, for a newly created worker caste, one giant leap for the Hymenoptera (figure 1).

Exactly what kind of group selection drives the species across the threshold? Concrete examples of this adaptation and the transition it affords are provided by halictid sweat bees and

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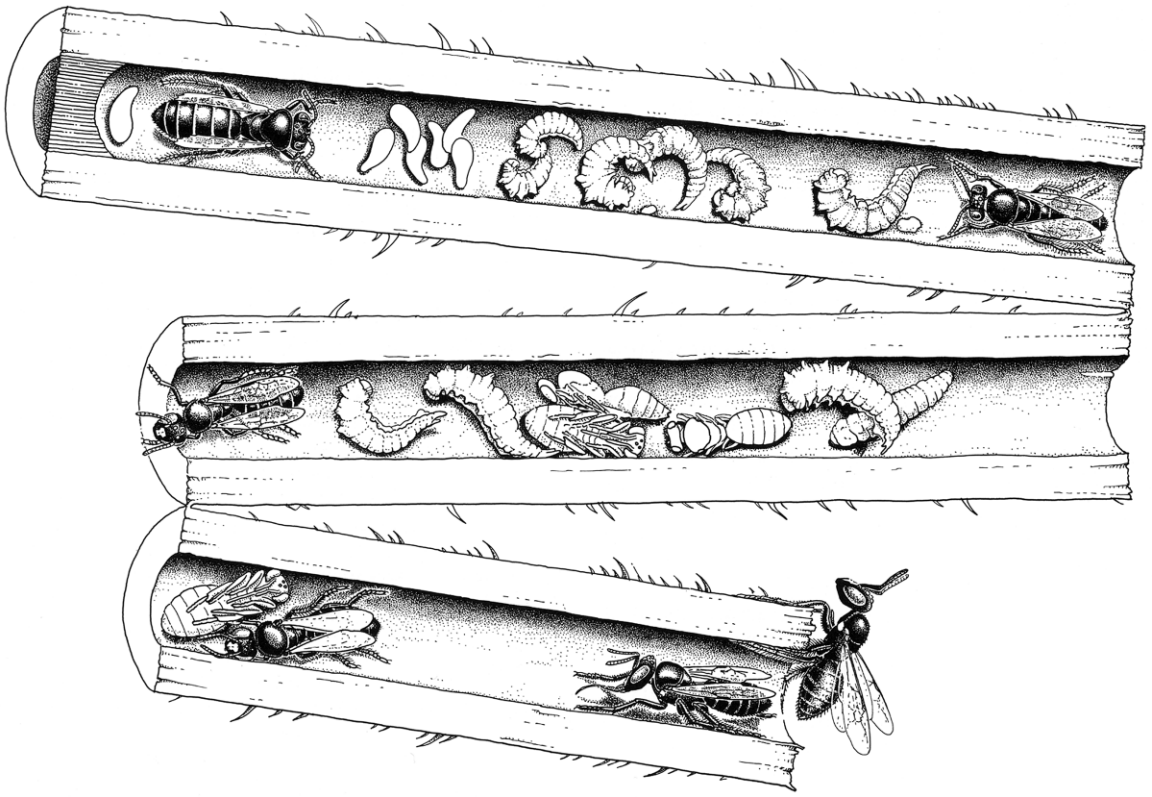


Figure 1. A colony of a primitively eusocial Formosan bee* (Braunsapis sauteriella) *nesting in a hollow* Lantana *stem. The queen, with giant eggs, is to the left in the top segment. The workers feed the grublike larvae progressively with lumps of pollen, which are placed on the stem cavity walls. Drawing by Sarah Landry, based on an illustration by Kunio Iwata in Sakagami (1960); reprinted with permission of the publishers from Wilson (1971).

polistine wasps. In one recently documented case, two species of sweat bees that switched from collecting the pollen of many plant species to collecting pollen from only a few plant species also reverted from a primitively eusocial life to a solitary life. Specialization on a limited array of plants as a source of food is advantageous in the environment in which the reverted species live. Such a change in life history, presumably genetic in origin, also shrinks the length of the harvesting season and removes the possibility of overlapping generations, and hence the formation of a eusocial colony and the advantage that might accrue from the presence of guard bees. Evolution in the reverse direction is easily conceivable, and very likely occurred: adaptation to a broader array of food plants set the stage for multiple generations, and thence for overlapping generations in the same nest (Danforth 2002). Similar evidence with respect to overlapping generations has been adduced for primitively eusocial wasps (Hunt and Amdam 2005). In crossing the line to eusociality, a single allele that disposes daughters to stay could be fixed in the populations at large if the advantage of the little group over solitaires sufficiently outweighs the advantage of each worker leaving to try on its own.

As an overarching principle, the final step to eusociality can occur with the substitution of only one allele or a small set of alleles. Throughout the great diversity of living ant species, for example, the coexistence of winged reproductive females and wingless worker females is a basic trait of colonial life. Judging from the phylogenetically well-separated flies (order Diptera) and butterflies (order Lepidoptera), wing development is directed throughout the winged insects by an unchanged regulatory gene network. More than 110 million years ago, the earliest ants (or their immediate ancestors) altered the regulatory network of wing development in such a way that some of the genes could be shut down under the influence of diet or some other environmental factor. Thus was produced a wingless worker caste (Abouheif and Wray 2002).

An equally informative example of a small genetic change amplified downstream into a greater social change is that affecting queen number and territorial behavior in the imported fire ant *Solenopsis invicta.* Colonies of the early US population, descended from colonies introduced by cargo out of southern South America by the mid-1930s, each contained one or a small number of functioning queens. The colonies also displayed odor-based territorial behavior when the nests were spread out. Sometime during the 1970s, this strain of fire ants began to yield to another strain, whose colonies possess many queens and no longer defend territories. It turns out that the differences between the two strains are due to variation in a single major gene, *Gp-9* (Ross and Keller 1998). The two

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Gp-9 alleles have been sequenced, and their product appears to be a key molecular component engaged in the olfactory recognition of nestmates. The effect of the many-queen allele is evidently to reduce or knock out the ability to discriminate members of other colonies, as well as to discriminate among potential egg-laying queens. As a result of the latter effect, colonies lose an important means of regulating queen number, with profound consequences (Krieger and Ross 2002).

The multiple forms of flexibility

The exact nature of the genetic step to the earliest degree of eusociality is still unknown, unlike the cases of winglessness and colony odor, but it is immediately accessible to genetic research. Hunt and Amdam (2005) have suggested that the genetic base of the flexible worker-versus-queen difference in *Polistes* paper wasps is the same as the genetically based developmental physiology that regulates diapause in solitary Hymenoptera. Such a change in response to the environment may indeed be important. Oddly, the change need not be an allele or ensemble of alleles that appears by mutation and then spreads from low frequencies by group selection. Instead, the key polyphenic allele (or allele ensemble) may in theory be previously fixed in the population by individual direct selection (as opposed to group selection), with solitary behavior the norm in most environments and eusocial behavior in other, rare and extreme environments. With a shift in the available environment in space or time, eusocial behavior would become the norm. That a species on the brink of eusociality might follow this path is shown by the Japanese stem-nesting xylocopine bee *Ceratina flavipes.* The vast majority of the females provision their nests with pollen and nectar as solitary foundresses, but in slightly more than 0.1% of the nests, two individuals cooperate. When this happens, the pair divides the labor: one lays the eggs and guards the nest entrance while the other forages (Sakagami and Maeta 1987).

Another example of genetic flexibility at the eusociality threshold is provided by the ground-nesting halictid sweat bee *Halictus sexcinctus.* The species appears to be genetically polymorphic at one locality within its range in southern Greece, with colonies of one strain founded by cooperating females, and those of a second strain founded by a single, territorial female whose offspring serve as workers (Richards et al. 2003).

Countervailing forces of selection

Although some individual direct selection may play an auxiliary role in the origin of eusociality, the force that targets the maintenance and elaboration of eusociality is by necessity environmentally based group selection, which acts upon the emergent traits of the group as a whole. An examination of the behavior of the most primitively eusocial ants, bees, and wasps shows that these traits are initially dominance behavior, reproductive division of labor, and, very likely, some form of alarm communication mediated by pheromones. A species in the earliest stage of eusociality is a kind of neurogenetic chimera: on the one hand, the newly emergent traits favor the group, while on the other hand, much of the rest of the genome, having been the target of individual direct selection over millions of years, favors personal dispersal and reproduction.

For the binding effects of group selection to outweigh the dissolutive effects of individual direct selection, the candidate insect species evidently must have only a very short evolutionary distance to travel, such that no more than a very small number of emergent traits are needed to form a eusocial colony. The reduction of that distance is achieved by a particular set of preadaptations. The rarity of these preadaptations, in just the right combination, when added to the high bar to eusociality set by countervailing individual direct selection, may be enough to explain the general phylogenetic rarity of eusociality.

The only genetic change needed to cross the threshold to the eusocial grade is possession by the foundress of an allele that holds the foundress and her offspring to the nest. The preadaptations provide the phenotypic flexibility required for eusociality, as well as the key emergent traits arising from interactions of the group members. Group (colony-level) selection then immediately acts on both of these traits.

Passing the point of no return

In the earliest stage of eusociality, the offspring remaining in the nest would be expected to assume the worker role, in conformity with the preexisting behavioral ground rule inherited from the pre-eusocial ancestor. Subsequently, a morphological worker caste can emerge by a further genetic change in which the expression of genes for maternal care is rerouted to precede foraging, thus reversing the normal sequence in the adult developmental ground plan of the ancestor (Amdam et al. 2006, 2007). The rerouting is programmed to remain part of the phenotypic plasticity of the alleles that prescribe the overall ground plan. This origin of an anatomically distinct worker caste appears to mark the "point of no return" in evolution, at which eusocial life becomes irreversible (Wilson 1971, Wilson and Hölldobler 2005).

Does kinship matter?

It might seem that the more closely interrelated the collateral kin of a group (kin other than parents and offspring), the more likely they would be to behave altruistically toward each other. Such was the proposition of early sociobiological theory. The more alleles shared with other group members through common descent, it was believed, the more the altruist's alleles would be multiplied as a result of those same alleles surviving in the other group members benefited by the altruism. Further, if the amount of benefit were correlated with the degree of relationship, the altruistic alleles would be benefited all the more.

However seductive this notion may be (and it has been very seductive, off and on, for four decades), it turns out that other circumstances and forces work in the opposite direction, and sometimes powerfully. They deserve much more inten-

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sive investigation in field and laboratory studies, and much more attention in future sociobiological theory.

Greater genetic variability in the workforce, and hence lower relatedness, can be favored by group selection. In the harvester ant *Pogonomyrmex occidentalis,* for example, colonies with greater genetic variation have overwhelmingly higher rates of growth and reproduction than those with less variation (Cole and Wiernasz 1999). This rise in fitness may be due to the enhancement of labor division by spreading tasks among workers with genetic predispositions to specialization. Such a disposition has been discovered in the polymorphic worker caste of the Florida harvester, *Pogonomyrmex badius:* some heritability occurs in adult worker size, which, with the allometric growth of imaginal disks during adult development in the final larval instar, differentiates colony members into small-headed minors and large-headed majors (Rheindt et al. 2005). On the other hand, no correlation of colony efficiency with degree of relatedness was detected in experiments on the Argentine ant *Linepithema humile* (Rosset et al. 2005).

As an alternative explanation, increased genetic diversity among workers might easily arise as a means of improving overall resistance to disease (Sherman et al. 1988, Schmid-Hempel 1998, Traniello et al. 2002, Stow et al. 2007). Such a correlation between genetic diversity and disease resistance has been found in colonies of the leaf-cutter *Acromyrmex echinatior* in the control of a virulent soil fungus (Hughes and Boomsma 2004). Further correlative evidence favoring the hypothesis of disease resistance has been obtained in species of ants and other social insects in which the queen increases the genetic diversity of her worker progeny by mating with multiple males (Crozier and Fjerdingstad 2001, Denny et al. 2004). On the other hand, in the fungus-growing ants as a whole, including many species with singly mated queens (and regardless of the aforementioned case of *A. echinatior*), the evidence for the enhancement of disease resistance by genetic diversity remains ambiguous (Murakami et al. 2000). Favoring the disease hypothesis is the recent discovery that the potency of antimicrobial defenses in bee populations rises steeply from solitary species to semisocial species and beyond to advanced eusocial species (Stow et al. 2007).

It may be argued that the genetic advancement of labor efficiency or resistance to pathogens occurs only in advanced stages of eusocial evolution, when mature colonies are large and complexly organized. But the possible difference between primitive and advanced species is an open question and subject to empirical testing. There would seem to be sufficient genetic variation even among full sisters of small haplodiploid colonies to allow such an enhancement.

In a third functional category, an increase in the genetic diversity of honeybee nestmates is positively correlated with increased stability in hive temperatures (Jones et al. 2004). This homeostatic effect appears to arise from the enhanced flexibility of colonies that harbor bees with innately different patterns of response. A similar conclusion has been tentatively advanced for genetic variation in worker specialization, as documented in the ant *Formica selysi* (Schwander et al. 2005). Homeostatic regulation of colony environments includes even the most primitive social bees, wasps, and ants.

Still another effect expected to diminish a positive influence of collateral kin selection is nepotism. If individual workers in a colony acted to favor their siblings or other close relatives, the result would be competition among subgroups. The result of such conflict is more likely to diminish the productivity of the colony, and hence to be countered by colony-level selection (Wilson and Hölldobler 2005).

A final force that could drive incipient colonies away from a high degree of relatedness during evolution might be the loss of genetic fitness by inbreeding. In communal associations of bees, group members occupy a single nest. They cooperate in brood care, but without surrendering their personal reproduction. This form of sociality, which occurs in all six of the taxonomic families of bees, could lead to eusociality by the subordination of some of the nest occupants, although no such shift has yet been documented. Conversely, preexisting subsociality (extended parental care of offspring) can turn into the communal condition if offspring come to share the nest. In fact, most communal species do occupy nests over many generations. Yet females tend to leave the nests, abandoning their close relatives. Why does this occur, despite the potential advantage of cooperating with kin instead of unrelated individuals? Kukuk and coworkers (2005) found that females of the halictid bee *Lasioglossum hemichalceum* tend to disperse when the nests are large and their brothers are present. The latter condition heightens the chance of inbreeding, and dispersal reduces it. Hence, "the occurrence of within-nest mating in communal species, combined with strong selection against inbreeding in the Hymenoptera, appears to select for female-biased dispersal. This in turn results in a population-wide decrease in intracolony relatedness, thereby maintaining cooperation among nonkin in communal Hymenoptera" (Kukuk et al. 2005, p. 1305). It may be argued that the result is not relevant if it turns out, as just suggested, that eusociality rarely or never emerges in communal societies. But that is precisely the point. Incest avoidance appears to be a strong dissolutive force in social evolution, at least when mating occurs at or close to home.

If neither the direction of collateral kin selection nor even its existence can be decisively deduced from first principles, what then does the evidence show? Many studies have been designed to discover kin recognition in colonies of social insects, a sign that collateral kin selection may be occurring. The results have been mixed. In the ants *Formica pratensis* (Pirk et al. 2001) and *Iridomyrmex purpureus* (Thomas et al. 1999), and in the primitively eusocial bee *Lasioglossum euphyrum* (Greenberg 1979), workers are more likely to live together without aggression if they are closely related and, as a result, more likely to share similar body odors. On the other hand, most such research on ants, bees, and wasps has yielded results that are either ambiguous or negative (Hölldobler and Wilson 2008). This much evidence combined should give pause to the idea that collateral kin selection is an im-

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portant binding force in eusocial evolution, at least when such selection is based on the recognition of degrees of kinship within colonies.

In fact, there is a good reason to suppose that eusocial insects fail to employ odor differences as a measure of genetic relatedness. In all social hymenopterans whose colony odor has been studied carefully, the workers learn the odor by an imprinting process during the first days following their emergence as adults (Hölldobler and Wilson 1990, 2008). The phenomenon of imprinting was discovered over a century ago by Fielde (1903), who found that when workers of different species of ants, even of different genera and subfamilies, were placed together within 12 hours of their emergence as adults, they lived thereafter harmoniously (more or less) as a group, and presumably would have been hostile to biological sisters from their natal colonies.

On the basis of phylogenetic reasoning, Fielde's phenomenon should be thought unsurprising. The immediate solitary ancestors of primitively eusocial bee and wasp species find their nests from a distance by visual cues, and at close range they almost certainly further use olfactory cues particular to the immediate site of the nest. This information has to be quickly secured and rendered steadfast—in other words, imprinted. With the attainment of eusociality, little further evolution is required for the nest odor to be based upon the cuticular hydrocarbons of the colony members. In fact, throughout the ants, the social insects most intensively studied for this phenomenon, the odor is acquired variously from combinations of diet, nest materials, and, to some degree, endogenous sources; and it is homogenized throughout the colony by grooming and food exchange (Hölldobler and Wilson 1990, 2008).

In summary, the known background biology of the eusocial insects, in particular the hymenopterans, gives no reason to presuppose that pedigree kinship is a key causative element in the origin and early evolution of eusociality. Two other lines of evidence, in fact, lean against such a role. First, when eusociality emerges in evolution from the progressive provisioning bottleneck, the first offspring of the founding mother must be siblings, whether or not collateral kin selection has occurred or is destined to occur. If close pedigree kinship is significant, we should expect members of primitively eusocial species following the first generation of workers and reproductives to remain closely interrelated. That expectation is not generally met. Instead, relatedness decays with time. In the primitively eusocial wasp *Eustenogaster fraterna,* for example, founding females have lower relatedness than sisters, and because of high adult turnover, the relatedness of unmated females has been documented as far lower ($r = 0.21 \pm 0.171$, 95% confidence intervals) (Landi et al. 2003). Relatedness among nestmates of the primitively eusocial wasp *Parischnogaster mellyi* also descends with colony growth (bimodal with overall relatedness of 0.31 ± 0.06) (Panelli et al. 2004). Similar results have been obtained from at least a few species of the primitively eusocial wasp *Ropalidia* and the somewhat primitive species of *Polistes* (Strassmann 1996).

In the realm of phylogenetic patterns, the evidence also leans against a binding role of close kinship. If the pedigree kin hypothesis is correct, we should expect eusociality to be widespread among clades with the intrinsically closest kinship in families. In evaluating such evidence, it is worth stressing that the attainment of eusociality has been a rare event in the evolutionary history of animals. Of the approximately 2600 living taxonomic families of insects and other arthropods (Parker 1982), only 15 are known to contain eusocial species (Wilson and Hölldobler 2005). Six of the eusocial families are termites, the living species of which apparently derived from a single ancestor, while eusociality originated in three independent events in both bees and wasps (Danforth 2002, Hines et al. 2007). The total number of known origins of eusociality in arthropods overall is 13.

Examining this small subset of clades, a role of relatedness in the origin of eusociality is opposed by the collapse of the famous "haplodiploid hypothesis," first suggested by Hamilton (1964). This early stanchion of the pedigree kin selection hypothesis, made theoretically defensible when worker bias toward production of new female reproductives is added, has been abandoned since the discovery in recent years of enough phylogenetically separate diplodiploid eusocial lines to render the association of haplodiploidy and eusociality statistically independent, and thus evidently not causally connected (Choe and Crespi 1997, Wilson and Hölldobler 2005). The same argument applies to the lack of a discernible trend toward eusociality among the multitude of insect and other animal species with parthenogenetic lineages, many of which are also clonal. The failure of the haplodiploid hypothesis is logically seen as evidence *against* pedigree kin selection, no less than when the hypothesis was accepted as evidence *for* pedigree kin selection.

Overall, the weight of empirical evidence leans toward, but does not definitively prove, the following proposition: while close pedigree kinship among group members inevitably accompanies the origin and early evolution of eusociality, the association is a by-product of preadaptation and not a causative condition. Two conditions working together, key preadaptations and strong proportionate group selection, are from the evidence necessary and sufficient for eusociality. Close genetic relatedness and collateral kin selection are not necessary.

The status of kin selection theory

The past four decades of research on social insects have seen enormous progress in our understanding of communication, caste, colony life cycles, and colony self-organization of the social insects. This advance has been achieved by empirical research augmented by midlevel theoretical models, that is, specialized models closely linked to documented phenomena. Virtually all of it has been guided by the concept of group selection, in other words, selection that targets traits emerging from the interaction of colony members.

During the same period, kin selection theory, also called inclusive fitness theory, has evolved a life of its own, based on

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increasingly sophisticated top-down models. The goal that has driven it, the creation of a general, all-inclusive theory of sociobiology, is admirable. I heavily promoted it in my first general syntheses of sociobiology (Wilson 1971, 1975). But what has it contributed to the present large body of empirical knowledge and empirically based theory? It has stimulated measurements of pedigree kinship and made them routine in insect social biology, a very valuable contribution. Researchers have used the data to predict accurately some cases of the perturbation of sex investment ratios (Trivers and Hare 1976, Bourke and Franks 1995), as well as the moderating effect of pedigree kinship on dominance behavior and policing (Ratnieks et al. 2006, Wenseleers and Ratnieks 2006). For the remainder of insect eusociality, however, the theory has contributed little or nothing not already understood from field and experimental studies, often combined with midrange theoretical models.

Kin selection theory is not wrong; it is simply relatively ineffective, even inapplicable in its present form to most empirical research. This basic weakness has a great deal to do with what its defenders also stress as its basic strength, its all-inclusiveness (Frank 1998, Foster et al. 2006a, 2006b, Grafen 2006). The fundamental parameters fed into the models of the origin of altruism (and hence eusociality) are, with reference to the inclusive fitness of individual genotypes, cost (c), benefit (b), and degree of relatedness (r), as first formulated by Hamilton (1964). These parameters will flesh into life, kin selection theorists assume, when empirical data can be folded into them. The concept works mathematically, and can cover all conceivable trajectories of social evolution, but only by defining the parameters so flexibly as to cover all categories of evolution, including even the origin of solitary behavior (e.g., "all solitary behavior originates by kin selection"). That stretch is a source of major confusion (reviewed historically by Wilson and Wilson [2007]). Where the coefficient of relatedness was originally used as a measure of pedigree kinship (as by Haldane [1955] and Hamilton [1964]), and is still widely conceived as such, some mathematical theorists now use it to describe the sharing of a single allele, regardless of the remoteness of common ancestry (e.g., Foster et al. 2006a, 2006b). The coefficient of relatedness can express the increase of genetic fitness in the average carrier of an altruism allele by the actions or presence of fellow group members, whether they are pedigree kin or not.

Although multilevel selection has been viewed as paramount in the origin of altruism since Darwin's *The Descent of Man* (1871; see, e.g., Traulsen and Nowak 2006), and although group selection must by definition occur, group selection is still alluded to by many writers as a non-Darwinian impossibility, as in the premier textbook *Animal Behavior: An Evolutionary Approach* (Alcock 2005). Other authors, bypassing the fundamental distinction between targets of selection at different levels of biological organization in order to focus on inclusive fitness, accept group selection but describe it as being the same as kin selection (Lehmann et al. 2007). The Wynne-Edwards hypothesis of group selection as a density-dependent population control is thought on one side to be theoretically all but impossible (West et al. 2006a, 2006b), and on the other to be a good possibility (Goodnight 2000, Werfel and Bar-Yam 2004, Kerr et al. 2006). Depending on definitions, group selection and individual direct selection are considered the key to the origin of eusocial evolution, with pedigree kin selection playing a minor role at best (Wilson and Hölldobler 2005); or on the opposite side, kin selection is considered the key to eusocial evolution (Foster et al. 2006a, 2006b).

It is often said in research reports on social insects that some particular set of empirical data is "consistent with kin selection theory." But the same can be said of almost any other imaginable result, and the particular connection of data to the theory remains unclear. Hence, kin selection theory is not wrong. It is instead constructed to arrive at almost any imaginable result, and as a result is largely empty of content. Its abstract parameters can be jury-rigged to fit any set of empirical data, but not built to predict them in any detail, nor have they been able to guide, with a few exceptions, research in profitable new directions. If good theory rests on the three-legged stool of generality, precision, and realism (Levins 1966), kin selection theory is strong on the first of these qualities but ineffectually weak on the last two.

Until that disjunct is repaired, empirical studies and midlevel theory will together continue the largely independent momentum that has succeeded so well. Eventually, kin selection theory can be collated with them. It is dangerous to predict the future of any discipline, but at least the following areas seem to promise a rich future for empirical studies: the identification and sequencing of the alleles that are substituted at the origin of eusociality and the point of no return; the identification of the developmental processes prescribed by these transition alleles; the ecological pressure leading to effective group selection at the two key thresholds; and, through a greatly expanded scientific natural history, the discovery of new phenomena of multilevel selection that underlie the proximate phenomena of colonial life.

Finally, it needs to be added that the explanation of the origin and evolution of eusocial colonial life advanced here is meant to apply only to nonhuman animal species, and insects in particular. Human social behavior arose with different preadaptations, and may have been driven by a very different pattern of fundamental selection forces. (Or it may not have been so driven.)

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Robinson, and David S. Wilson, who are hereby absolved from factual or logical errors the article may contain.

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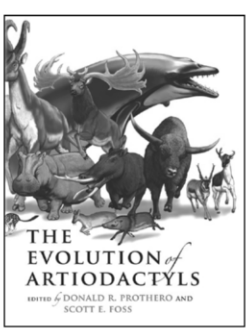
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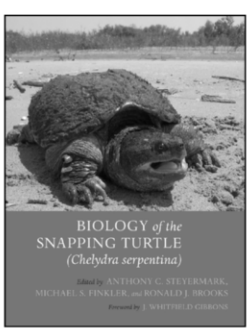
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