Recurrent Evolution of Dependent Colony Foundation Across Eusocial Insects

Adam L. Cronin,[1,*] Mathieu Molet,[1] Claudie Doums,[1,2] Thibaud Monnin,[1] and Christian Peeters[1]

[1]Laboratoire Écologie & Évolution CNRS UMR 7625, Université Pierre et Marie Curie, 75 005 Paris, France; email: adamcronin@gmail.com, mathieu.molet@umpc.fr, claudie.doums@umpc.fr, thibaud.monnin@upmc.fr, cpeeters@snv.jussieu.fr

[2]Laboratoire Écologie & Évolution CNRS UMR 7625, École Pratique des Hautes Études, 75 007 Paris, France

*Corresponding author

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Abstract

The spectacular success of eusocial insects can be attributed to their sophisticated cooperation, yet cooperation is conspicuously absent during colony foundation when queens are alone. Selection against this solitary stage has led to a dramatically different strategy in thousands of eusocial insect species in which colonies are started by groups of nestmates and the benefits of sociality are retained continuously. Dependent colony foundation (DCF) evolved recurrently multiple times across the ants, bees, and wasps, though its prevalence in termites remains unclear. We review adaptations at both the colony level (reproductive investment shifts from sexuals to workers) and the individual level (wingless queens evolve in ants), and other consequences for life history (invasiveness, parasite transmission). Although few studies have focused on DCF, the accumulated data from anecdotal reports, supported by indirect information including morphology, population genetics, and colony demographics, make it clear that this strategy is more diverse and widespread than is usually recognized.

INTRODUCTION

Independent colony foundation (ICF): queens found new colonies without any help from nestmate workers

Nonclaustral ICF: the founding queen must leave her nest to find food for the first brood of workers, exposing herself and her brood to predation

Claustral ICF: the founding queen uses metabolic reserves to rear the first brood of workers and does not forage outside the nest

Social insects (most notably all termites and ants and some bees and wasps) represent around 2% of all insect species but have a huge ecological importance in all terrestrial habitats (56). Their success is due to the benefits of efficient cooperation and separation of tasks among nestmates. This cooperation is conspicuously absent, however, when new colonies begin: Most species use independent colony foundation (ICF), during which the queen (queen and king in termites) is alone as she attempts to establish a new nest and produce the first generation of workers. This vulnerable solitary stage can last several weeks, and the vast majority of attempts will fail (43, 56, 73, 89, 128).

The risks of solitary founding are highest in species in which the queen must forage for food (nonclaustral ICF; **Table 1**). In higher (formicoid) ants, the survival of the queen and her brood is improved by claustral ICF (98), whereby queens have large metabolic reserves that are sufficient to feed the first brood without foraging outside the nest. Similarly, claustral ICF occurs in many termites, as cellulose can be obtained from the nesting substrate (115). Other variants of ICF can also reduce mortality during the solitary stage (**Table 1**): In some ants (8, 9, 119), wasps (37, 103), and bees (94, 111), several queens cooperate to establish a new nest (pleometrosis), typically increasing the success of incipient colonies. These queens disperse alone before forming a pleometrotic association and consequently are usually unrelated. Furthermore, they compete for reproduction and, depending on the species, most become infertile subordinates or are killed or ejected from the nest once the first generation of workers emerges (3, 9, 103). Another strategy employed by solitary queens to reduce the risks of ICF is to invade an established host colony (of the same or a foreign species), and exploit it as a resource to produce her own offspring (**Table 1**). Social parasitism, like pleometrosis, can be considered a form of ICF, because founding queens disperse alone and do not cooperate with nestmate workers (99).

Although these alternative forms of ICF can increase foundress success, high foundress mortality has led repeatedly in other species to the evolution of a remarkably different strategy that eliminates the solitary phase altogether. In thousands of ants, bees, and wasps, established colonies regularly divide into smaller autonomous colonies, a process known as dependent colony foundation (DCF). DCF is also thought to be a strategy additional to ICF in some termites, but its

Table 1 Characteristics of ICF and DCF

Mode of colony foundation	Number of individuals in each propagule	Composition of newly founded colony	Risk of mortality for incipient colony
ICF: solitary founding (nonclaustral or claustral)	One	Isolated founding queen (royal couple in termites)	High: founding queen remains alone for weeks or months as she rears her first brood
ICF: pleometrosis	One	Few founding queens (nonnestmates, nestmates by chance, sometimes heterospecifics)	Medium-high: brood production is more rapid than in solitary founding
ICF: social parasitism	One	Founding queen plus hosts	High while entering a host colony, low if takeover is successful
DCF (fission, budding, swarming)	Several[a]	Founding queen(s) plus nestmate workers	Low as queen is never alone[b]

[a]In addition, ants allocate brood to propagules, and stingless bees allocate food and propolis; honey bees and wasps allocate only adults.

[b]Queens in bees and wasps are vulnerable during a short solitary phase while mating on the wing. In all DCF ants, queens mate in the vicinity of the nest and benefit from the protection of workers.

Abbreviations: DCF, dependent colony foundation; ICF, independent colony foundation.

INDEPENDENT COLONY FOUNDATION

ICF, in which new queens disperse alone, is well studied in the red imported fire ant, *Solenopsis wagneri* (formerly *S. invicta*) (128). The monogynous form of this species founds colonies by claustral ICF. Mature colonies produce approximately 700 sexuals, with a sex ratio of 1:1 on average. Between their emergence as adults and their departure to found new colonies, young queens accumulate so much energetic reserves (storage proteins and fat) that they triple their weight. Each queen mates with a single foreign male and disperses a few hundred meters. Once she finds a suitable nesting site, she sheds her wings, excavates a nest, and seals herself in. Within a week she lays 30 to 70 eggs, and uses her energetic reserves and now useless flight muscles to rear a first generation of 5 to 35 workers, losing half her body weight in the process. These workers become the first foragers of the new colony, and the queen need not leave the nest again.

DEPENDENT COLONY FOUNDATION

Honey bees and army ants are the archetypes of reproduction by DCF but do not reflect the true diversity of this strategy. A lesser-known example is the ant *Cataglyphis cursor* (24, 27). Monogynous colonies of approximately 700 workers rear sexuals with a 1:4 female-to-male ratio (24, 96). Young queens mate at the nest entrance in the company of workers, while males disperse on the wing to find foreign colonies. Workers find suitable sites to establish new colonies and begin nest construction, on average 7 m from the mother colony. In a process requiring approximately 1 to 3 days for each propagule, workers then transport gynes, brood, and other workers to the new site. In this way each colony splits into two to seven new colonies over a period of 1 to 9 days, with each new colony containing a dramatically different number of workers (3–71% of the workforce of the colony before fission). A viable workforce is available from the outset and the size of new colonies may be tailored according to ecological conditions (27).
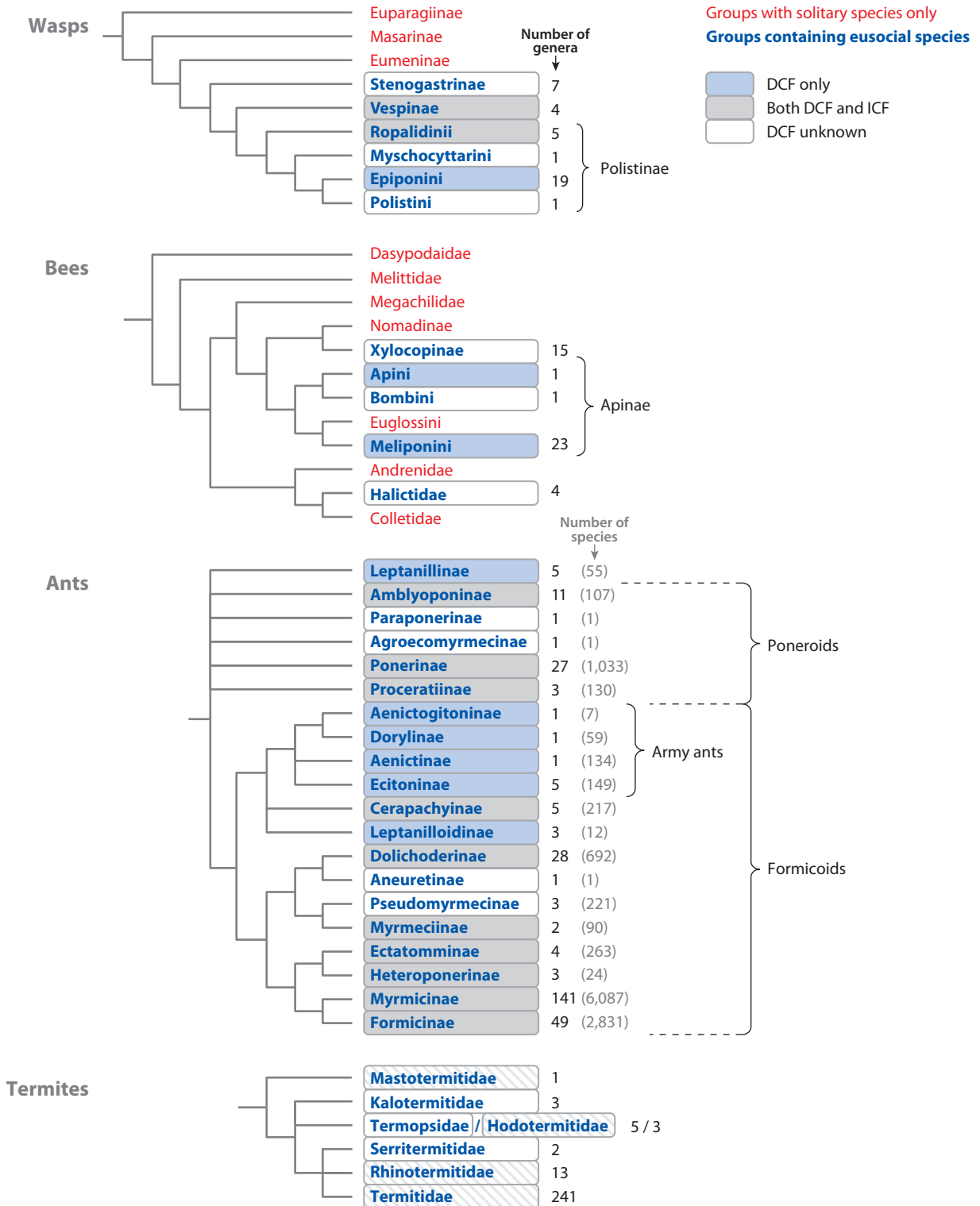
prevalence is currently unknown. Depending on the species, the mother colony produces one or more propagules that consist of a variable number of highly related nestmate queens and workers (**Table 1**). The founding queen(s) is continuously helped and protected by nestmate workers who forage and care for the brood, greatly improving the success rate of colony establishment (67, 99). Various terms (fission, budding, swarming) have been used in the literature to describe such colony division, but in the absence of reliable and consistent criteria distinguishing these (98), we follow Peeters & Molet (99) in uniting them under the umbrella of DCF (**Table 1**). DCF is a strategy of colony foundation and thus, unlike some previous uses of the terminology (e.g., 51, 108), we exclude cases in which newly mated reproductives are readopted by their natal colony without the formation of a new colony. In this review, we examine the phylogenetic distribution of DCF and compare ICF and DCF strategies in terms of reproductive investment, dispersal range, population genetic structure, and other life-history traits.

Dependent colony foundation (DCF): queens found colonies with help from nestmate workers and are typically incapable of succeeding without this help

DIVERSITY OF DCF STRATEGIES

Recurrent Evolution of DCF

Recent phylogenetic analyses permit us to infer that DCF has evolved at least three times in wasps [in Vespinae, Ropalidinii, and Epiponini (swarm-founding wasps); 67, 82, 116], twice in bees [in Apini and Meliponini (stingless bees); 84], and numerous times in ants (97) (**Figure 1**).

Wasps

	Number of genera
Euparagiinae	
Masarinae	
Eumeninae	
Stenogastrinae	7
Vespinae	4
Ropalidinii	5
Myschocyttarini	1
Epiponini	19
Polistini	1

Polistinae

Groups with solitary species only
Groups containing eusocial species

DCF only
Both DCF and ICF
DCF unknown

Bees

	Number of genera
Dasypodaidae	
Melittidae	
Megachilidae	
Nomadinae	
Xylocopinae	15
Apini	1
Bombini	1
Euglossini	
Meliponini	23
Andrenidae	
Halictidae	4
Colletidae	

Apinae

Ants

	Number of species	
Leptanillinae	5	(55)
Amblyoponinae	11	(107)
Paraponerinae	1	(1)
Agroecomyrmecinae	1	(1)
Ponerinae	27	(1,033)
Proceratiinae	3	(130)
Aenictogitoninae	1	(7)
Dorylinae	1	(59)
Aenictinae	1	(134)
Ecitoninae	5	(149)
Cerapachyinae	5	(217)
Leptanilloidinae	3	(12)
Dolichoderinae	28	(692)
Aneuretinae	1	(1)
Pseudomyrmecinae	3	(221)
Myrmeciinae	2	(90)
Ectatomminae	4	(263)
Heteroponerinae	3	(24)
Myrmicinae	141	(6,087)
Formicinae	49	(2,831)

Poneroids

Army ants

Formicoids

Termites

Mastotermitidae	1
Kalotermitidae	3
Termopsidae / **Hodotermitidae**	5 / 3
Serritermitidae	2
Rhinotermitidae	13
Termitidae	241

The situation is not clear in termites: Although DCF has been reported or implied in specific groups (61, 115, 125, 126), it is thought to be uncommon in general (133). DCF has evolved many more times in ants than in the other eusocial Hymenoptera, though ICF remains the predominant strategy in almost all ant lineages (with the exception of army ants). Furthermore, in contrast with the scattered distribution of DCF in ants, DCF tends to be confined to particular taxonomic groups in bees and wasps.

Evidence for DCF is based on direct, though often anecdotal, observations in wasps, bees, and some ants. However, DCF can also be inferred indirectly. In ants, the absence of winged queens in species belonging to at least 50 genera suggests that, with few exceptions (e.g., 69), they reproduce via DCF (97), because flying ability is unlikely to be selected against under ICF. The annual production of only a few gynes in the colony is also suggestive of DCF, because ICF species usually produce many gynes (see below).

Organized or Opportunistic DCF?

DCF occurs in many species as a regular stage of the colony cycle, and consequently it follows a precise schedule. Following intrinsic triggers (e.g., colony size; 12) or extrinsic triggers (e.g., season, in army ants, 10, 42; and wasps; 67), the colony produces new queens prior to division. In many taxa, foragers may explore and select a new nesting site (67, 135), and DCF proceeds with the movement of queen(s) and workers to the new nest(s) (4, 24, 91, 135). In ants, this includes transport of brood and food.

This highly structured process contrasts with opportunistic DCF, when a group of nestmates accidentally becomes separated from the mother colony. This can occur in species in which the colony is distributed among several physically distinct nests (i.e., polydomy). These nests may become isolated from one another because of a gradual decrease in traffic between them or, especially in arboreal species, because of accidents severing physical links between nests (54). Opportunistic DCF can also occur in species with frequent nest emigrations, because the colony can become fragmented (81, 105, 125). Despite an element of randomness, such opportunistic DCF can be adaptive. However, for colony fragments to become autonomous they must have a queen (as can occur under polygyny) or have the ability to requeen (e.g., 49, 72, 107, 133). Opportunistic DCF can easily be overlooked because the growth and reproductive phases are not conspicuously different, and because it can co-occur with ICF.

Ecological Conditions Favoring DCF

DCF has been linked with a range of ecological factors, including habitat patchiness, nest site limitation, competition, predation, climate, resource availability, and nest site instability (reviewed

←——

Figure 1

Phylogenetic distribution of dependent colony foundation (DCF) among wasps (2, 53, 101), bees (21, 29, 70), ants (16, 88, 137), and termites (65, 77). Blue, bold text represents groups containing eusocial species, whereas red text represents groups with solitary species only. A light blue background represents groups in which only DCF occurs, a gray background represents groups in which both DCF and ICF (independent colony foundation) occur (usually within the same genus), and a white background represents groups in which DCF is unknown. For termites, a gray-and-white hatched background represents groups in which DCF has been reported or inferred. Numbers of genera are given and are based on genera containing eusocial species only. The number of species (gray text in parentheses) is given for ants only, as accurate estimates are unavailable for other taxa. Occurrence of DCF is based primarily on published accounts, though it is also based on morphology (lack of winged queens) in ants. Data were obtained from References 67, 82, and 116 for wasps, References 84 and 85 for bees, Reference 97 and AntCat (**http://www.antcat.org/**) as of December 2011 for ants, and References 61, 115, 125, and 126 for termites.

in 13, 14, 48, 52). However, many of these arguments focus on ants, and especially DCF species that are polygynous, based on the premise that selection against solitary founding leads to queen readoption, which in turn permits colony division. These arguments are less appropriate for monogynous DCF species [e.g., ants (11, 24), honey bees, and stingless bees (84)]. Furthermore, in many cases the benefits of either ICF or DCF vary depending on the ecological context. ICF may be advantageous for reaching new patches or escaping degrading patches, whereas DCF may allow rapid exploitation and long-term domination of patches. In this regard, a mixed strategy combining ICF and DCF can bestow multiple benefits. Whereas many ants are mixed strategists (17, 48, 59, 76, 86, 87), this is currently unknown in bees and wasps. Some factors that may consistently favor DCF over ICF are high levels of intraspecific competition and high predation risk, both of which require colonies to have an effective workforce from the beginning (13, 17, 52, 86).

REPRODUCTIVE INVESTMENT UNDER DCF

Propagules Consist Mostly of Workers, Not Queens

Parents face trade-offs in resource investment between somatic maintenance and reproduction, and over the quantity and quality of offspring (28, 117). ICF necessitates the production of a large number of female sexuals to balance their low probability of success, and this investment may be considerable [e.g., 244–1,261 queens in some ICF Vespinae (67), and 1,000–2,000+ queens in *Formica truncorum* (123)]. In contrast, investment in queens is markedly lower in DCF and colonies may be limited to only a few queens (24, 38, 42, 67, 112). However, it is essential to consider also the substantial investment in workers required to help the new queens under DCF (95). This worker component of the reproductive investment is difficult to quantify because workers are helpers in the mother colony before becoming helpers in daughter colonies. Workers thus contribute to both colony growth and reproduction, and only their residual value should be considered toward the reproductive investment (see 28). The lower investment in female sexuals under DCF means numerical (operational) sex ratio is male biased (28, 95, 96), and often dramatically so (42), but calculation of sex investment ratios is complicated by the inclusion of the worker component of the investment (95).

Security and Flexibility of Reproductive Investment

Colonies with obligate ICF risk a massive loss of invested resources because founding queens are irreversibly committed to establish new colonies once they have left the colony, and the vast majority of attempts will fail [the survival rate of dispersing queens is less than 1% in some ants (56, 128) and termites (73, 89) and less than 23% in *Vespula* wasps (43)]. This risk is much reduced under DCF for two reasons. First, propagule survival is improved vastly by cooperative founding. Second, workers leaving their natal colony are not irrevocably committed but can, at least in some cases, return to the natal nest to be reallocated if the attempt to start a new colony fails (24, 27) (**Figure 2**). By adjusting the number of workers in each propagule, investment can also be tailored to environmental variation up to the moment of dispersal (24). In species where propagules remain in contact with their mother colony for an extended period, investment can also be adjusted after dispersal (62, 129).

Factors Influencing Resource Allocation

Models of resource investment predict that after DCF the mother colony should remain larger than offspring colonies, and that offspring colonies should be of equal size (19, 28). However,
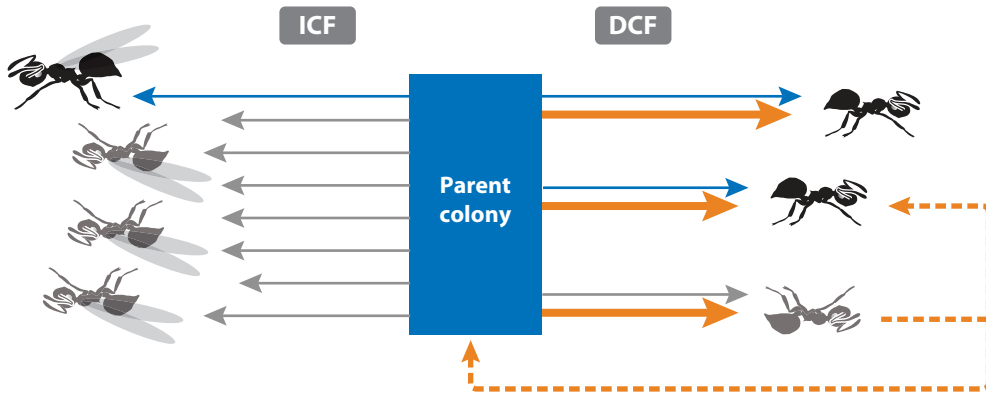
Figure 2

Investment in female reproductives under independent colony foundation (ICF) is high, and many dispersing queens will not survive (*gray lines*). Fewer new queens are produced under dependent colony foundation (DCF), but each has a higher chance of survival because of the investment in workers to accompany the queen (*orange lines*). Furthermore, in some species, resources (workers) invested in failing propagules may be reallocated (*dashed lines*).

resource allocation may be subject to bet-hedging strategies (24, 92) and conflicts of interest between mother and daughter colonies (19, 28, 95), as well as demographic, environmental, and life-history factors (e.g., 10, 100). Relatedness asymmetries often exist in social insect colonies and can influence resource allocation. For example, in polygynous and/or polyandrous species, workers might be expected to preferentially join a propagule with a more highly related queen because of indirect fitness benefits. Furthermore, hymenopteran workers are differently related to their mother and sister queens and this can lead to a bias in preference (95, 100). For instance, in monogynous and monandrous colonies, workers should prefer to be with their mother and raise sisters, rather than be with their sister and raise nieces. However, although one study on the ant *Proformica longiseta* (114) showed that workers undergoing DCF did not segregate randomly with respect to kinship, other studies of ants (50), swarm-founding wasps (118), and honey bees (74, 102) have found no evidence of nepotism.

Life-history and ecological factors also place constraints on both reproductive investment and propagule size. For example, in species where large colony size is essential for survival, one can expect the production of only one or very few large propagules. The army ants (e.g., *Eciton burchellii*) are mass predators, requiring a huge number of workers, and colonies split into two every three years (35) (**Figure 3**). At the other extreme, if the survival of small propagules is high, then producing small but numerous propagules may be the best strategy (19). Laboratory colonies of *Monomorium pharaonis* split into as many propagules as possible, depending on available nesting sites, until a critical minimum propagule size is attained (18). Recent models suggest that under some conditions, producing offspring (here propagules) of varied size can be most advantageous (92), and this may explain unequal resource allocation among propagules in the ant *Cataglyphis cursor* (24).

The above arguments suggest that resource allocation under DCF is subject to a wide range of influences, and indeed, the available data indicate the number and size of propagules are highly variable between species. Whereas honey bees and army ants invest roughly 50% of their available workforce in a single propagule (42, 112), this investment is only 10–30% in the stingless bees *Trigona laeviceps* and *Tetragonisca angustula* (63, 129), and 34% and 23% in the ants *Cataglyphis floricola* and *Proformica longiseta*, respectively (1, 33). Other species studied produce multiple propagules
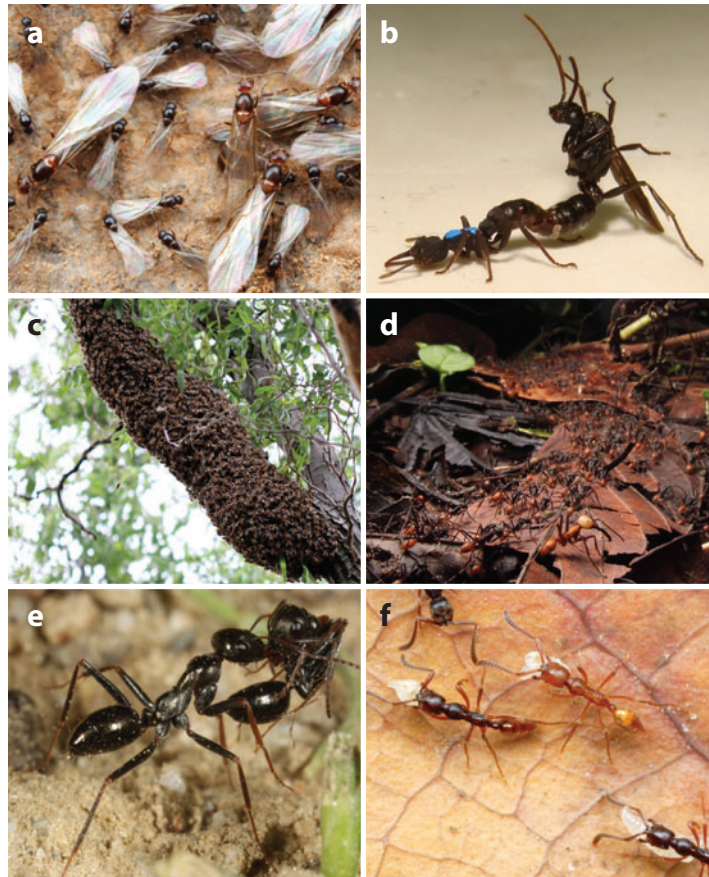
Figure 3

The evolution of dependent colony foundation (DCF) has wide-ranging life-history implications for social insects. (*a*) Large numbers of *Forelius mccooki* independent colony foundation (ICF) queens and males prepare to depart the nest on the wing, whereas (*b*) an ergatoid queen of *Mystrium oberthueri* mates outside its laboratory nest where it is protected by workers. (*c*) Honey bees (*Apis mellifera*) have excellent group coordination, and swarms, guided by scouts, can travel many kilometers. (*d*) In contrast, *Eciton burchellii* army ants must disperse on foot, and their reliance on mass-predation means that only one very large propagule is produced. Ants employ a range of strategies to make dispersal on foot more efficient, and only ants are able to transport brood to new nests. (*e*) A *Cataglyphis cursor* worker transports a nestmate to a new nest, and (*f*) *Simopelta* sp. workers transport brood. Panels *a*, *c*, *d*, and *f* copyright Alex Wild, reprinted with permission; panel *b* courtesy of Mathieu Molet; and panel *e* courtesy of Thibaud Monnin.

of variable size: One colony of *Monomorium* (*Chelaner*) sp. invested only 12% of its workforce in 16 propagules (17) (see sidebar, Dependent Colony Formation). Although these data are limited, they clearly demonstrate a wide spectrum of investment strategies under DCF.

DISPERSAL AND POPULATION GENETICS

The ability to fly has contributed greatly to the evolutionary success of insects (104, 136). Dispersal is particularly important as a means of limiting local resource competition and escaping unstable or

Table 2 Association between dispersal capabilities and founding strategy in different social insects[a]

Taxa	Maximum range of DCF	Maximum range of ICF	Maximum range of foraging	References
Ants	32 m	1.6 km	–	1, 24, 33, 128
Termites	<10 m	>1 km	–	60, 126, 132
Swarm-founding wasps	320 m	–	1 km	15, 34
Stingless bees	300 m	–	2.1 km	64, 75, 129, 140
Honey bees	10 km	–	15 km	68, 112, 113, 134

[a]Range of foraging flights is given as an indicator of dispersal in species in which ICF does not occur. Because of the paucity of available data, these figures represent a wide range of species and are meant to be broadly indicative only.

Abbreviations: DCF, dependent colony foundation; ICF, independent colony foundation

patchy environments (13, 120), and restricted dispersal may be evolutionarily unstable (46). DCF can in some cases limit dispersal, because whereas an ICF queen is an independent entity during dispersal, a DCF queen is constrained by the dispersing ability of nestmates in the propagule.

Colony-Founding Strategy and Dispersal Range

All social bees and wasps have winged workers and thus disperse by flight regardless of the mode of colony founding. Swarms of honey bees are guided to a predetermined site by scout bees (4) and can disperse over very long distances (**Table 2**). However, the coordinated movement of a large group of individuals is a complicated process that can restrict dispersal range in other species (90, 116, 135). In swarm-founding wasps and stingless bees, scouts lay a chemical trail to the new nest prior to swarming by marking objects along the intended path (15, 30, 66, 116). Dispersal thus relies on an array of suitable substrate and/or topographic features between the mother and daughter colonies (15, 139), and substrate-deficient areas and/or barriers such as large rivers can limit dispersal (34, 67). Dispersal may also be restricted by the need to maintain temporary contact with the mother colony: In stingless bees, the transfer of materials (wax, food) and workers from the mother to the daughter colony can continue for up to six months after swarming (63, 129, 140). Most notable with respect to dispersal, however, is the fact that ant and termite workers are wingless, and thus DCF entails obligate dispersal on foot (**Figure 3**). Dispersal distances are accordingly very low compared to distances of independent flying queens (**Table 2**).

Consequences of Restricted Dispersal for Population Genetic Structure

Restricted dispersal has implications for population genetic structure, which is itself intimately tied with local adaptation, genetic drift, and ultimately, speciation (47). Restricted dispersal of social insect queens performing DCF, particularly in species without aerial dispersal, can lead to population genetic viscosity (106), a condition in which colonies that are physically nearby in a continuous population are genetically more similar than colonies that are further away. It has been argued that population viscosity, and the associated higher level of resource competition among female kin, could increase selection against aggressiveness between nests, a key parameter in the success of invasive (39) and ecologically dominant (141) species. Some theoretical arguments also suggest that population viscosity could favor the evolution of altruistic behaviors (45, 78). A further potential effect of limited dispersal is increased mating between close relatives, which can lead to

inbreeding depression (a decrease in the fitness of inbred individuals) and production of diploid males (in Hymenoptera). This is particularly important in social insects because of small effective population sizes (most individuals are nonreproductive workers; 22).

Whereas restricted queen dispersal can lead to population genetic viscosity of maternally inherited mitochondrial genes (mtDNA), biparentally inherited nuclear genes may be unaffected, because males can be efficient dispersers and can mitigate the effects of restricted queen dispersal. In termites, both neotenic males and females are wingless and inbreed, implying that if DCF were to occur, genetic viscosity would be very high. In ants, sex-biased dispersal can lead to higher population genetic viscosity in mitochondrial genes than in nuclear genes. This pattern has been observed in many DCF species (e.g., 6, 25, 31, 41, 44, 58), though the viscosity of nuclear DNA can vary both within and between species (e.g., 23, 25, 124). Male-biased dispersal can also counter the effects of inbreeding, and very few studies of DCF ants have uncovered evidence of inbreeding except in rare cases in which DCF is associated with loss of male dispersal (e.g., 127).

In bees and wasps, genetic studies of population genetic viscosity are rare and often have conflicting interpretations. In the Asian giant honey bee, *Apis dorsata*, colonies within nest aggregations were genetically related, suggesting limited dispersal of swarms (93), whereas no such pattern was found in stingless bees (20). In termites of the families Rhinotermitidae and Kalotermitidae, very few studies of natural populations have found population genetic viscosity (130–132), except in introduced populations in which colonies are headed by neotenics (32, 79, 80). This has been interpreted as an indication of infrequent DCF. However, the absence of population viscosity of nuclear markers should not be taken as convincing evidence of the absence of DCF (39), and further studies are needed. The available data thus suggest that although limited dispersal associated with DCF in some species can lead to population genetic viscosity and inbreeding, this is in many cases countered by male-biased dispersal.

LIFE HISTORY AND ECOLOGY

Colony-founding strategy can influence how species interact with their environment. The lack of a solitary phase, and dispersal on foot in ants and termites, has implications for a range of phenomena, including morphological constraints on reproductive individuals, parasite transmission, and invasiveness.

Age of First Reproduction

ICF colonies must produce a workforce before switching to reproduction, and because the growth rate of incipient colonies can be low (in ants at least), it may take several years before colonies start producing sexuals (e.g., 55, 128). In contrast, DCF colonies bypass the incipient stage as they start with a viable workforce (including brood in ants). Young DCF colonies could thus benefit from a higher growth rate than incipient ICF colonies and may reproduce earlier, even though DCF propagules are more expensive to produce than ICF queens. It has been proposed that in ants, colonies of species reproducing by DCF can start reproducing at a younger age than colonies of species reproducing by ICF (99), which has profound implications for fitness (121). Although this may be true when comparing species in which all else is equal, colony reproductive cycle is subject to a variety of other life-history traits that must also be considered: take for example the higher rate of swarming in African honey bees (*Apis mellifera scutellata*) compared to that of European honey bees (*Apis mellifera*) (110). Furthermore, whereas all ants form perennial colonies, most ICF bees and wasps are annual and may in many cases reproduce earlier than perennial DCF species. Thus, although DCF can provide a head start to species requiring significant time to

produce a sufficient workforce before their first reproductive event, this can be assessed properly only by comparing closely related species that differ only in reproductive strategy, and such data are currently unavailable.

Relaxation of Morphological Constraints in Ants

An important consequence of dispersal on foot is that morphological constraints for flight are relaxed in queens. In ants, this has repeatedly led to the evolution of ergatoid (permanently wingless) queens as well as gamergates (reviewed in 51, 52, 98, 99). This trend is widespread, as several hundred species from at least 50 genera have completely replaced winged queens with wingless reproductives (97). In general, ant queens that engage in DCF are characterized by reduced or absent wings (**Figure 3**), lower metabolic reserves and, in some species, smaller size relative to their ICF counterparts. As a consequence, they can be cheaper to produce (98), and this reduced cost of queens may also contribute to an increased efficiency of DCF (99). Interestingly, there is no parallel loss of winged queens in termites (72, 89) and ICF continues to occur in all species. Wingless neotenic reproductives in termites are produced to increase both the size and longevity of colonies; unlike ergatoid queens in ants, neotenic reproductives mate with each other or with the primary king, and if DCF does occur it may not be obligate.

Parasite Transmission

Pathogens can be transmitted vertically from mother to offspring or horizontally among conspecific or heterospecific individuals, and the pattern of transmission can determine the evolution of virulence in pathogens and resistance in the host. In ICF species, the mother colony transmits her pathogens vertically to daughter colonies only via the founding queen. This acts as a bottleneck and potentially limits parasite transmission (7). DCF propagules, on the other hand, can contain a few dozen to hundreds of thousands of individuals according to species, any of which may carry pathogens (36). DCF species can thus transmit most or all their pathogen community from the mother colony to the propagule(s), and such strong vertical transmission could affect host resistance and pathogen virulence. However, high parasite pressure can be counteracted by various defense mechanisms at the individual (e.g., higher immune defenses) and colonial (e.g., higher level of genetic diversity or more efficient social prophylactic defenses; 26, 109) levels. Pathogen transmission may also affect propagule size, but it is difficult to make clear predictions: Smaller propagules may transmit fewer pathogens, but larger propagules may have more efficient colony-level defenses.

Does Founding Strategy Influence Invasiveness?

Social insects are among the most damaging invasive species. After a species has been transported to nonnative habitats through human activities, colony-founding strategy can affect its potential to become invasive. We follow Suarez et al. (122) in defining invasive species as nonnative species that displace the local fauna, in contrast to nonnative species that establish stable populations but do not displace the local fauna. This distinction is necessary because many species have established stable populations in habitats to which they have been introduced but only a few of those have excluded local species (83, 122). Our knowledge of the biology of invasive ants is still fragmentary and more ants may be invasive than currently acknowledged (49), but the available information suggests that these ants reproduce predominantly by DCF, or a mix of ICF and DCF (49, 57, 122). Although the prevalence of DCF remains unclear in termites (132), the existence of neotenics that

remain in their natal colony can clearly facilitate human-mediated introductions (e.g., 40, 80). In contrast, there are at present no records of invasive wasp species employing DCF (5).

Is DCF Associated with Either Monogyny or Polygyny?

DCF is often linked in the literature with polygyny (multiple queens per colony). Indeed, one study of higher (formicoid) ants in temperate regions showed that ICF species tend to be monogynous, whereas DCF species are more likely to be polygynous (71). Similarly, in termites, colonies founded by ICF are initially monogynous but become polygynous when neotenics begin to reproduce, and DCF may then occur in some taxa (126). Polygyny is also ubiquitous in swarm-founding polistine wasps (67). However, the link between polygyny and DCF does not hold in many other cases. Monogyny is the norm in many DCF ants including army ants (42, 87), as well as in DCF vespine wasps (82) and most DCF bees (most stingless bees and *Apis*). This suggests that there is no causal link between DCF and polygyny, and that co-occurrence of the two factors may be due to selective pressures that separately favor the evolution of each.

DISCUSSION

ICF is the most widespread reproductive strategy among social insects. The high failure rate of founding queens under ICF is generally countered by producing them in large numbers. Alternative variants of ICF such as pleometrosis and social parasitism may reduce the risk of solitary founding, but a significant trend is the repeated evolution of DCF across a broad range of taxa (**Figure 1**). The multiple origins of DCF imply that this carries strong advantages under various environmental conditions. DCF brings the benefits of sociality to all stages of the life cycle, resulting in improved survival of propagules and reduced loss of resources invested in reproduction. However, it has costs of its own, primarily a limited number of breeding attempts and dispersal on foot in ants and termites. This restricted dispersal limits the probability of escape from patchy or isolated habitats that have become unfavorable, and makes populations subject to stronger local resource competition.

The benefits of DCF can more easily outweigh the costs when these costs are significantly reduced. For example, the impact on dispersal is reduced or absent in species in which all castes are winged. We might thus expect widespread DCF in bees and wasps, but the available data suggest this is not the case. The various DCF bees and wasps are phylogenetically clumped (e.g., all species of *Apis*, stingless bees, and swarm-founding wasps). In contrast, DCF ant species are scattered among clusters of ICF species (**Figure 1**), suggesting that DCF may be more evolutionarily stable in flying than in nonflying insects. Whereas DCF may be a highly successful strategy for the latter over the short term, limited dispersal may be costly over the long term (e.g., 46). DCF ants are phylogenetically clumped only in taxa with very specific life-history traits, such as those that rely on mass predation and cannot function below a critical size (army ant syndrome; 42, 55). The absence of DCF in other bees and wasps may stem from life-history constraints precluding DCF, such as an annual life cycle.

Evolutionary reversions are possible for complex traits such as social behavior (138), and factors selecting against DCF could favor reversions to ICF. However, an obstacle to such reversions is the loss of ability of DCF queens to function without workers. For example, queens of honey bees and stingless bees are completely helpless without workers, who feed and groom them. Ants show by far the highest number of transitions from ICF to DCF, with 10 subfamilies displaying both strategies (**Figure 1**), and may thus be a good group to investigate reversions from DCF to ICF. However, demonstrating reversions is at present impossible because it requires a

species-level phylogeny and knowledge of the colony-founding strategies in all related species. In addition, DCF in ants is often associated with loss of winged queens (52, 98), and this may restrict reversions. Reversion may also be constrained by life history in some groups such as army ants (**Figure 1**), for which the simultaneous evolution of an alternative foraging strategy in incipient colonies would be necessary. Reversion is therefore more likely in less derived species, and one candidate group is *Ropalidia* wasps: Morphological castes are weak or absent, both ICF and DCF species exist, and DCF may be facultative in some cases (37).

The diversity of DCF strategies results from recurrent evolution in phylogenetically distinct species. Although the broad distribution of DCF species suggests universal selective forces, the diversity of strategies and paucity of empirical data, particularly for some groups such as the termites, makes attempts at generalizing premature at present. Understanding the principles underlying the evolution and maintenance of DCF is nonetheless important because of the ubiquity and ecological importance of many DCF species. Comparative studies, both within and between species, are needed and will yield further insights.

SUMMARY POINTS

1. The solitary stage inherent in ICF is very risky, and the high mortality of young queens is compensated for by their production in large numbers. In contrast, DCF retains the benefits of sociality at all stages of the life cycle, leading to increased survival of young colonies.

2. DCF is more widespread than generally acknowledged. It evolved recurrently from ICF, and this accounts for the great diversity of patterns and mechanisms. Direct evidence can be hard to obtain in some groups (e.g., ants and termites) but can be supplemented with morphological and population genetic data. Opportunistic DCF may often have been overlooked.

3. Unlike ICF, which relies on a large number of sexuals, workers are the major component of reproductive investment in DCF and many fewer sexuals are produced. Colonies using DCF can divide into a limited number of daughter colonies, hence limiting the number of breeding attempts, but there is greater security and flexibility in reproductive investment.

4. Dispersal is severely constrained in DCF species with wingless workers (ants and termites), which can lead to population genetic viscosity. Nonetheless, in ants at least, dispersal by winged males can maintain gene flow and thus decrease viscosity for biparentally inherited nuclear DNA.

5. Evolutionary shifts to obligate DCF can lead to the loss of queen autonomy as a result of either behavioral or morphological adaptations. Permanently wingless queens have evolved only in ants.

6. DCF is phylogenetically clumped only in taxa in which the costs of group dispersal are reduced (flying species) or that have particular life histories (e.g., army ants).

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