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Natural selection drives the evolution of ant life cycles

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The genetic origin of advanced social organization has long been one of the outstanding problems of evolutionary biology. Here we present an analysis of the major steps in ant evolution, based for the first time, to our knowledge, on combined recent advances in paleontology, phylogeny, and the study of contemporary life histories. We provide evidence of the causal forces of natural selection shaping several key phenomena: (i) the relative lateness and rarity in geological time of the emergence of eusociality in ants and other animal phylads; (ii) the prevalence of monogamy at the time of evolutionary origin; and (iii) the female-biased sex allocation observed in many ant species. We argue that a clear understanding of the evolution of social insects can emerge if, in addition to relatedness-based arguments, we take into account key factors of natural history and study how natural selection acts on alleles that modify social behavior.

sociobiology | claustrality | adaptive radiation | inadequacy of inclusive fitness

Comparative studies have revealed that from the moment of the evolutionary origin of animal eusociality, which is at first facultative in nature, each worker is in a tug-of-war between it and the colony of which it is a part. As colony-level selection becomes more important, however, individual survival and reproduction become less important to the worker's personal genetic fitness, and the survival and reproduction of the colony become more so. Finally, in obligatory eusociality, the capacity for worker reproduction within the genome ceases, creating the ultimate insect superorganism (1, 2). Ultimate superorganisms, in which the female workers lack any capacity to reproduce, are found in doryline army ants, *Atta* fungus growers, and the ant genera *Solenopsis*, *Pheidole*, *Monomorium*, *Tetramorium*, and *Linepithema*. Workers in the last five genera lack ovaries altogether. On the other hand, in a few clades of species the capacity of workers to reproduce has returned or at least has been augmented by secondary evolution, allowing individual workers to assume the role of queen (3, 4). At the extreme superorganismic phase, the level of selection becomes the genome of the queen and the sperm she stores, and the workers can be viewed as the robotic extensions of her phenotype (5).

Conflict between colonies may arise by direct physical contact, resulting either in retreat or complete destruction ("myrmicide") of the losing colony. Examples that have been well studied include fire ants of the genus *Solenopsis* (6), weaver ants (*Oecophylla*), and honeypot ants (*Myrmecocystus*) (7). Comparable programmed warfare occurs

in the primitive termite species *Zootermopsis nevadensis*. During encounters of two adjacent unrelated colonies nesting under bark, the single or multiple queens and kings of one of the *Zootermopsis* colonies are killed in combat, and their surviving offspring merge into one colony. Members of both colonies then cooperate as a single unit. Replacement reproductives develop from helpers of both original colonies and may interbreed (8).

Competition between colonies of the same ant species does not consist exclusively of overt combat and predation by large colonies on small colonies of the same species. It also includes competition through the preemption of nest and foraging sites as well as superiority in harvesting nest materials and food. Theoretical and experimental studies combined have demonstrated that all these colony-level endeavors depend primarily on colony size, a genetically determined group-level phenotype, as displayed in monogynous-versus-polygynous strains of many ant species (2, 6) and thought to precede the distinction of closely related species (2, 6). The number of participating workers alone has a profound effect on the colony's metabolic growth rate, life cycle, reproductive allocation, and mature size. The relationships mirror the metabolic scaling laws for mass and physiology of individual organisms (9). Mathematical modeling suggests that the critical demographic factor in the competitive growth of insect colonies is the initial fecundity and expected life-time of the founding queen (5).

A popular testing ground of inclusive fitness theory has been the colony life cycles and within-colony behavior of eusocial

insects, especially ants, leading to superorganisms (10–14). However, in almost all cases precise models of social interactions and evolutionary dynamics have not been formulated but instead have been replaced by arguments based on imaginary inclusive fitness concepts, which are not grounded in a mathematical description of evolution. Here we approach the issue in a novel manner, from geological history, phylogeny, and the details of comparative colony life cycles.

The Geological Origins of Eusociality

Although theory must be built upon facts, factual information makes little sense unless woven together as evolutionary history. Within biology, this principle is illustrated by every aspect of social evolution.

In tracking the historic origins of eusociality, we recognize that eusociality is a rare and relatively late arrival in the very long evolution of insects as a whole. It was the last of the great evolutionary advances through geological time, following (in chronological order) winged flight, the folding of wings over the back, and complete metamorphosis. It arose only after repeated diversifications of the insects and other hexapods across 325 million years.

The oldest known parainsectans, comprising neanurid (15) and isotomid collembolans

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(16), date to the Early Devonian (419–393 Mya). The earliest fossil, a pterygote insect at *ca.* 415 Mya, is *Rhyniognatha hirsti* (17). It is not the most basal, however; other evidence points to the primitively wingless Archaeognatha in that role (18). It is very likely that the earliest insects had a common ancestor that appeared bristletail-like (18) but actually would not have been part of the crown-group Archaeognatha. The Paleozoic evolution of the insects, paralleling that of the vertebrates and other invertebrates, then passed through two successive phases. The first, lasting until the start of the Late Carboniferous (about 323 Mya), was characterized by a scarcity of fossils and potentially limited biodiversity (19). The second phase was a major adaptive radiation during the Early–Late Carboniferous boundary, resulting in the origin of winged insects and an abundance of new insect orders (20) including the appearance of the most advanced major lineage of insects, the Holometabola characterized by an egg-larva-pupa-adult development (21). By the late Paleozoic Era, the fauna had begun to acquire a strong modern cast, although the main part of the process was ushered in by the mass extinction at the end of the Permian Period. Of the 28 insect orders alive today (the number recognized varies slightly according to taxonomic opinion), 14 were present at that time. The Paleozoic survivors include many of our most familiar insects: barklice, thrips, hemipterans such as treehoppers and shield bugs, dobsonflies and other neuropterans, mayflies, dragonflies, orthopterans, cockroaches, stoneflies, and beetles (especially archostematan) (20, 22, 23). Of the 14 orders known to have originated in the following Mesozoic Era, all are present today.

The late Paleozoic insects not only were abundant, diverse, and relatively advanced anatomically (24) but also, as evidenced by the amount of fossil leaf damage, constituted a major environmental force in the peat-accumulating forests and nearby better-drained habitats that dominated the land. By the end of the Permian Period, herbivory, called by Beck and Labandeira (25) “the basic trophic machinery of insects,” reached one-third that in modern rain forests for one lineage of seed plants, the gigantopterids.

Across the span of the second phase of Paleozoic evolution (323–252 Mya), the rich fossil record left no known evidence of eusocial insects. Some species might have existed in sparse populations, as exemplified today by modern *Microstigmus* wasps, or have lived in hidden niches, as do present-day scolytid beetles and gall-forming thrips. As yet, however, no trace has been detected

of an anatomically distinct worker caste, the hallmark of obligatory eusociality (26–33).

This evidence, albeit negative, deserves attention because of its relevance to the general theory of eusocial evolution. It supports the conclusion that eusociality—or at least its advanced, obligatory level—has been rare and came late in geological time. Additional support for this perception comes from the continued sparseness of the origination of eusociality in the Mesozoic and Cenozoic Eras. The number of known events that created obligatory eusociality in contemporary animals as a whole is only 18: three in synalpheid shrimps; two in the vespid wasps, scolytid beetles, and bathergid mole-rats; and one each in ants, termites, sphecid wasps, allodapine bees, augochlorine bees, corbiculate bees, halictine bees, thrips, and aphids (22, 34). A cockroach species (*Sociala perulicida*) from the Early Cretaceous has been interpreted as being eusocial from a single specimen (35), but the claim needs additional evidence. On the other hand, a more immediately plausible case might be made for including human beings, because of the existence of the postmenopausal “caste” of grandmother helpers (36).

Other examples, especially among arthropods, almost certainly will be found, but we doubt that the number ever will rise to more than the tiny fraction of all the animal phylads and of the species the phylads comprise. For example, all the known species of ants, termites, and eusocial bees and wasps make up only about two percent of the nearly 1 million known insect species (2).

The origins of the living insect eusocial lines were scattered across the Mesozoic and Cenozoic Eras. Termites were the earliest among them, projected to have evolved from cockroach-like ancestors during the Middle Triassic to Early Jurassic (237–174 Mya) (37). The eusocial corbiculate bees, particularly the bumble bees (tribe Bombini), honey bees (Apini), and stingless bees (Meliponini), evidently originated variously toward the end of the Cretaceous Period, as far back as 87 Mya, and during the early Paleogene Period (27, 28). The origin of eusociality in halictid bees occurred during the mid-Paleogene Period, 35 Mya (27, 28). The ants appeared, evidently from a single aculeate wasp ancestor (29), during the Cretaceous Period, about 140 Mya (29–31). By the Paleogene Period and likely during the very Late Cretaceous, most or all of the contemporary 21 ant subfamilies had separated (29–31).

The Approach of and Breakthrough to Eusociality

Why was eusociality so late in coming, and why has it remained so rare, when it has proven so ecologically successful? Numerous candidate phylads and environmental opportunities to advance into eusociality have been present on the land as well as in the fresh and shallow marine waters since the first terrestrial invasion by multicellular life. At least tens of thousands, more likely hundreds of thousands, of insect species were present and diversifying during the late Paleozoic and early Mesozoic Periods, during which they occupied a wide range of niches. The Pennsylvanian tree fern *Psaronius*, for example, was host to at least seven insect groups with different feeding habits, including external foliage consumption, piercing and sucking, stem boring, galling, spore consumption, and ingesting litter and peat at the base of the tree (33). Many types of life cycles and dispersal mechanisms have existed from that time onward. Also, various degrees of relatedness, from clonal to unrelated, probably were present in groups of individuals, as they are today in modern lineages of Paleozoic origin.

At the present time social aggregations of ancient origin, still short of eusociality, occur in different patterns and degrees of complexity in a majority of the insect orders. Massed offspring are tended by mothers and sometimes fathers as well. In a few cases these offspring are led by their parents from one place to another. According to species, the young are either protected by nests or kept in the open. For example, long-term care and protection of young has been observed in membracid treehoppers, scutellerid jewel bugs, belostomatid giant water bugs, gall-dwelling aphids, tingid lacebugs, praying mantises, earwigs, and argid sawflies. Tight masses of larvae, adults, or both, in some cases capable of organized movement, occur in species as diverse as gyrinid whirligig beetles, psocopteran barklice, embiidid web-spinners, noctuid and lasiocampid moths, acridid lubber grasshoppers, tenthredinid and pamphilid sawflies, and cockroaches (38, 39).

From this evolving mélange of subsocial insect and other animal species has arisen the very small subset of independent lines of living eusocial taxa. The key to their origin is that all these lines, with no known exception, first attained the same relatively rare pre-adaptation comprising progressive care of the young until maturity, by regular feeding or inspection or both combined with protection against conspecific competitors and other

enemies (34). The rearing of multiple larvae by such progressive care in protected nests has been of special importance as a presocial adaptation in the Hymenoptera (36, 38, 40–42). From nest construction and progressive care, only one short step is needed to achieve eusociality, namely the silencing, by as little as a single mutation, of the propensity of the mother and offspring to disperse (34).

The ultimate cause of the critical preadaptation (progressive care of offspring in a protected nest) remains open to speculation. The cause may have been nothing more than the advantage conferred by the possession of a residence, providing parents and offspring with a protected site from which they could forage and to which they could reliably return. The lack of a protected site leaves a subsocial family open to higher per-capita mortality and lower per-capita available food. (Compare, for example, the habitat of a population of subsocial insects confined to the canopy of a single tree, exposed to the elements and enemies, with that of a population of wasps living in a manufactured fortress within a tree branch from which scouts can travel abroad for food.)

Once dispersal is silenced, the adult stay-at-home daughters immediately subordinate themselves to their mother in the role of nonreproductive workers. Why does this seemingly non-Darwinian behavior occur, even if only partially? The answer, for hymenopterans at least, is that adults have a preexisting propensity to form dominance hierarchies in which later occupants yield rank to earlier occupants. Adults are strongly predisposed (“spring-loaded”) to become eusocial when forcefully kept together. For example, *Ceratina* and *Lasioglossum* bees, when experimentally confined together in very close quarters, proceed to divide labor variously in foraging, tunneling, and guarding of the nests (43–45). The dominant female stays at the nest as the reproductive caste. This propensity for forming dominance hierarchies sets the stage for the evolution of eusociality. In one well-studied case, with a pattern that may be widespread in temperate halictine bees, females mate in the autumn and form multiple-female colonies in the spring. In each colony one of the foundresses, as a rule the largest or oldest, becomes the queen, guarding the nest entrance and thereby inducing her cofoundresses to function as workers (46, 47).

Spring-loading as a step in the origin of eusociality did not come out of the blue. It is consistent with the fixed-threshold model documented in the origin of division of labor in well-formed insect societies. Behavioral studies have shown that, in general, members

of insect colonies vary in their responses to different tasks. When two or more individuals interact, the individuals with the lowest thresholds for each localized task are the first to undertake it. The activity of the initiators inhibits their colony-mates, who then are more likely to move on to whatever tasks remain available (48, 49).

Monogamy and Origin of Eusociality

A closely linked circumstance in early eusocial evolution is the “monogamy window hypothesis” (50). The generalization is well enough documented to be called a principle: All currently available evidence indicates that obligatory sterile eusocial castes arose only via the lifetime association with monogamous mothers.

At least in ants and other social Hymenoptera, the reason for the monogamy window principle is open to several alternative explanations that are relevant to the origin of eusociality. The first explanation is based on direct observation of natural history. A single mating, with the sperm stored in the mother’s spermatheca, provides the same amount of genetic variation as matings by individual solitary (noneusocial) species. Because the earliest eusocial colonies consist of a relatively small number of individuals, the number of sperm from a single mating (paid out through the spermathecal valve) is adequate to last for the founding female’s usually brief lifetime as queen. Another selection pressure favoring this explanation of monogamy was seldom invoked by previous authors but also is confirmed by direct observation: The mortality of the eusocial foundresses is very high from the moment they leave the mother nest and mate until they finish constructing a nest. Time is of the essence in the interval between leaving the relative safety of the mother nest and entering the relative safety of the new one. The agents of the increased mortality during exposure are many, both biological (chiefly through predation) and physical (because of the scarcity of nest sites and hour-by-hour vicissitudes in the environment). The large magnitude of the resulting hecatomb of would-be foundresses has been commonly observed in species that release large numbers in nuptial flights. Tschinkel (6), for example, has described the death of the vast majority of imported fire ant (*Solenopsis invicta*) queens from the first minute they take flight, subjecting themselves to “predation by birds and insects and the chance of heat death, starvation, execution, and usurpation.” As the queens settle to the ground, “a further fraction is taken by ground-based predators, especially other ants” (6). When predators are abundant, as

few as five percent of the queens succeed in building a nest (51). Similar mortality rates have been observed in the mating swarms of other ant species with large mature colonies, including representatives of the genera *Atta*, *Pheidole*, and *Pogonomyrmex* (2, 52).

Continuing this first explanation of the monogamy window principle, it is likely, although difficult to demonstrate, that high rates of mortality also exist for dispersing queens of primitively eusocial species, even though the starting numbers are much smaller. Such is demonstrably the fate of facultatively eusocial wasps. Among 19 species studied, 38–100% of the nests constructed by lone foundresses, who then were subjected to high risk both on the nest and during foraging, failed before the first brood emerged (53). When foundresses of the Neotropical stenogastrine wasps *Liostenogaster fralineata* and *Eustenogaster fraterna* disappear, the orphaned subordinate helpers, whether kin or nonkin, rear her brood while starting their own. Thus, they create an “insurance-based” advantage to the cooperators—and to the origin of eusociality (54, 55).

In summary, the monogamy window principle can be explained logically through direct observation as the consequence of individual-level natural selection. It exists because there is little relative advantage to a foundress to mate more than once. The advantage of acquiring greater genetic diversity in the small cohort of first offspring is outweighed by the protection afforded by a constructed nest. To the extent that some of the early worker broods are fertile, as often happens in primitively eusocial species, natural selection becomes multilevel: The fitness of the genomes of both the queen and each of her potentially reproductive workers derives from their inherited traits expressed in early colonial life.

Another consequence of the monogamy principle is that the first offspring of monogamous founding queens are closely related, as sisters. Primitively eusocial hymenoptera species are monogamous, as pointed out by Hughes et al. (56). Data are still lacking, but closely related solitary species are under the same predation-selection pressure, and they, too, can be expected to be monogamous. Because there are hundreds of extant related solitary species and only six known hymenopteran eusocial lines, the kinship-based hypothesis of Hughes et al. (56) does not explain why only a few of the monogamous lines evolved eusociality.

The Cretaceous Adaptive Radiation

Ants were born among dinosaurs of the Cretaceous Period (29–31). Most of their

fossils are found in cupressaceous amber from New Jersey, Alberta, Siberia, and Myanmar (formerly Burma) and also as fossils in rock compressions occurring in sub-Saharan Africa, Eurasia, and South America. The still very imperfect emerging picture is a possible (but far from proven) Gondwanan fauna featuring the myrmeciomorph clade, represented today by *Myrmecia* and *Nothomyrmecia* in Australia and the nearly worldwide Pseudomyrmecinae, and a Laurasian fauna, consisting of the extinct sphecomyrmines and other contemporary genera within or close to the poneroid clade. Of the derivative formicoid clade, destined during the early Eocene to expand to vast diversity and abundance worldwide, only a single formicine, *Kyromyrmex neffi* (57), and a dolichoderine, *Chronomyrmex medicinehatensis* (58), are known at present. Also present were members of the Aneurinae (represented today by a single, endangered species in Sri Lanka) and a species identified as either a primitive myrmeciine or a myrmeciine-sphecomyrmine intermediate (59).

The limited diversity of documented Mesozoic species, despite the considerable breadth of their apparent adaptive radiation, must result in part from the small sample size of specimens available. However, in contrast to their overwhelming abundance among insects in Eocene and later amber, ants are genuinely scarce in Cretaceous amber (60). These lower densities may be a consequence of the often small, cryptic colonies and low population densities that characterize most phylogenetically primitive species in the modern ant fauna.

The most anatomically primitive ants from the Mesozoic fauna were members of the extinct tribe Sphecomyrminae, the workers of which possessed a mosaic of ant and wasp traits—hence the name given them, “wasp ants.” The basal rooting of present-day Martialinae and Leptanillinae places the origin and early diversification of ants as far back as Early Cretaceous times. Molecular phylogenetic studies of these and other living species place the origin of almost all the living subfamilies in the early or middle Late Cretaceous or the Early Paleogene Periods (29–31). The history of the ants as a whole, however, appears not to extend as far back as the Jurassic Period (29–31).

Evidently the key event fostering the phylogenetic expansion of ants in general was the replacement in the mid-Cretaceous of a large part of the predominantly gymnosperm-dominated forest by the angiosperms (flowering plants). These insects flourished in tropical to warm-temperate forests,

which covered a much smaller fraction of the land and which were farther poleward than is the case today. The soil and ground litter of angiosperm-dominated forests are, and evidently always have been, far more diversified in structure and physiochemical conditions than those of more gymnosperm-dominated forests. In particular they inevitably created, as they do today, a much greater variety of both dwelling places and food for ants and other invertebrates. In addition, both the diversity and abundance of ants appear to have been greatly enhanced by claustrality, an innovation in the colony life cycle that deserves special attention in sociobiological theory.

The Claustral Revolution, Ecological Success, and Sex Allocation

Today, of the 21 extant ant subfamilies recognized by systematists as of 2013, four are dominant in terms of geographic spread, population density, and species diversity: Ponerinae (1,264 known species, 8.59% of the total 14,710 known and described ant species), Dolichoderinae (828 known species, 5.63%), Myrmicinae (7,087 known species, 48.18%), and Formicinae (3,794 known species, 25.79%) (61). The ponerines, represented by common species of *Ponera* and *Hypoponera*, are especially abundant in the litter and soil of tropical forests. Most of their species form small colonies that feed primarily or exclusively on fresh prey or on the remains of invertebrates newly killed by other predators. However, they are outnumbered more than fivefold in species and individuals by the myrmecines (62). Above the ground, from several meters high to the canopy, the formicines and dolichoderines dominate.

In north temperate forests ants nest primarily on and in the ground and vegetational litter. The species among them are overwhelmingly myrmecines and formicines.

Monogynous (single-queened) colonies of species in the Myrmicinae, Formicinae, and Dolichoderinae, the world-dominant crown groups of the formicoid clade, share claustrality, the habit of the newly inseminated queen of sealing herself in a chamber while rearing her young. Claustrality is an evolutionarily derived and nearly unique feature of their life cycles. This trait is the decisive factor in the sex allocation of resources. It is demonstratively adaptive, appearing in fact to be basic to the ecological success of the three subfamilies. Except in species that are socially parasitic or in which mated queens rejoin the mother colony (both of which also are derived traits in evolution), the virgin queens are much larger than the males. The queens

in each of these species are fattened by the workers, and they grow massive wing muscles. In many species virgin queens and males fly from the nest to form mating swarms. Males mate once, and the queen, depending on species, mates once or several times.

After mating each male dies, usually on the day of mating and principally by predation. The newly inseminated queen, carrying the sperm within her spermatheca, flies a distance that varies among species and then sets out to construct a nest and lay her first batch of eggs. Thereafter she does not leave the nest to secure food but instead feeds the growing larvae with regurgitated glandular food manufactured by materials and energy from her fat bodies and catabolized wing muscles. By the time the first brood matures, typically emerging into adulthood as tiny, short-lived “minim workers,” her reserves are depleted. Tschinkel (6) has appropriately characterized the queen of the fire ant *Solenopsis invicta* at this critical point as an “emaciated wraith.” She has raised a first brood of between 5 and 35 minims, who then set about to enlarge the nest and search for food to feed her. On average the fire ant queen’s weight during her seclusion falls from 14 mg to about 7 or 8 mg. Because most of her stored reserves consisted of fat, which possesses higher per-gram caloric content than lean body components, the claustral fire ant queen has lost two thirds of her starting total energy reserve, much of it in maintenance cost.

The claustrality of queens in the Formicinae, Myrmicinae, and Dolichoderinae confers an enormous advantage that is observed routinely in field studies. The young queen starts by acquiring a lifetime of sperm, enough to last over a period of years to decades. She can fly a substantial distance from the mother nest—up to 8 km in *Solenopsis invicta* (63)—and then raise a force of workers without leaving the safety of the nest in search of food. Claustrality thus removes most of the threat from predators and also from enemy ants of the same species (2, 6).

Studies of both monogamous and polygynous claustral ant species have revealed that the ratios of the number of queens to number of males produced are close to but below the 1:1 Fisherian ratio. On the other hand, the ratio of energy costs invested in females vs. males is understandably much higher. For example, in one large dataset of 42 monogynous (single mother queen) species summarized by Pamilo (64), the ratio of the number of virgin queens to males averaged 0.436, whereas the ratio of energy costs invested in virgin queens vs. males averaged 0.631.

Full claustrality is limited almost entirely to the subfamilies Myrmicinae, Formicinae, and Dolichoderinae, and herein lies a point of

considerable importance to sociobiological theory. These three phylads dominate the North Temperate Zone in colony and worker abundance and become increasingly dominant poleward. American and European researchers have focused largely on North Temperate species, and the result has been an unintended bias. For example, all but four of the 40 species cited in Pamilo's (64) study of sex allocation belong to these three families, out of the 21 subfamilies worldwide.

Full claustrality was derived from the basal condition of partial claustrality, which is practiced generally by the other subfamilies. The same condition occurs in solitary and primitively eusocial bees and wasps that progressively rear their young. In partial claustrality the foundress, sometimes assisted temporarily by cooperating foundresses, raises the young in a nest but forages outside to obtain part of the food supply (65). One rare exception is the ponerine *Pachycondyla lutea* (66), which is fully claustral.

From the broad stock of partially claustral clades have arisen several specialized life cycles, including single-queen army ant colonies that multiply by fission. From the fully claustral subfamilies have emerged species and strains with polygynous colonies (multiple queens) that multiply by budding (3, 4). In this latter assemblage, young queens mate on or near their home nests and return to the home nest to participate in reproduction. Having no need to carry on-board reserves, the virgin queens of polygynous species are smaller in size and receive a resource investment from their mother colony more closely matching that provided to males. Pamilo's (64) estimate of the queen-to-male resource-investment ratios from 25 polygynous species averaged 0.444, much closer to monogynous parity. Parasitic species in the same subfamilies also need no on-board reserves. As also expected, in slave-making species the queen-to-male resource-investment ratios have been found to be close to parity (average 0.483).

Taking the evolutionary history of the ants into account, and from direct inspection of colony founding in modern species, it is quite clear that the pattern of sex allocations can be explained fully as the product of natural selection acting on alleles that modify sex ratios. In contrast, explanations based on inclusive fitness theory usually are unsubstantiated inferences that neglect key aspects of evolutionary history, phylogeny, and the details of colony life cycles.

One of the persistent basic assumptions of inclusive fitness theory in explaining the much greater investment in virgin queens than in males in monogynous species has

been that workers are in control and skew the sex allocation to the virgin queens because of their closer genetic relationship. However, this assumption also is an error. The mother queen, not the workers, is in principal charge of which sex is preferred. If she "decides" to produce all females, she can hold her spermathecal valve open; if, on the other hand, her preference is all males, she can keep the valve closed. If she chooses a certain percentage of virgin queens and males, and the workers wish otherwise, the workers can change the ratio by killing one sex or another, a process observed in *Formica exsecta* and *Linepithema humile* (67, 68). However, the process is energetically costly, and there is no reason to assume that the advantage of the culling is to the advantage of the workers as opposed to that of the queen and colony as a whole. Furthermore, there is no evidence at present that such culling is practiced widely, although very few studies have addressed this issue. The workers also may inform the queen of the sex ratio needed, but such a feedback loop has yet to be found.

Workers of the ant colony nevertheless might be thought to control the production of virgin queens (providing the queen chooses to create females in the first place) by influencing the female larvae to develop into either virgin queens or workers. However, in the myrmicine *Myrmica ruginodis*, the most thoroughly analyzed case of female caste determination in ants to date, at least five factors have been implicated. Emanating (in macrogyne colonies) variously from the mother queen and the workers, these factors are larval nutrition, exposure to winter hibernation nest temperature, queen presence or absence, egg size, and queen age (69, 70). The condition of the egg before leaving the oviduct also has been implicated in the formicine *Formica polyctena* (71). The relative importance of these factors and the degree of their interactions have not been worked out, but collectively they point either to the phenotypic traits of the colony as a whole or to

those of the mother queen exclusively during colony foundation as the targets of natural selection.

Inadequacy of Inclusive Fitness and Beyond

The evolution of social insects often is presented as a testing ground for inclusive fitness theory. It has been claimed that inclusive fitness can explain sex allocation, worker policing, conflict resolution, and evolution of eusociality (14), but precise calculations of inclusive fitness do not exist for any of these phenomena. Relatedness-based arguments, such as the monogamy window hypothesis, are not necessarily wrong but rarely provide a complete picture; moreover, one cannot rely on inclusive fitness to determine when they are correct. The failure of inclusive fitness theory to provide exact calculations is not surprising, because a mathematically meaningful approach to inclusive fitness (72) cannot be performed for the majority of evolutionary processes (5), and the linear regression method (73–75) does not provide meaningful insights and cannot make empirical predictions (76). In general it is not possible to study social evolution from the perspective of an individual by evoking the virtual quantity of inclusive fitness. Instead we should focus on how natural selection acts on alleles that modify social behavior. On the level of genes or alleles, there is no inclusive fitness: Mathematical descriptions of the evolutionary dynamics of genetic mutations do not require a partition of fitness effects (which usually is impossible anyway) or any other aspect of inclusive fitness theory. We advocate the development of precise theories that are grounded in a good understanding of the life cycles and evolutionary history of social insects.

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