

C

Colony Foundation



Christian Peeters
Institute of Ecology and Environmental Sciences,
Sorbonne Université, Paris, France

Efficient cooperation and division of tasks among nestmates are the strength of insect societies, yet in most species this cooperation is absent while new colonies are beginning. For several weeks, a lone founding queen (queen and king in termites) faces the same challenges as solitary insects to produce her offspring. Although her brood survives better in the safety of a rudimentary nest, foraging is always associated with high mortality risk. A proportion of social Hymenoptera have reduced risks by evolving two very distinct adaptations: (i) in three large subfamilies of ants (80% of all species), solitary founding queens no longer forage, because the first larvae can develop on their mother's internal metabolic reserves, or food obtained from mutualistic fungi or scale insects, or food obtained from parasitism of foreign ant colonies; (ii) in many species across all lineages, established colonies can split into daughter colonies, so that founding queens are helped by nestmate workers who feed and protect the brood.

Two Alternative Founding Strategies

In independent colony founding (ICF), a lone queen (founding pair in termites) needs to raise the first brood of offspring without the help of nestmates. Following aerial dispersal and mating with one or more foreign males, the queen excavates, builds, or takes over an existing shelter and lays a first batch of eggs. During the next few weeks or months, she must guard and feed the first larvae. In social bees and wasps, as well as in a minority of ants, ICF necessitates risky foraging trips away from the brood that is temporarily undefended. In many unrelated lineages, ICF has been replaced by a strikingly different founding mode whereby queens are never alone. This is known as dependent colony founding (DCF) or swarm founding. In DCF species, existing colonies divide into two or more daughter groups, which soon become autonomous. This allows the queen(s) to be continuously protected by nestmate workers that take all the risks involved in foraging.

The evolution of DCF was an evolutionary breakthrough, allowing the benefits of social life to be retained at all stages of the ► [colony cycle](#) [2]. DCF evolved in many social wasps and bees, but it is particularly suited to the biology of ants, since the eggs, larvae, and pupae are mobile items that are easily carried to a new nest. This contrasts

with bees and wasps in which brood develops in fixed cells of wax or paper, so that nest emigration implies that all existing brood must be abandoned. Accordingly, new daughter colonies begin without any brood, and as the older foragers die, colony size tends toward a minimum.

In several lineages of social Hymenoptera, a number of foundresses cooperate in building the nest and producing the first workers (pleometrosis). As a rule, once the first workers emerge, only one queen survives since the others are expelled or executed. In various species, pleometrosis is a facultative strategy influenced by the local density of dispersing queens [12].

Unlike ant queens, independent foundresses in social bees and wasps must retain the ability to fly and so cannot metabolize their wing muscles as a source of brood food. They must forage intensively to rear the first brood of daughters, increasing the probability of mortality. In various ► *Polistes* species showing ICF, 42–84% of incipient colonies fail before the emergence of the first offspring [15]. Such a low success rate is likely to account for the broad distribution of DCF in social wasps and bees [6, 11, 13]. Nonetheless, ICF occurs in most polistine wasps, as well as all ► *stenogastrine* and ► *vespine wasps* (*Provespa* excepted) as well as ► *Bombus* bees. Among polistine wasps, *Belonogaster*, ► *Mischocyttarus*, *Polistes*, and many ► *Ropalidia* species show ICF [3], but other genera (e.g., *Polybia* and *Metapolybia*) reproduce by DCF. Polistine species that show colony fission are polygynous, and mean colony sizes range from a few dozen to a few thousand females. *Provespa* wasps, all ► *stingless bees*, and ► *Apis* are monogynous and show DCF. An interesting difference is that the old queen flies away in *Apis*, but this is almost impossible in stingless bees, because queens become physogastric, hence it is the young queens that disperse with nestmate workers. Colony division is abrupt in *Apis*, but more gradual in stingless bees, as workers from the daughter colony temporarily return to the mother colony for building materials and food supplies.

In termites, evidence for colony fission is scanty or ambiguous [2] and ICF appears to be

the rule. Risky foraging trips are not needed when dead wood provides both a nest and cellulose for food [14], although most species of Termitidae do not nest in their food supply. Importantly, hemimetabolous development in termites results in autonomous immatures (nymphs) that do not rely on the founding queen and king for nourishment.

Winglessness in Ant Workers Impacts Both ICF and DCF

Ant workers are permanently wingless, and one of the many consequences is that queens spend almost all of their lives on the ground. Indeed, queens fly only briefly to disperse from the maternal nest. They break off and discard their wings shortly after mating, and wing muscles are converted to amino acids to feed the first larvae. Two major trends in ants are a striking queen-worker dimorphism in body size and the evolution of permanently wingless queens. Both are associated with a diversity of founding strategies (Table 1) that greatly exceeds that found in social bees and wasps.

- (1) **Non-claustral ICF** is the ancestral strategy in ants, resembling the behavior of solitary parasitoid wasps. In these, a mother provisions each offspring with paralyzed insects. Similarly, dealate ant queens hunt on the ground just like workers. This unspecialized ICF predominates in the ► *poneroid subfamilies* Amblyoponinae and Ponerinae, as well as in three formicoid subfamilies (Ectatomminae, Myrmeciinae, and ► *Pseudomyrmecinae*) (Table 1). In Formicinae and Myrmicinae, the few non-claustral species (scattered in, e.g., ► *Cataglyphis* and ► *Pogonomyrmex*) represent an adaptive response to local environmental conditions, hence a secondary modification from claustral ICF [10].
- (2) A majority of ICF species in ants have evolved **the ability to found colonies claustrally, i.e., without relying on food obtained outside the nest**. In most species of Dolichoderinae, Formicinae, and

Colony Foundation, Table 1 Patterns of colony-founding strategies across the different ant subfamilies (47 genera for which founding behavior is known). Evidence for DCF is either direct (e.g., field observations) or indirect (e.g., absence of winged queens, genetic differentiation data [10]). The first five subfamilies are poneroids, while others are formicoids

Subfamily	ICF					DCF
	Non-claustral	Claustral (metabolic reserves)	Claustral (mutualism, etc...)	Pleome-trosis	Social parasite	
Amblyoponinae	👍					👍
Leptanillinae						👍
Paraponerinae	👍					
Ponerinae	👍			👍		👍
Proceratiinae	👍		👍			👍
Dolichoderinae		👍	👍	👍	👍	👍
Dorylinae	👍					👍
Ectatomminae	👍					👍
Formicinae	👍	👍	👍	👍	👍	👍
Myrmeciinae	👍				1 sp.	?
Myrmicinae	👍	👍	👍	👍	👍	👍
Pseudomyrmecinae	👍		👍			?

Myrmicinae, dispersing young queens carry large metabolic reserves (fat and specialized storage proteins) that are accumulated before leaving the natal nest; the wing muscles are hypertrophied to carry this extra load [4]. Hence young queens can feed their first offspring without taking any of the risks involved in foraging outside (Fig. 1). In these lineages, the significance of metabolic reserves is amplified by the large size difference relative to the worker caste. This makes it possible for a founding queen to produce many small offspring. Moreover, these first workers are often smaller than average (*nanitics*), another adaptation for claustral ICF. None of the social bees or wasps show claustral ICF, which is a true novelty of the ants. The three ant subfamilies (Dolichoderinae, Formicinae, Myrmicinae)

that show claustral ICF make up almost 80% of known species, and claustrality is arguably a contributing factor to their evolutionary success.

- (3) In a small number of genera, **claustral ICF is possible due to a mutualism with sap-feeding insects or with fungi**. During the mating flight of *Acropyga* and *Tetraoponera*, foundresses carry a gravid pseudococcid (scale insect) to the stem cavity where they settle. Being clonal, the sap-suckers multiply rapidly and supply sufficient ▶ [honeydew](#) to feed the first worker brood. In attine species, dispersing queens carry hyphae of the mutualistic fungus in their infrabuccal pocket, and this will be the nucleus of future ▶ [fungus gardens](#). Similarly, ▶ *Azteca* foundresses bring an ascomycete fungus to the *Cecropia* domatium in which they settle. Parenchyma



Colony Foundation, Fig. 1 A claustral *Lasius* foundress queen raises her first crop of workers sealed in an underground chamber. She feeds the developing larvae with reserves from her own body. (Photo ©Alex Wild)

tissue is scraped from the walls and processed by the fungus that is then used as food for the first larvae, so the foundress does not need to forage outside.

In contrast to these examples of vertical transmission, foundresses in other genera need to find scale insects or fungi near the newly established nests (horizontal transmission). *Cladomyrma* lives together with mealybugs (also a scale insect), whose first instars (crawlers) disperse to settle into incipient nests of the ants. *Melissotarsus* and *Rhopalomastix* live in a mutualism with diaspidid scale insects inside living trees, and it is likely that crawlers locate tunnels newly chewed by founding queens. Acquisition of the mutualistic partner is always an essential step in the successful establishment of a new colony.

In *Discothyrea oculata*, a specialized predator on spider eggs, founding queens locate the silken egg sacs of spiders to begin their nests, so that the first larvae can feed on spider eggs and queens do not need to forage. In conclusion, claustrality is possible in various species having queens that lack large metabolic reserves, provided that food is available inside the nest. This is analogous to claustral ICF in termites that feed on the decomposing wood in which they nest.

- (4) **Social parasitism is an independent founding strategy.** In several ant lineages, newly mated queens attempt to enter existing colonies of their own or other species, following which their offspring are fed and raised by host workers. ► **Social parasitism** is a form of ICF, because queens are not helped by nestmate workers [10]. Founding queens disperse alone and take considerable risks in trying to enter the host colonies. The latter are nothing more than a resource of the environment to be exploited, similar to insect prey. Many authors have considered parasitism to be DCF because queens depend on their host colonies, but claustral queens depend just as much on their metabolic reserves, while non-claustral queens depend on the food they gather outside. What is crucial in DCF species is that queens rely on *nestmate* workers, and there is convergence of genetic interests since they are close relatives. This is clearly not the case in social parasitism, in which founding queens use colonies of other species as stepping stones for founding their own colonies, and long-lasting coexistence with the hosts only occurs in few species [1]. Parasites are typically winged and able flyers, and they do not need to carry substantial metabolic reserves for colony founding [1]. In terms of resource allocation and dispersal distances, social parasitism is comparable to non-claustral colony founding.
- (5) **Dependent Colony Foundation** (DCF, also called colony fission or budding) occurs widely in both poneroid and formicoid lineages (Table 1). As already mentioned, ant brood is easily transported to new nests, allowing for higher viability of daughter colonies. DCF is found in both monogynous and polygynous species. The terms “colony fission” and “colony budding” exist in the literature, but they are used inconsistently, and this distinction does not seem heuristic. DCF is the only mode of colonial reproduction in many species, whereas it exists as an alternative to ICF in a minority of species. Since DCF queens disperse on foot with nestmate workers to a new nesting site, the shift from ICF is often

accompanied by the evolution of ► [flightless reproductives](#). Ergatoid (no wings) and brachypterous (short-winged) queens exist in species from over 50 ant genera [9].

Individual-Level Adaptions in Ants: Queen Morphology

As noted above, claustral ICF is only possible in species where workers are substantially smaller than queens; the finite metabolic reserves of a foundress must allow a minimum number of larvae to develop to adulthood. A significant component of these reserves is huge wing muscles that are unknown in ICF wasps and bees. Since wing muscles are broken down after the mating flight, this considerable reserve of amino acids ensures the development of more larvae, hence more first workers can go out foraging sooner. The dramatic hypertrophy of wing muscles constrains the geometry of head muscles inside the prothorax. The reduced head muscles of claustral queens are consistent with the lack of worker-like foraging [5].

Another unique feature of ants is the evolution of permanently flightless queens in most species exhibiting DCF [9]. Many social wasps and bees also practice DCF, but flight ability persists due to the universal retention of flying workers. This constraint is relaxed in ants: wingless workers are the major players during the division of established colonies, hence the queens walk with them, and flight ability is selected against. A significant number of species show intraspecific queen polymorphism, ranging from physiological differences (wing muscle development or quantity of metabolic reserves), to bimodal distributions in body size (macro- and microgynes, both of which can fly), to a winged/wingless dimorphism. Such species combine the benefits of both ICF and DCF (reviewed in Ref. [9]). While expensive flying queens are always required in social wasps and bees, ants can replace them with flightless queens at certain times of the life cycle; for example, secondary reproductives can extend colony lifespan after the death of the winged ICF foundress.

In fewer than 200 ant species belonging to three subfamilies, workers have retained a

functional spermatheca and can reproduce sexually. Such *gamergates* have completely replaced winged queens in a number of species, so that DCF is the obligate strategy. Other species have winged queens together with gamergates, and the latter function as secondary reproductives [8].

Colony-Level Adaptions: Reproductive Investment

The establishment of a new colony in ICF species requires the production of a large number of female sexuals every year to compensate for heavy mortality. Moreover, these sexuals are expensive per capita in species showing claustral ICF: (i) production costs are high because of hypertrophied wing muscles and large size relative to workers and (ii) large metabolic reserves are accumulated before leaving the natal colony. In some species, queens emerge as adults several months before dispersal and mating, and their fresh weights increase significantly during this interval (up to triple in the ► [fire ant *Solenopsis invicta*](#)).

In sharp contrast to this are the majority of DCF species, in which very few female sexuals are reared annually. This makes sense, because (i) the mortality of DCF queens is considerably reduced and (ii) existing colonies can divide into only two or very few daughter groups, hence producing excess queens would be wasteful of resources (exceptions exist, see Ref. [7]). Moreover, the lack of wing muscles makes DCF queens cheaper to produce. However, lower investment in queens is offset by the necessary production of numerous workers, which must be present in sufficient numbers for daughter colonies to be viable.

Mating Strategies Are Distinct from Founding Strategies

Colony founding usually follows very soon after mating, but these are two very different events affected by distinct selective pressures [10]. ICF queens in some species mate close to their natal colony (*female-calling*) before dispersing, while

in other species, they mate far away (*male-aggregation*). DCF queens mate near their natal colony or even inside it. This seems true even in DCF species with queens that are capable of flying: since newly mated queens stay in their natal nest, they cannot fly to distant male aggregations. Female calling is associated with lower mortality, since it eliminates the risks of predation or getting lost.

Future Studies

The founding strategies of a majority of ant species remain unstudied (Table 1). Indeed, there are no published data about colony foundation even for several large genera. This scarcity of information results from the necessity of studying colony foundation in the field at a particular season, when new sexuals are present. DCF is especially difficult, because in various tropical species it occurs unpredictably throughout the year, and it needs to be distinguished from simple nest emigrations [2].

In species whose manner of colony founding is unknown, data on queen morphology can generate testable hypotheses. The thorax architecture of queens and workers reflects the size and geometry of head muscles [5]. Among species with flying queens, some have strong neck muscles (similar to those of workers), because they need to forage outside the incipient nests (non-claustral ICF), and their prothorax is larger than in claustral species [5]. In wingless queens, the absence of wing muscles is associated with a highly simplified thorax (i.e., fusion of sclerites), and such queens generally perform DCF.

Cross-References

- ▶ [Cataglyphis](#)
- ▶ [Fire Ant](#)
- ▶ [Pogonomyrmex](#)
- ▶ [Pseudomyrmecinae](#)

References

1. Buschinger, A. (2009). Social parasitism among ants: A review (Hymenoptera: Formicidae). *Myrmecological News*, 12, 219–235.
2. Cronin, A., Molet, M., Doums, C., Monnin, T., & Peeters, C. (2013). Recurrent evolution of dependent colony foundation across eusocial insects. *Annual Review of Entomology*, 58, 37–55.
3. Gadagkar, R. (2012). *The social biology of Ropalidia marginata – Toward understanding the evolution of Eusociality*. Cambridge, MA: Harvard University Press. 384pp.
4. Helms, J. A., & Kaspari, M. (2015). Reproduction-dispersal trade-offs in ant queens. *Insectes Sociaux*, 62, 171–181.
5. Keller, R., Peeters, C., & Beldade, P. (2014). Evolution of thorax architecture in ant castes highlights trade-off between flight and ground behaviors. *eLife*, 3, e01539.
6. Michener, C. D. (2007). *The bees of the world* (2nd ed.). Baltimore: John Hopkins University Press. 992pp.
7. Molet, M., Fisher, B., Ito, F., & Peeters, C. (2009). Shift from independent to dependent colony foundation and evolution of ‘multi-purpose’ ergatoid queens in *Myrmium* ants (subfamily Amblyoponinae). *Biological Journal of the Linnean Society*, 98, 198–207.
8. Monnin, T., & Peeters, C. (2008). How many gamergates is an ant queen worth? *Naturwissenschaften*, 95, 109–116.
9. Peeters, C. (2012). Convergent evolution of wingless reproductives across all subfamilies of ants, and sporadic loss of winged queens. *Myrmecological News*, 16, 75–91.
10. Peeters, C., & Aron, S. (2017). Evolutionary reduction of female dispersal in *Cataglyphis* desert ants. *Biological Journal of the Linnean Society*, 122, 58–70.
11. Peeters, C., & Ito, F. (2001). Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annual Review of Entomology*, 46, 601–630.
12. Peeters, C., & Molet, M. (2010). Colonial reproduction and life histories. In L. Lach, C. Parr, & K. Abbott (Eds.), *Ant ecology* (pp. 159–176). Oxford, UK: Oxford University Press. 424pp.
13. Ross, K. G., & Matthews, R. W. (Eds.). (1991). *The social biology of wasps* (678pp). Ithaca: Cornell University Press.
14. Shellman-Reeve, J. S. (1997). The spectrum of eusociality in termites. In B. Crespi & J. C. Choe (Eds.), *The evolution of social behaviour in insects and arachnids* (pp. 52–93). Cambridge, UK: Cambridge University Press. 552pp.
15. Turillazzi, S., & West-Eberhard, M. J. (1996). *Natural history and evolution of paper-wasps*. Oxford: Oxford Science Publications.