

Colony Founding in Social Insects

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Introduction

From our anthropocentric perspective, we tend to think that the world is full of social or group-living animals, like human societies. On the contrary, the majority of species, at least in the animal kingdom, are solitary in their life-style. And yet, undeniably, some of the most ecologically successful animals spend much or all of their lives in organized social groups called colonies. According to the definition given by E. O. Wilson in his 1971 book *The Insect Societies*, a colony is 'a group of individuals, other than a single mated pair, which constructs nests or rears offspring in a cooperative manner.' Insect colonies, in particular, have long fascinated biologists because the members of a colony, however distinct they are as individuals, often act like a single organism, and are hence called superorganisms. Such a society exhibits features of organization and function analogous to the physiological properties of a multicellular organism.

In this article, I will limit my discussion to social insects because their colonies are most intricately organized and thus most rigorously investigated of all animal species with an exception of *Homo sapiens*. The term 'social' has a very broad and not easily delineated boundary. Here, I use the categorization scheme for insect social systems (Table 1) modified from the one proposed in the book by Choe and Crespi, *The Evolution of Social Behavior in Insects and Arachnids*. According to the Crespi–Choe categorization, eusocial systems exhibit qualities such as parental or biparental care, shared breeding site, cooperation in brood care, alloparental care, and irreversible caste formation. The following taxa are considered eusocial: essentially all species of ants (Formicidae) and termites (Isoptera); other hymenopteran families/subfamilies of wasps and bees – Stenogastrinae, Sphecidae, Vespidae, Apidae, Anthophoridae, and Halictidae contain eusocial species; and thrips (Thysanoptera) and aphids (Aphididae) with specialized 'resource defenders,' and ambrosia beetles (Scolytinae and Platypodinae). Such a broad definition of eusociality permits more extensive comparative tests for the origin and evolution of sociality. Research findings for insects falling within this broad definition of eusociality are the subjects of this review.

A colony of organisms has a lifecycle much like the cycle an individual organism goes through. George Oster and Edward O. Wilson conveniently divided the colony cycle into three stages – *founding*, *ergonomic*, and *reproductive*. The founding stage is a critically important phase in

that the risk of mortality is the highest in the life of a colony. High mortality during this phase of life history has led to adaptations for colony founding that are diverse as for the reproduction patterns of individual organisms. The process of colony founding provides a unique window of opportunity to test a variety of models for the origin and maintenance of eusociality, because individual reproductives may theoretically choose among various reproductive options.

Honeybees (*Apis* spp.) and some species of ants, such as Argentine ants (*Iridomyrmex humilis*), pharaoh ants (*Monomorium pharaonis*), and army ants (*Eciton* spp.), produce new colonies by the breakaway of a group of colony members from a mature colony. This process resembles vegetative propagation in some plants and various modes of asexual reproduction in single-celled organisms and invertebrate animals. In the majority of social insects, however, new colonies are founded independently, without the help of workers. Reproductives of social insects have the options of either initiating a new colony from scratch or taking over an existing young colony, which could be either a conspecific or another species. Unlike *coups d'état* in human society, usurpers of social insects work alone and thus do not derive any somatic investment from the mother colony. No 'helper' members of the original colony accompany reproductives.

In their highly influential 1977 paper, Bert Hölldobler and E. O. Wilson drew up a comprehensive diagram illustrating the possible routes of colony foundation and maturation in social insects. Figure 1 presents a modification of their scheme that concentrates on the founding stage and includes colony usurpation as a legitimate founding mode. In this classification scheme, all modes of colony founding can be sorted into one of two categories that depend upon whether reproductives initiate colonies by themselves or are accompanied by workers. *Independent colony founding* involves the initiation of a new colony by reproductives without the aid of workers, while colony founding by budding and fission are grouped as *dependent colony founding*. Independent colony founding is further divided into two modes – usurping existing colonies or creating anew.

Independent Colony Founding

Among all the modes of colony founding, independent founding requires the least amount of investment by the

Table 1 Types of insect social systems

Type of society	Brood care	Shared breeding site	Cooperative brood care	Alloparental brood care	Castes
Subsocial	+				
Colonial	—	+			
Communal	+	+	+		
Cooperative breeding	+	+	+	+	
Eusocial	+	+	+	+	+

This categorization scheme modifies the one proposed by [Crespi and Choe \(1997\)](#). Here, brood care includes both parental and biparental care. Shared breeding sites are those that involve multiple females. Whether they cooperate in brood care or not is an important parameter in the evolution of sociality. Alloparental brood care refers to the presence of behaviorally distinct groups, with individuals specializing to be reproductives or helpers to those who reproduce. Following the definition given by [Crespi and Yanega \(1995\)](#), castes refer to 'groups of individuals that become irreversibly behaviorally distinct at some point prior to reproductive maturity.' This scheme allows the broadest possible taxonomic scale of comparative tests for explanation of the genetic, phenotypic, and ecological causes of variation in social systems.

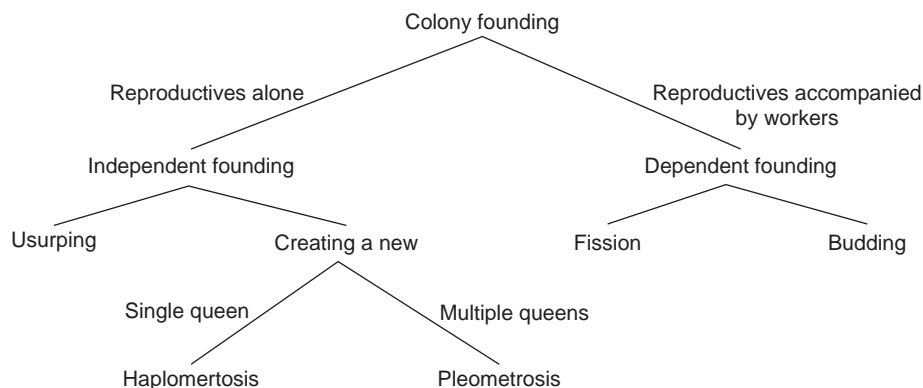


Figure 1 Modes of colony founding in social insects. Depending upon whether or not colony founding is accompanied by workers, it can be divided into dependent and independent founding. Dependent founding occurs in the form of either fission or budding. Independent founding has two types as well. The majority of social insect queens found a new colony singly (haplometrosis) or in group (pleometrosis). A sizeable minority usurp already established colonies of the same or different species.

mother colony. Inseminated females initiate new colonies alone or in a group. Unlike in budding and fission, the mother colony makes little investment as no workers accompany founding queens. This means that the colony of independently founding social insects passes through a solitary phase, however short it may be. This is curiously analogous to the reproductive cycle of multicellular organisms when they go through a single-celled haploid phase of sperm or egg. Under some ecological conditions, natural selection should favor independent founding, because independent reproductives can cover greater distances or wider areas than the ones escorted by workers. Independent founding is observed in a majority of ants and termites, halictine sweat bees, bumble bees (*Bombus*), hornets and yellow jackets (Vespinae), paper wasps (*Polistes*, *Parapolybia*, *Mischocyttarus*, and *Ropalidia*) as well as social aphids, thrips, and beetles.

Independently founding queens of social insects have the option of joining with other queens as a cofoundress in addition to starting one of their own. Although the majority of newly initiated colonies are founded by single

queens (*haplometrosis*), a significant minority are founded by multiple queens (*pleometrosis*). Foundress associations during the colony founding stage are observed in a number of social insect groups, including ants, bees, wasps, termites, aphids, and thrips. Compared to the early recognition of worker sterility or queen–worker conflicts as a critically important topic in the evolution of insect sociality, students of social insects had not paid much attention to queen–queen conflicts until the mid-1980s, with a possible exception of wasp biologists, most notably, Mary Jane West-Eberhard. For the past two decades, however, facultative pleometrosis has been investigated with greater rigor, because these systems provide opportunities to analyze the relative contributions of genetic and ecological factors to the evolution of cooperation.

As far as the kin structure of colonies is concerned, it is interesting that cofoundresses are typically unrelated in ants and some bees. An exception to this ‘rule’ is *Lasius pallitarsis*, in which solitary and kin-pair queens produce workers, whereas nonkin pairs of queens do not. In eusocial wasps and bees, however, cofounding queens are generally

close relatives. Transactional skew theory views foundress associations as a form of social contract that guarantees mutual benefits to both the dominant and subordinate foundresses. Skew models predict more or less evenly shared reproduction among genetically unrelated cofoundresses, because a greater incentive to help is required of nonrelatives. Indeed, low reproductive skew is reported among cofoundresses of ants and some bees. In contrast, reproductive outputs are highly skewed in foundress associations of eusocial wasps and many bees, in which per capita brood production generally declines as the number of cofoundresses increases. Like the counter-example found in ants, exceptions to the rule have also been discovered in paper wasps (*Polistes* spp.), tropical hover wasps (*Parischnogaster mellyi*), and social thrips *Dunatothrips aneurae*. The philopatric nature of foundresses naturally facilitates cofounding by nestmates from the previous year. In these insects, however, DNA microsatellite analyses revealed that their social organizations are much more diverse than previously assumed. Reproduction is often shared between related and nonrelated foundresses in some nests.

Evolution of Claustal Founding

Independent foundresses may be claustral, in which they confine themselves within the nests until the first brood of workers ecloses. Alternatively, they may be nonclaustral or semiclaustal, so that they forage outside of the nests while raising the first brood. In bees and wasps in which reproductives retain their wings throughout their lives and nests are essentially open all the time, the basal mode of colony establishment is independent, nonclaustral founding. Founding queens forage outside the nest to bring food to rear the brood. The dominant of a cofoundress association forces subordinate foundresses to forage, in which case she becomes functionally claustral but still does not exhaust her bodily resources like ant and termite queens. Foundresses of social gall aphids and thrips are also basically claustral, but have no need to forage outside or drain off their bodily energy reserve because their nests contain feeding sites. Founding females remain within the gall (or other types of domiciles) feeding on plant cell contents and producing offspring that develop to adulthood inside. They are so-called 'fortress defenders' in the terminology developed by David Queller and Joan Strassmann in their 1998 paper, exhibiting a form of resource-based sociality. When sites for shelter and food coincide, selective pressure is strong for the defense of expansible and food-rich nest sites. Indeed, this favored the evolution of morphologically specialized defenders or soldiers in both gall aphids and thrips.

Claustal colony founding is most common among ants. The ability to metabolize wing muscles is a preadaptation to the evolution of claustral founding. Claustal

founding is also characterized by a suite of other physiological and behavioral adaptations, such as wing dropping after nuptial flight, the ability to pack away large amount of body fat, and ingluvial feeding, that is, feeding larvae on metabolized nutritional reserves. Mortality risk during foraging for founding queens is quite obviously the selective pressure that has led the evolution of claustral founding. The so-called 'higher' ants in the subfamilies Formicinae and Myrmicinae typically found new colonies claustrally, whereas semiclaustal founding is rather prevalent in the morphologically and socially more primitive ants of Paraponinae, Ponerinae, Myrmecinae, and Nothomyrmecinae. This suggests that claustral colony founding is a derived state, while semiclaustal founding is an ancestral character in the evolution of colony-founding modes.

Contrary to the previous belief, however, recent studies revealed that semiclaustal colony founding occur at least in 28 species of 12 genera of myrmicine and 2 genera of formicine ants. Semiclaustal founding is obligate for foundresses of fungus-growing ants, *Atta* and *Acromyrmex*, because their fungus gardens would not survive without a constant supply of fresh leaves. Because they lack sufficient stored proteins for claustral founding, foundresses of *Messor andrei* also appear to be obligately semiclaustal. At least one species of harvester ants, *Pogonomyrmex californicus*, founds new colonies semiclaustally in the laboratory setting. For most semiclaustal ants, their colony foundation habit seems facultative. Environmental variability may allow foundresses to adopt semiclaustal founding as a bet-hedging strategy.

Although claustral queens may benefit from much reduced predation, they must rely on the histolysis of their no longer needed wing muscles and stored fat bodies to supply the energy resources required to rear the first brood of workers. Thus, claustral foundresses can be called *capital breeders*, whereas nonclaustral or semiclaustal foundresses act like *income breeders*. Depending on the size of the capital, an obligately claustral foundress suffers a burden of trade-off between the number and size of brood. Despite a higher risk of mortality, a semiclaustal foundress may be able to practice a strategy to maximize the number and/or size of offspring within the capacity of a given environment. A colony founded by a capital breeder begins as a society of closed economy and then switches to an open economy once the workers start provisioning resources from the outside. A claustral breeder must budget her capital, that is, bodily resources, so that they are not exhausted before producing a sufficient worker force. Time and efficiency are the names of the claustral game.

Evolution of Foundress Associations

Among ants, pleometrosis occurs mostly in the 'higher' subfamilies, namely, Formicinae, Myrmicinae, and

Dolichoderinae, with possible occasional exceptions in Ponerinae and Nothomyrmecinae. Ants of the three subfamilies have evolved remarkably similar sets of modifications and variations on pleometrotic colony development. Cofoundress associations have also been observed among wasps of eusocial Polistinae, Stegogastrinae, and Sphecidae. All observed cases of pleometrosis among bees come from Halictini, Augochlorini, Ceratinini, and Allodapini. Among termites, soil-nesting species are more frequently pleometrotic than wood-dwelling species.

Cofounding has its own costs. Per capita reproductive output is likely to decrease, competition over resources increases, and close proximity can make the transmission of parasites and pathogens easy. Despite all these potential costs, however, pleometrosis is widespread, occurring in nearly all eusocial insect groups. This means that there must be sufficient benefits for cofounding counterbalancing the costs. A list, not necessarily mutually exclusive, of the advantages of pleometrosis suggested thus far is:

1. Production of the first worker cohort much larger and/or faster

In a number of species, colonies founded by multiple queens produce greater worker forces in the first brood, and in some cases, do so in less time. Producing a larger worker force in a given time or more quickly accrues a host of benefits in terms of colony defense, brood raiding, and foraging success. Pleometrosis appears to be an adaptation for intercolonial competition. Better success in defense, brood raiding, and foraging give multiple-queen colonies a competitive edge among incipient colonies. Colonies initiated by large numbers of queens better resist usurpation attempts. Larger or more rapidly formed worker forces can eliminate neighboring incipient colonies, but the importance of brood raiding in the colony-founding stage is debatable. The majority of brood-raiding observations are from laboratory studies and its prevalence in the field awaits further research. Brood raiding occurs frequently and is an important ecological parameter in *Solenopsis invicta*, an invasive species with an extremely high density of incipient colonies. On the other hand, a carefully planned field study on *Messor pergandei* turned up no evidence of brood raiding occurring in the field. Instead, increased foraging success by larger worker forces appears to clearly enhance colony survival and growth. *Cecropia*-nesting *Azteca* colonies with multiple queens produce more workers in less time than those with solitary queens, and those workers which chew their way out of the internode first can monopolize the supply of glycogen-rich Müllerian bodies secreted by *Cecropia*. The outcome of this scramble competition is the starvation of all other incipient colonies inhabiting the same *Cecropia* sapling. When many incipient colonies are clumped in an area, early brood production is

particularly important, given the probability of intercolonial brood raids and/or intense competition for limited food resources.

2. Increased survival of foundresses

To determine whether cofoundresses on average have higher survivorship than solitary foundresses, one has to analyze queen mortality due to intracolony competition and intercolonial competition separately. Although enhanced survivorship may be a major benefit for foundress associations, most studies of pleometrosis have measured only mortality from intracolony competition; the relationship between the number of cofoundresses and mortality is not always significant. Once intercolonial mortality caused by interference or scramble competition is added to the analysis, however, it becomes obvious why pleometrosis is favored over haplometrosis. Even though an individual foundress' probability of becoming the ultimate survivor of a foundress association decreases as the number of foundresses increases, the selection still favors pleometrotic associations because of the decisive advantages of larger worker forces during competition among incipient colonies.

3. Earlier maturation to the reproductive stage

Colonies with larger and more rapidly produced worker forces tend to survive better and produce reproductive offspring earlier than the ones with small or slowly produced worker forces. Enhanced production of workers may increase an individual foundress' reproductive output. Although a haplometrotic queen does not suffer from intracolony competition, the pressures from intercolonial competition may be so great that joining other queens in colony founding may be the only way a queen can survive. Despite the heavy odds against surviving to become the ultimate reproducing queen in a pleometrotic colony, a queen may have a better overall chance of reaching the reproductive stage if she begins a colony with other foundresses than if she founds alone.

4. Better protection from parasites and predators

In the case of nonclaustral and semiclaustral founding, unattended nests and broods experience higher incidences of attacks from natural enemies. In *Polites* and *Mischocyttarus* wasps, foundress associations greatly reduce the rate of nest destruction by conspecifics and predators. Colonies started by solitary foundresses tend to leave their nests unattended for longer periods of time while foundresses are out foraging. Frequent switching and continuous guarding by communally nesting sweat bees effectively protect their nests from the attacks of kleptoparasites. The social thrips *D. anueriae* also has better protection against kleptoparasites than solitary thrips. Although multiple foundresses confined to close proximity may facilitate easier transmission of parasites and pathogens, cofoundresses can

groom each other, which may reduce the mortality caused by fungal attacks.

5. Reduction of costs of nest construction and maintenance

Joint colony founding can also yield more immediate and direct benefit in terms of construction, defense, and repair of nests. Cofounding queens of several ant species cooperate in nest excavation and those of wasps and bees cooperate in building up the nest during the founding stage. In *S. invicta*, queens attempting to usurp other colonies are less successful when attacking a three-queen colony than a one-queen colony regardless of how many workers are present. Cooperating wasp cofoundresses also defend their nests from usurpers better and repair damaged nest more rapidly.

6. Assured fitness returns

Raghavendra Gadagkar argues that the subordinate cofoundresses can have the advantage of assured fitness returns by joining a foundress association. A foundress has no fitness gain if she chooses to start a colony alone but dies before her offspring reach the age of independence, but she is assured some fitness returns if she joins a pleometrotic colony and even assumes the role of helpers. Even if she cares for some larvae during their early stages and dies long before they grow to become independent, some other helpers are likely to care for the same larvae and bring them to independence. This model is most applicable to a life cycle of the sort exhibited by polistine wasps in which larvae are progressively provisioned and pupae need continuous protection by adults.

Cofoundress associations are dynamic systems of conflict and cooperation. The propensity for cooperation varies, and diverse ecological conditions may favor cooperative colony founding. Individual foundresses in a pleometrotic colony must contribute enough to enable their colony to outcompete neighboring incipient colonies, but at the same time, they must also carefully budget their energy reserves in order to outcompete fellow cofoundresses for the eventual ownership of the colony. They cooperate to survive during the early phase of the founding stage, but when the first workers eclose, they begin fighting fiercely, typically to the death. It is unclear whether workers actively choose the surviving queen and kill off other queens or if they passively eliminate already injured and less competitive queens. Cofounding queens of *Lasius niger* differ with respect to their oviposition rates and workers preferentially feed more fecund queens. Therefore, selection may favor queens that balance their energy budgets well and maintain good body condition until worker emergence.

Primary polygyny or extended coexistence of pleometrotic queens to the reproductive stage is extremely rare.

The transition from closed to open economic system provides a major explanation for the transition from pleometrosis to secondary monogyny. In claustral multiple queen associations, all available energy to rear the first brood comes from the stored bodily reserves of cofoundresses and there is a good reason why they must be cooperative. When the first workers start bringing food from outside, however, the colony's economy switches to an open system and cooperation among foundresses begins to collapse. This explanation is not complete because in most *Polistes* wasps, which are clearly nonclaustral, cofounding females stay together well into the reproductive stage, but a single female usually lays most or all of the reproductive-destined eggs. Primary polygyny has also been observed in semiclausal *Acromyrmex* ants.

Unisexual founding in termites

Unisexual colony founding by female reproductives is the norm in the hymenopteran social insects but is an exception in termites. Colony founding in termites typically involves both sexes. In the case of pleometrotic founding, discussions often center around the adaptive significance of polygamous mating (mating between a single male with multiple females) in comparison to the usual monogamous mating. In the subterranean termite, *Reticulitermes speratus*, female reproductives which fail to mate sometimes found colonies alone or in female-female pairs. Foundresses without males reproduce through thelytokous automictic parthenogenesis. If a male is introduced to a female pair in the laboratory, only one female survives. If a partner male is absent, two females, but never more than two, found a colony in which they produce the first brood of workers in a cooperative manner. Recently, Kenji Matsuura and his colleagues discovered that secondary neotenic queens of *R. speratus* are produced almost entirely parthenogenetically by the founding primary queens, while workers and winged reproductives are produced by normal sexual reproduction.

Mixed-species pleometrosis in Azteca ants

Among all the observations of colony founding in social insects, the most enigmatic is cooperative founding by queens of two different species of *Azteca* ants. Dan Perlman conducted an extensive field study on the colony-founding processes of *Cecropia*-nesting *Azteca* ants in Monteverde, Costa Rica. Several species of *Cecropia* are myrmecophytes, obligately inhabited by *Azteca* ants. In Monteverde, *Cecropia* saplings (mostly *C. obtusifolia*) are occupied by two sympatric *Azteca* species, *A. constructor* and *A. xanthacra*. *Azteca* colonies are founded in three distinct ways: by single queens, by single-species groups of queens, and by mixed-species groups of queens. Pleometrotic colonies of both single species and mixed species outperform haplometrotic colonies by producing larger first worker cohorts, and by eventually

taking control of the entire tree through the monopolization of the main food source, Müllerian bodies grown by *Cecropia*. Field observations revealed that mixed-species foundress associations are nearly as cooperative and successful as their single-species counterparts throughout the founding stage. This means that mutualism is as important a selective factor as inclusive fitness for the evolution of pleometrosis.

Soon after landing on a *Cecropia* sapling, a newly inseminated queen explores the young upper internodes of the plant for a while, sheds her wings, and begins to chew into a thinner, unvascularized area in the wall of one of the uppermost internodes. *Cecropia*-nesting *Azteca* queens appear to settle in the first tree upon which they land, but once the tree is chosen, they appear to examine and choose among internodes. It is reasonable to presume that the queens can discriminate a recently occupied internode from an unoccupied one based on the presence of the loosely plugged entry hole. On the other hand, it may be rather difficult for late-arriving queens to estimate the number of foundresses that have already joined the association before entering the internode.

A queen can take as long as 2 h to push herself through the hole into the plant. She then plugs the hole with parenchymal tissue scraped from the inner wall of the internode. A late-arriving queen has options: she could choose to make a hole to enter an unoccupied internode or she could join other queens in already-excavated internodes. If she chooses the latter option, it takes only 5–12 min, thus saving energy and reducing exposure time to predation risk. A mature *Cecropia* tree is invariably occupied by a single colony with a single queen. Selection to produce a large worker force as quickly as possible to outcompete neighboring colonies in the same tree leads not only to foundress associations but also to the evolution of this remarkable case of interspecific cooperation in colony founding. Mixed-species colonies are quite common. One out of five queens is engaged in mixed-species foundress associations. All cofounding queens contribute to the production of workers whether they belong to single-species or mixed-species colonies. Like other pleometrotic species, *Azteca* queens start fighting against one another regardless of species identity, once the workers begin foraging and stockpiling Müllerian bodies. Colony founding in *Azteca* ants offers an ultimate testing arena for investigating the relative importance of genetic and ecological factors in the evolution of sociality and further studies will surely turn up many more exciting new discoveries.

Colony Founding by Usurpation

Queens that failed in attempts to found new colonies independently or that are subordinates in multiple-queen colonies can employ the alternative founding strategies of

usurping established colonies or adopting orphaned colonies. Attempting to start a new colony when the season is well underway is hardly a viable option. Taking over nest, brood, and/or workers produced by other queens is clearly parasitism and therefore colony foundation by usurpation or adoption is called social parasitism. Such parasitism occurs within species as well as between species and the usurping queens taking possession of a colony of a different species are called 'inquilines.'

In wasps, usurpers typically kill eggs and early-instar larvae of the colony they have taken over. The usurper lays eggs while letting later-instar host larvae and pupae complete development so that they can be forced to provide care for the brood of the usurper. The success rate of usurpation is sufficiently high that selection could favor this as a primary founding strategy. Usurpers can save the energy required for founding a new colony and instead sit-and-wait to take advantage of another queen's investment. Special adaptations of more extreme social parasites include enlarged heads and mandibles of usurping queens as well as evolutionary loss of the worker caste. Social parasites exhibit a wide spectrum of integration with their host colonies. For instance, parasitic queens of the 'ultimate' inquiline ant *Teleutomyrmex schneideri* harmoniously coexist with the host ants of *Tetramorium* by allowing the host queen to continue to lay worker-destined eggs while the parasite produces reproductive offspring.

Dependent Colony Founding by Fission and Budding

At the opposite side of the colony-founding continuum, relatively large colonies of some species propagate vegetatively by forming a swarm that consists of reproductives and a sizeable worker force. This mode of colony founding has been called swarm founding, or more specifically, hessmosis in ant literature and sociotomy in termite literature. But the term 'swarm' is also used to refer the mating swarm of reproductives during nuptial flight and this dual usage creates occasional confusion with the colony-founding swarms. Dependent colony founding may be more accurately described as either fission or budding.

Colony fission occurs when a monogynous colony first produces a clutch of reproductives and then divides into two daughter colonies of roughly equal sizes. When daughter colonies are led by new queens, their worker forces are more or less even. When one of the daughter colonies retains the old queen, however, its sister colony with a new queen is often smaller in size. Colony fission is the norm of founding in honeybees, stingless bees, army ants, and some wasps. It appears generally the case that fission is the mode of colony founding adopted by species that achieve a very large colony size, but not all large-colony species reproduce by dependent founding. Fungus-growing ants

of the genus *Atta*, *Vespula* wasps, and 'higher' termites of the Termitidae all attain colony sizes of thousands or millions of workers, yet invariably reproduce by independent founding.

When colony fission is present, it is the exclusive mode of colony founding for the species; facultative fission is unknown. Colony budding is a much less stereotyped process that often occurs concurrently with more standard independent colony founding. Colony budding involves the departure of already inseminated queens from polygynous colonies with a relatively small number of workers. Unlike fission, in which the daughter colonies disperse far enough to become independent, budding colonies remain in close proximity with one another and the mother colony. They often interchange workers among themselves, yielding a polydomous colony structure, in which a single large colony has multiple nests.

Dependent founding has evolved under the ecological conditions in which independent founding is not an option because colonies below a certain size are not viable. Colony fission and budding have clear selective advantages over independent founding, because the accompanying workers can construct the nest quickly and immediately begin colony-level performances via task specialization. Indeed, queens of species practicing dependent founding store much less body fat than independent founding queens.

Unanswered Questions and Future Studies

Considerable research has focused on foundress associations. Theoretical models assume that foundresses have the ability to assess costs and benefits of joining others. Data on the process of cofoundress formation and nestmate selection under field conditions are still needed. Provided that workers have little influence on the accession decision among cofoundresses, it is important to know how individual foundresses balance their energy budgets between individual and colony-level investment. In this both competitive and conflicting game of egg laying, she must lay as many eggs as possible if she hopes her colony to outcompete the neighboring colonies. At the same time, however, she should not exhaust herself before the physical combat against other cofoundresses. We must measure relative contributions of individual foundresses and observe whether foundresses can induce others to contribute more or prevent others from contributing too much.

For both pleometrosis and haplometrosis, long-term field studies are needed. Few studies of colony founding have followed queens long enough to estimate lifetime reproductive success. Surviving queens in pleometrotic colonies may be able to reproduce earlier and/or for a longer period of time than haplometrotic queens. Colony founding provides an excellent arena for testing various hypotheses for the evolution of sociality, and the approach of long-term ecological research will give us a much more complete picture.

See also: Ant, Bee and Wasp Social Evolution; Division of Labor; Kin Selection and Relatedness; Queen–Queen Conflict in Eusocial Insect Colonies; Reproductive Skew; Termites: Social Evolution.

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