
Ant Ecology

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Colonial Reproduction and Life Histories

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9.1 Introduction

The spectacular ecological success of ants can be attributed to the benefits of both division of labour and morphological specialization among adults. Unlike solitary insects that sequentially perform the various tasks leading up to successful reproduction, in social species different tasks are performed in parallel by individuals with distinct behavioural profiles. Furthermore, in the ants, this division of labour is more efficient because functional differences between queens and workers are amplified by morphological differences. Queens (usually winged) start new colonies and produce offspring, while workers (never winged) raise the brood, build the nest, and forage for food. The degree of size dimorphism between queen and worker castes varies dramatically across ant species, and there is a clear phylogenetic pattern behind this. Molecular data provide very strong support for a ‘formicoid’ clade, not revealed by previous morphological studies (Ward 2007c). This clade comprises 14 of the 21 extant ant subfamilies (including Myrmicinae, Dolichoderinae, and Formicinae) and about 90% of all described ant species. The ‘poneroid’ group, comprising five subfamilies (including Amblyoponinae and Ponerinae), exhibits a larger proportion of ancestral traits (see Chapter 1). Moreover, winged queens and wingless workers in the poneroids are often similar in size and morphology, and this is associated with small colony sizes (e.g. *Harpegnathos saltator*; Peeters *et al.* 2000). The degree of queen–worker dimorphism generally increases sharply in the formicoids, but not always; in many species one large highly fertile queen pro-

duces numerous tiny workers, which leads to a dramatic increase in colony size.

The colonial life cycle can be conveniently broken into three stages – colony foundation, growth (production of workers), and reproduction (production of sexuals) (see Figure 9.1) – and we review existing knowledge about these. The relative importance of these three stages is deeply affected by the way colonies begin. Thus, it is impossible to understand life cycles without contrasting the two main strategies of colony founding. Independent colony foundation (ICF) – where queens found new colonies alone – is widespread in all taxonomic groups except the army ants. Yet, in many species across all subfamilies, this strategy has been repeatedly selected against, and replaced by dependent colony foundation (DCF), where queens cannot found a colony without the help of workers from the natal colony. In addition to a substantial decrease in dispersal distance, this shift led to crucial adaptations of individuals (queens become wingless or they are replaced by reproductive workers) and colonies (more workers are produced as part of the reproductive investment). We illustrate how each stage of the colony life cycle is influenced by the strategy of colony reproduction, and we analyse the causes and consequences of the frequent shifts from ICF to DCF.

9.2 Colony life histories, mating biology, and dispersal

Hölldobler and Wilson (1990) as well as Bourke and Franks (1995) reviewed the tremendous diversity in

life histories and mating patterns in ants. Young winged queens ('gynes') and males are generally reared once a year. The gynes remain in the maternal nest for a variable period, during which they usually accumulate metabolic reserves. Following a change in weather conditions (e.g. temperature, humidity), gynes and males exit the nests synchronously. According to species, the sexuals disperse at various distances from the natal nests (Table 9.1). At one extreme, gynes stay close to their natal colony and wait on the ground or low vegetation for foreign males flying singly. The latter usually have larger eyes than the queens, suggesting the importance of vision to locate single gynes or nests. Males also detect pheromones released by the gynes, hence the term 'female calling'. Following copulation, the females can disperse farther by flight to avoid local competition and reach new habitats, or in other species, shed their wings and initiate new colonies in the vicinity. At the other extreme, gynes and males converge to fixed aggregation sites where mating occurs. Large-scale nuptial flights are of limited duration and involve sexuals from many colonies; thus, they result in maximum dis-

persal. They seem possible only in species with relatively dense colonies, and a large seasonal production of gynes. In contrast, because the number of sexuals produced is too low for mating aggregations to be possible (Peeters and Ito 2001), female calling is found in ants exhibiting small colonies, including many Ponerinae (references in Peeters 1991). Permanently wingless ('ergatoid') queens also remain near their natal nests and wait for flying males (see Section 9.6.4). The dichotomy between 'female calling' and 'male aggregations' focuses on the mechanism of locating sexual partners and is not a reliable indicator of dispersal distances. Gynes that mate close to their natal nest can either fly away to do ICF in some species, or re-enter the nest in other species (Table 9.1). Once back in their natal nest, they can either stay, or leave alone (ICF), or with a group of workers (DCF), depending on species. In *Carebara vidua*, gynes fly to a distant male aggregation, but then settle on vegetation and 'call' for males (Robertson and Villet 1989). Aerial dispersal that precedes mating is very unlikely to result in inseminated gynes returning to their natal nest (Bourke and Franks 1995); hence it is always

Table 9.1 Comparison of various mating strategies in ants. The category 'female calling' is heterogeneous and cannot predict dispersal distance or founding strategy. Only gynes that do not fly prior to mating can be involved in DCF.

	Historical terminology		
	Female calling	Male aggregation	
	Location of mating (relative to gyne's origin)		
	Inside/outside of nest	Outside of nest	Away from nest
Behaviour of gynes	Wait for foreign males (if outside: can return inside after mating)	Fly, then wait for foreign males	Fly and search for aggregation
Behaviour of males	Fly individually, search for trails, nests or ants	Fly individually, search for ants	Fly and search for aggregation, select partner
Synchronized exit of males and females?	No	Yes	Yes
Dispersal distance	Low	Moderate?	High
Risk from predators	Low (exit not predictable, protection of nest)	Low (not predictable, no aggregation)	High (mass exit from nest, aggregation)
Colony foundation strategy	DCF (rarely ICF)	ICF	ICF
Gyne morphology ^a	EQ, G, BQ, AQ (can dealate before mating)	AQ	AQ

^a EQ = ergatoid queen, G = gamergate, BQ = brachypterous queen, AQ = alate queen

associated with ICF. Mating in aggregations likely leads to greater mortality of gynes (e.g. predators, desiccation) compared to mating near natal nests. It appears that aggregations were selected against in various species and replaced by female calling, although in other species, female calling is an ancestral trait. To understand evolutionary diversification in reproductive strategies, mortality associated with dispersal and mating needs to be considered separately from mortality during colony founding because the selective pressures are distinct.

Unlike various social bees and wasps with annual colonies, all ants have perennial colonies, even in temperate and boreal environments. Colonies are started in one of two completely different manners: ICF or DCF. During ICF, queens work alone for several weeks up to a few months (depending on species), feeding and caring for the brood until these become adult workers. This founding stage is reminiscent of the life of solitary insects, because failure in any of the steps needed before the first workers become active outside the nest is fatal. In contrast is DCF (also called 'fission' or 'budding' as discussed in Section 9.4), where an established colony divides into two or more autonomous colonies. DCF is obviously possible only in insects that are social, and it should lead to much decreased mortality rates of queens (which are never without the workers). However, DCF in ants necessitates a loss of aerial (i.e. long-range) dispersal, because ant workers are strictly wingless. This founding strategy is unlike DCF in social wasps and bees, where the winged workers can disperse together with the queens (i.e. swarming) (Peeters and Ito 2001). Nevertheless, thousands of ant species exhibit DCF, and this strategy is obligate in species with permanently wingless ('ergatoid') queens (at least 60 genera out of 283; C. Peeters, unpublished data). DCF occurs across all the subfamilies, in species having both tiny and huge colonies and irrespective of monogyny or polygyny. A literature review indicates that it evolved in numerous unrelated taxa as a substitute for ICF (C. Peeters, unpublished data). Indeed, ICF is ancestral in ants, which is intuitive since they evolved from solitary wasps (the synapomorphy of ants is the metapleural gland that produces antimicrobial

substances necessary for underground life; see Box 9.1).

9.3 Independent colony foundation (ICF): queens work without nestmates

We consider ICF to include all instances of queens that found colonies without the help of workers originating from their own colony. ICF foundresses disperse individually, and are often alone until the first brood become adult workers. According to the species, foundresses exhibit a variety of strategies to improve their survival: foraging outside the nest (Section 9.3.1), expanded wing muscles and other metabolic reserves (Section 9.3.2), cooperating with randomly encountered conspecific foundresses (Section 9.3.3), invading established colonies of other ants (Section 9.3.4), or exploiting other living organisms as a food source (Section 9.3.5). All these adaptations make use of available resources in the environment in order to increase founding success.

9.3.1 Non-claustral ICF

In hundreds of species, founding queens perform non-claustral ICF, i.e., they need to hunt outside their nests in order to feed the first generation of workers. This is the ancestral strategy in ants, and occurs widely in poneroid species (e.g. Ponerinae and Amblyoponinae; Peeters 1997). These ants typically exhibit a low queen-worker dimorphism; given that they must raise workers that are almost the same size as they are (Plate 7), the queens lack sufficient metabolic reserves (notably obtained from the histolysis of wing muscles; Roff 1990; Zera and Denno 1997) to feed their first brood without foraging outside the nest. Once the first workers have emerged, they start performing all non-reproductive tasks from brood care to hunting, and queens can shift to egg-laying only. Non-claustral ICF is intuitively associated with a low probability of foundress survival (Brown and Bonhoeffer 2003; Peeters 1997). Ant workers suffer high mortality during foraging (e.g. Schmid-Hempel and Schmid-Hempel 1984) and similarly, hunting queens are vulnerable. Survival is particularly poor in environments that provide low or unpredictable resources. Moreover, the brood is

Box 9.1 Antimicrobial defences in ants: pure and applied science

Andrew J. Beattie

Ants possess a variety of antimicrobial defences including two biochemical systems, one external and one internal. Antimicrobial compounds are secreted externally by the paired thoracic metapleural glands (Beattie *et al.* 1986). Protein and lipid products have been characterized, but little is known about how they vary or about the genes behind their production or regulation. A few genera (e.g. *Camponotus*), and male ants, do not possess these glands, possibly because their tenure in the nest is relatively brief. Male ants isolated from gland-bearing workers quickly develop large microbial loads, illustrating the hazards of not possessing them.

Internally, ants have a sophisticated immune system. Workers of *Myrmecia gulosa*, when challenged with strains of *Escherichia coli*, produced antibacterial peptides, rich in proline with *N*-acetylgalactosamine *O*-linked to a conserved threonine. The synthetic non-glycosylated form was ineffective, showing that glycosylation was necessary for maximum antibacterial activity (Macintosh *et al.* 1998). These biochemical properties were of both evolutionary and commercial interest (see later). A defensin gene has been identified from *Formica aquilonia* and compared with the defensin genes of the Hymenoptera *Apis mellifera* and *Bombus ignitus* and with three other insect species. It differs from each of them with respect to the number and length of the introns and exons, providing insights into the role of selection in the evolution of defensin in ants.

The case of leaf-cutting ants

The regulation of subterranean fungal cultures by antibiotics is well known, but the complexity of the ant—microbial interactions is still being revealed. Currie *et al.* (1999) showed that *Acromyrmex octospinosus* harbours a mutualistic, antibiotic-producing bacterium, *Pseudonocardia* on the cuticle, and that its secretions are potent against the parasitic fungus *Escovopsis* (see Chapter 6). Mutualistic bacteria with similar functions have been discovered in

other Hymenoptera, hence the question arises as to how much antibiotic production is ultimately microbial. *Acromyrmex octospinosus* also exhibits immune responses to fungal pathogens.

Behavioural defences

Ants are known to forcibly remove diseased and moribund individuals from the colony, and the colonies of many species have obvious trash heaps and/or graveyards with workers assigned to their care. Ants groom one another, removing fungal spores, in some cases storing them in an infrabuccal cavity. Incomplete disposal of the infrabuccal pellet can result in fungal contagion of the colony; a mechanism that has been used to spread control agents in colonies of pest ants. This cleaning activity may also extend to the nest infrastructure. Ants may avoid areas of high infection or even move the colony in response to microbial invasion (Roy *et al.* 2006). The leaf-cutting ant *Atta colombica* responds to unwanted fungi by physically removing the spores from their fungal gardens and, if the substrate is already infected by them, the ants remove it in a highly specialized set of behaviours known as ‘weeding’. These activities can be very effective against generalist fungal invaders, but the specialist parasite, *Escovopsis*, appears to have evolved counter adaptations that result in its persistence in the gardens (Currie and Stuart 2001).

Antimicrobials and the evolution of sociality

The idea that the evolution of sociality required the synchronous evolution of increased defences against microbial attack has recently been addressed in detail. Pursuing the hypothesis that increased crowding and decreased genetic diversity within colonies provided ideal conditions for microbial pathogens, Stow *et al.* (2007) demonstrated that the strength of antimicrobial compounds increased along a gradient of solitary, semi-social, and eusocial native Australian bee

continues

Box 9.1 continued

species. Such increased defences appear critical to the evolution of eusociality as the most primitively semi-social bee species showed an increase in antimicrobial strength, an order of magnitude greater than solitary species. Such comparisons cannot be made among ant species, which are exclusively eusocial. However, a similar evolutionary pathway may be inferred by the presence of the two chemical antimicrobial defence systems in ants. The presence of 'social immunity', demonstrated in termites, where previously unchallenged individuals are more resistant to disease if they have been in contact with immunized nestmates, has not been demonstrated in ants.

Commercial aspects of research into ant antimicrobials

Ecologically driven bioprospecting provides many commercial possibilities, not least among

ants (Beattie 1995). The field relies on a deceptively simple question: Where has the desired product already evolved? Among insects, as Stow *et al.* (2007) have shown, strong antimicrobials have evolved especially in social species, suggesting that commercial bioprospecting should be most profitably focused on social species. Ants have yielded two patents, one based on metapleural secretions, the other from immune peptides (Macintosh *et al.* 1998). Bioprospecting for biologically active molecules in ants and other social insects is still in its infancy, but holds the promise of chemical novelty, a prerequisite for the new generation of antibiotics. In an interesting role reversal, patents have been taken out for fungal entomopathogens to control invasive ant species such as the red imported fire ant (*Solenopsis invicta*).

exposed to predators and parasites whenever the nests are left unattended.

9.3.2 Claustral ICF

In many species belonging to formicoid subfamilies, founding queens never leave the incipient nests because they are able to feed the first brood using just their metabolic reserves. Such winged queens are often larger than workers (Plates 6 and 7); they have enlarged wing muscles and are also provisioned with large amounts of lipids (Passera and Keller 1990) and storage proteins (Wheeler and Martínez 1995). Claustral ICF relies on capital breeding (i.e. resources are acquired prior to the reproductive period), whereas non-claustral ICF uses income breeding (resources are acquired during the reproductive period) (Johnson 2006). Increased isolation from the outside world likely results in a higher success rate relative to non-claustral queens, although the vagaries of aerial dispersal remain a constant for both types. Yet, reversals from claustral ICF to non-claustral ICF have oc-

curred in several formicoid ants that live in habitats where resources (mostly seeds) are massively available and predictable, and predation is low (e.g. *Messor andrei*; Brown 1999; *Pogonomyrmex californicus*; Johnson 2002). In these habitats, foundresses can raise more workers of higher quality than if they were confined inside their nest.

9.3.3 Unrelated queens unite together

Following aerial dispersal, foundresses meeting at random can increase their success by cooperating together. Such 'pleometrosis' is beneficial because division of labour allows for a quicker production of either more workers or higher-quality workers (Bernasconi and Strassmann 1999). Generally, once the first workers have emerged, only one queen survives while the others are killed by the workers. Only in a few species do foundress associations persist and lead to polygyny, i.e., several queens reproduce concurrently (e.g. *Pachycondyla cf inversa*; Heinze *et al.* 2001). Pleometrosis is relatively uncommon in ants, being confined mostly to

formicoid subfamilies with claustral ICF (Choe and Perlman 1997). However, there are exceptions, as in the non-claustral species *Pachycondyla villosa* and *Pogonomyrmex californicus*, where pleometrosis is an optional strategy (Johnson 2004; Trunzer *et al.* 1998). Pleometrosis involves both cooperation and conflict among foundresses, and individual contributions to the production of workers are highly variable. Cooperation can evolve among foundresses that are unrelated because survival probability needs to go up only slightly faster than the number of queens in a group (see game theory; Dugatkin and Reeve 2000). Pleometrosis can even involve foundresses from two species, as found in *Azteca* nesting inside *Cecropia* trees (Choe and Perlman 1997).

9.3.4 Solitary queens that parasitize established ant colonies

Some species have queens that parasitize the nests of closely related ants. Once the parasite queen has succeeded in entering a host colony (sometimes killing the host queen), she is protected and fed by the host workers. She benefits from their labour to produce her own workers and sexuals. In the most derived species (e.g. *Pogonomyrmex anergismus*; Johnson 1994), the worker caste has disappeared and the parasite queen only produces queen-destined eggs, making her completely reliant on her host (inquilinism).

Other interspecific associations are less parasitic. They involve species that are phylogenetically distant and generally exhibit very different body sizes (e.g. Kaufmann *et al.* 2003). *Pyramica maynei* (Myrmicinae) nests in close vicinity to *Platythyrea conradti* (Ponerinae) and collects food from the host's chambers (Yéo *et al.* 2006). Founding queens thus forage in a protected environment (i.e. inside the *Platythyrea* nest), which is a big advantage during non-claustral ICF.

9.3.5 Solitary queens that are mutualistic with other organisms

In various formicoid genera (e.g. *Acropyga*, *Aphomyrmex*, *Cladomyrma*, *Tetraoponera*) that are highly dependent on mutualistic associations with hemipterans, founding queens need to carry one of the

mutualists during the nuptial flights. Foundation is fully claustral. Plant-sucking hemipterans feed on roots or in galls; given their parthenogenetic reproduction, a new group is quickly generated and provides additional food (honeydew) to the incipient ant colonies (references in Passera and Aron 2005). Similarly, claustral foundresses of fungus-growing ants need to bring the spores of their symbiont; their faeces are used to nurture the fungus, and the latter will be food for the first generation of workers. In both cases, the added nutrition is likely to increase the success of claustral foundation. Such associations do not seem to exist in the case of non-claustral founding.

9.4 Dependent colony foundation (DCF): Queens and nestmate workers cooperate

In many ants, the young queen(s) start a new colony together with nestmate workers. There is no solitary phase, because the queen is continuously protected and her offspring cared for. Mating occurs close to or inside the maternal nest. The new nesting site may already be known by workers that have explored the surroundings of the maternal nest, so the dispersal phase can be quick and efficient. Because workers perform all non-reproductive tasks, this caste determines the success of incipient colonies and needs to be present in sufficient numbers. DCF is the only mode of colonial reproduction in many ants, among both poneroid and formicoid groups (Peeters and Ito 2001), while it exists as an alternative to ICF in a minority of species (see Section 9.6.1).

9.4.1 Does queen number affect DCF?

A persistent belief in the ant literature is that DCF is inherently linked to polygyny. This confusion stems from the fact that various congeneric species are either monogynous and exhibit ICF, or polygynous and exhibit DCF (e.g. Keller 1991; Rosengren *et al.* 1993). However DCF is also common in monogynous species spread across all subfamilies (Table 9.2). New gynes can be produced before or after colony division: either they mate in the presence of the old queen and coexist for a short time (e.g. *Cataglyphis cursor*; Lenoir *et al.* 1988; army ants;

Table 9.2 A selection of species that exhibit DCF (in few species, as an alternative to ICF) as observed in the field ('obs'), or otherwise inferred from population genetic data, colony demography, or morphological characteristics of reproductives (AQ: alate queens; EQ1: sole-purpose ergatoid queen; EQ2: multi-purpose ergatoid queen; BQ: brachypterous (i.e. short-winged) queen; G: gamergate; m: monogyny; p: polygyny).

	Morphol. of reprod.	Mono- or Polygyny	Colony size (mean \pm s.d.)	Direct or indirect evidence for DCF	References
Poneroids					
<i>Myrmica</i> 'red'	EQ2	p	56 \pm 42	Size EQ < workers	Molet <i>et al.</i> (2009)
<i>Onychomyrmex hedleyi</i>	EQ1	m	850 \pm 341	Nomadic; \leq 6 gynes/colony	Miyata <i>et al.</i> (2003)
<i>Diacamma cyaneiventre</i>	G	m	214 \pm 80	DNA markers	Doums <i>et al.</i> (2002)
<i>Leptogenys kraepelini</i>	EQ1	m	21 \pm 7	Frequent nest emigration	Ito (1997)
<i>Odontomachus coquereli</i>	EQ1	m	19 \pm 11	?	Molet <i>et al.</i> (2007a)
<i>Pachycondyla marginata</i>	AQ	m/p	881 \pm 332	Obs; mostly ICF	Leal and Oliveira (1995)
<i>Pachycondyla (Megaponera) analis</i>	EQ1	m	583 \pm 174	Frequent nest emigration \leq 50 m	Longhurst and Howse (1979)
Formicoids					
<i>Dorylus wilverthi</i>	EQ1	m	>10 ⁶	Obs; nomadic	Gotwald (1995)
<i>Rhytidoponera mayri</i>	G	p	577 \pm 281	DNA markers	Tay <i>et al.</i> (1997)
<i>Gnamptogenys striatula</i>	AQ + G	p	372 \pm 298	Obs; DNA; fat reserves	Giraud <i>et al.</i> (2000)
<i>Dolichoderus cuspidatus</i>	EQ1	m	>10 ⁴	Obs; nomadic	Maschwitz and Hänel (1985)
<i>Cataglyphis cursor</i>	AQ	m	654 \pm 596	Obs; queens do not fly; limited dispersal (DNA)	Clémencet <i>et al.</i> (2005); Lenoir <i>et al.</i> (1988)
<i>Proformica longiseta</i>	EQ	p	480 \pm 41	Obs 3.2 m	Fernández-Escudero <i>et al.</i> (2001)
<i>Aphaenogaster senilis</i>	BQ	m	1260 \pm 69	\leq 3 gynes per colony	Boulay <i>et al.</i> (2007b)
<i>Leptothorax</i> sp. A	AQ + EQ	m	<100	Size EQ < AQ	Heinze and Buschinger (1987)
<i>Monomorium</i> nr <i>rothsteini</i>	AQ + BQ	?	50,000	Obs; 16 daughter colonies after one split; ICF also	Briese (1983)
<i>Myrmecina</i> sp. A	EQ2	p	130 \pm 96	Size EQ = workers	Ito (1996)
<i>Ocymyrmex picardi</i>	EQ2	m	360, 108	Obs; 1 mated young EQ in daughter colony (150 m away)	Bolton and Marsh (1989)

Gotwald 1995), or they mate after the old queen has left with a group of workers (e.g. *Aphaenogaster senilis*; Ledoux 1973). A distinct mechanism of DCF is exhibited in some polygynous species that

have polydomous colonies, i.e., distributed over several nests that are separated in space (e.g. *Formica* and *Myrmica*, Rosengren *et al.* 1993; Walin *et al.* 2001). It seems that polydomy evolves initially as a

foraging strategy; by increasing the number of nests occupied by the colony, a larger territory can be explored and more resources gathered. Workers, brood, and food are readily exchanged among nests. Eventually, however, when exchanges stop between two or more constituent nests, these can become the nucleus of a new colony. This phenomenon, often termed as ‘budding’ (see Section 9.4.2) is facilitated by polygyny. However, most polygynous ant species are monodomous, i.e., they have a single nesting site, and colony division is not different from DCF in monogynous species. In this case, exchanges between daughter colonies probably stop quickly.

Field descriptions of DCF are scarce in ants (Table 9.2), unlike wasps and bees where open nest constructions make observations easier (see Peeters and Ito 2001). In the polygynous *Proformica longiseta*, 26 DCF events were observed over a period of 30 days, with brood and adults carried over a distance of 3.25 ± 0.33 m (mean \pm SE). All DCF propagules originated from populous parental nests ($1,185 \pm 236$ workers, $N = 4$) that were more than twice the average size for this species (480 ± 41 workers, $N = 50$) (Fernández-Escudero *et al.* 2001). Daughter colonies had 262 ± 42 workers ($N = 11$) with either 1–2 adult queens or 21 ± 6 gyne pupae. After 3–4 days, all exchanges of workers had stopped, but there was much excavation in the new nests. Chance observations of single DCF events have also been reported for *Cataglyphis*, *Monomorium*, *Ocymyrmex*, and *Pachycondyla* (Bolton and Marsh 1989; Briese 1983; Leal and Oliveira 1995; Lenoir *et al.* 1988). In army ants, where observations are possible because the nests are above ground (a huge number of workers simply cluster around the queen and brood), a few gynes are produced each year. However, only one is selected by the workers, and after she mates, the colony divides into two groups of equal size that migrate in opposite directions. The old queen remains in one group, while the new queen joins the other (Gotwald 1995).

DCF allows for faster colony growth, and accordingly earlier colony reproduction. In addition, it facilitates local spreading and competition with incipient ICF colonies. It is linked to the success of various invasive species that are initially transported by humans (Hee *et al.* 2000; see Chapters 13 and 14 and ‘jump dispersal’ in Suarez *et al.* 2001).

9.4.2 The terms ‘fission’ and ‘budding’

The terms ‘fission’ and ‘budding’ are both commonly used in the literature to describe DCF. ‘Fission’ was originally intended for monogynous species, like army ants, where colonies split into two independent parts, while ‘budding’ was meant for polygynous species that produce new nests that initially remain interconnected (polydomy). The definitions of both these terms have evolved over the years (see Peeters and Ito 2001), and authors have variously emphasized dispersal distance, number of queens, or size of the propagules. Both terms are sometimes used interchangeably. Ultimately, the consequences of budding and fission are the same: limited dispersal and enhanced local propagation. Since DCF has replaced ICF in many unrelated taxa, the exact processes are likely to be highly diverse. Propagules can vary a lot in their composition because multiple individuals from two castes are involved. Thus, propagules can range from very small (a trait originally used to define budding) to large (a trait used in the definition of fission), with all possible intermediates. Accordingly it is difficult to categorize DCF with a dual terminology (i.e. fission or budding). Some species, e.g. *Proformica longiseta*, exhibit traits from both ‘budding’ (small propagules) and ‘fission’ (no proximity of the mother and daughter colonies and no durable exchanges) (Seppä *et al.* 2008). Thus, describing DCF on a case-by-case basis remains necessary before we can hope to define general patterns. Given our lack of empirical knowledge in almost all ants, we advocate the use of only one neutral term, dependent colony founding (DCF). Determining whether DCF is obligate or facultative is crucial, and morphological specialization of queens (especially permanent loss of wings), as well as investment in sexuals may give reliable information about this (see Section 9.6).

9.4.3 Parasitism is not DCF

We think it is not heuristic to consider parasitism (see Section 9.3.4) as a special type of DCF. Host colonies are nothing more than a resource of the environment to be exploited, similar to insect prey. Parasitism is another adaptation to improve success

during ICF, just like pleometrosis (see Section 9.3.3). The crucial point is that the founding queen is not helped by relatives from her natal colony, hence the interests of protagonists diverge. Parasitism is a risky strategy, because a foundress needs to enter an alien colony by deceiving its workers and sometimes killing its queen. Workers from the parasitized colony have no interest in rearing unrelated brood, leading to the evolution of defensive mechanisms. An arms race is expected between the host and the parasite, the latter evolving ways to escape detection. Similarly, pleometrotic associations are based on selfish strategies to access direct reproduction, and only one queen generally survives once workers have emerged. In both pleometrosis and parasitism, queens disperse on their own without the protection of nestmates. Thus, foundresses have a high failure rate, and many individuals need to be produced annually. This matches the investment of species that rely on non-claustral or claustral ICF; large numbers of queens are produced to compensate for mortality, and nestmate workers are not a part of the reproductive investment. In contrast, with DCF, all participants have convergent interests because they are highly related (young queens and workers are generally sisters), and evolution favours utmost cooperation.

9.5 Colony growth and reproduction

Offspring number and quality (e.g. size, weight, and metabolic reserves) have crucial consequences on the capacity of living organisms to spread in their local environment and to colonize new habitats. Solitary insects can adjust the traits of their offspring to a limited extent, by trading-off quantity and quality, which are generally constrained by limited resources (e.g. Fox and Czesak 2000). Social insects with morphological castes have more complicated trade-offs, because quantity and quality of either the gynes or the workers can vary independently. In ants reproducing by ICF, the number and size of gynes produced by a colony follow the classic quantity or quality trade-off found in solitary organisms. Dramatic changes in individual size are impossible because functionality must be retained (Molet *et al.* 2008). However, by shifting to DCF, a much wider range of offspring phenotypes be-

comes possible, i.e. colonies can produce propagules with more or fewer workers and queens, and these can vary independently in quality. Hölldobler and Wilson (1990) described the colony life cycle as 'an orchestration of energy investments, in which workers are multiplied until [...] it is profitable to convert part of the net yield into new queens and males'. This maturation point differs markedly across species, and it is heavily influenced by the occurrence of either ICF or DCF.

9.5.1 Investment of resources in workers

Ants are holometabolous insects, meaning that the juvenile form (larva) hatching from the egg is very different from the adult (Plate 8). The larva is fed and grows during several weeks. Weight increase is continuous, but size increase is discrete and occurs only during regular moulting events, i.e. three to five larval instars depending on the species (e.g. Onoyama 1982). Once a critical size has been reached, the larva can undergo metamorphosis. By then, environmental factors have channelled female larvae towards either queen or worker caste. Nutrition determines castes in honeybees (quantity and quality of royal jelly), but in ants, abiotic parameters (e.g. cold) also seem to be involved. Once individuals are adults, there is no further growth (no more moulting). The size of the workers is thus fixed and cannot change as they age.

Only workers are reared during most stages of the colonial life cycle (Figure 9.1). Species with small colonies typically have monomorphic workers (i.e. exhibiting little variation in size and shape) because these must perform all tasks efficiently. In species with larger colonies, polymorphic workers can be produced because specialization for specific tasks becomes advantageous (Wilson 1983). Thus workers can vary markedly in size, either continuously or as discrete subcastes. In the latter, 'soldiers' are allometrically distinct from the rest of the workers, and these occur only in 42 (41 of which are formicoid) of the 283 genera of ants (Oster and Wilson 1978). Workers in poneroid ants exhibit much less variation in size, and division of labour is then based mainly on age (Peeters 1997). In many formicoid ants, founding queens produce a first brood of nanitic (i.e. undersized) workers

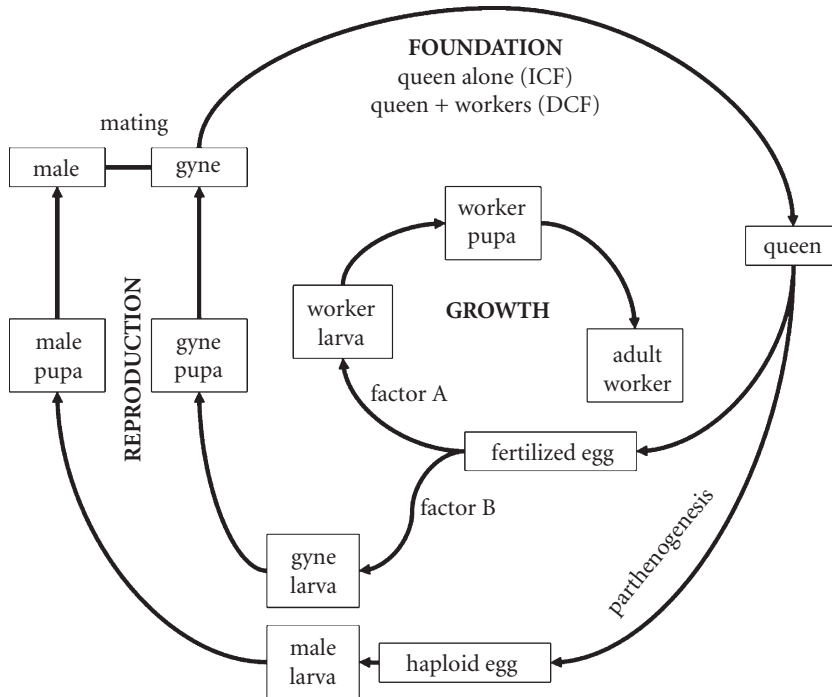


Figure 9.1 Typical life cycle of an ant colony. Newly founded colonies go through a growth phase during which all larvae are reared into workers. Once a critical size is reached, sexuals can be produced (reproductive phase): larvae hatching from the queen's fertilized eggs develop into gynes (exposure to biotic and abiotic environmental factors), while larvae emerging from unfertilized eggs develop into males. Males and gynes mate with foreign partners, and gynes then found new colonies either alone (ICF) or helped by nestmate workers (DCF).

termed 'minims' (Porter and Tschinkel 1986). Incipient colonies can thus reach a greater number of workers in a fixed time. Workers from subsequent broods progressively reach a normal size. In red imported fire ants (*Solenopsis invicta*), as colonies grow to about 200,000 workers, mean worker mass increases fourfold (Tschinkel 1993). In some species, colonies can alter the ratio between subcastes according to environmental influences. For instance in *Pheidole pallidula*, more soldiers are produced when high competition or predation makes nest defence a priority (Passera *et al.* 1996).

9.5.2 Investment of resources in sexuals of ICF species

During a certain period of the year, female larvae are reared into gynes instead of workers. In addition, unfertilized eggs are laid and develop into males

by arrhenotokous parthenogenesis (Figure 9.1). This is due to the 'complementary sex determination' system, where individuals that are heterozygous for the sex determination gene develop into females, whereas those that are not (e.g. are haploid) develop into males (Heimpel and De Boer 2008). Colonial investment in winged gynes varies tremendously across species that exhibit ICF and is affected by colony size, degree of dimorphism of gynes relative to workers, and the amount of reserves accumulated by gynes prior to dispersal (e.g. *S. invicta* gynes gain 290% in mass, mostly fat, before dispersal; Tschinkel 1993). In poneroid species, colonies generally have several dozens or hundreds of workers, these are not much smaller than queens, and the latter have few reserves. In contrast, in formicoid species, colonies can have thousands to millions of workers, these are often much smaller than queens, and the latter are provisioned with more metabolic reserves. In both

cases, gynes represent a large proportion of colonial resources, and this is necessary due to their poor individual success rate at dispersing and founding new colonies. For instance, among poneroids, *Harpegnathos saltator* colonies can produce as many gynes in one season as there are workers (e.g. 58 in a colony of 60 workers, Peeters *et al.* 2000).

The production of this large number of sexuals needs to be completed over a short time of the year (sexual activity is often limited to a few weeks or days), so it necessitates integrated colony operations. In some species, fat is stored in workers outside the reproductive season and is utilized to feed sexual larvae. This is the case in *Pogonomyrmex badius*, where a large number of sexuals are produced in early spring, at a time when foraging brings too few resources (Smith 2007; Tschinkel 1998). If stored resources are still insufficient, then investment in gynes is deferred to the following year, and more workers are produced instead. In *Solenopsis invicta*, colonial investment in sexuals does not rise gradually, but suddenly, once colonies reach about 50,000 workers, and then it remains constant at 33% (Tschinkel 1993). Workers keep on being produced once the colony has reached this maturation point to compensate for mortality or even allow for additional growth.

As we see in Section 9.6.2, the investment in gynes decreases considerably in DCF species.

9.5.3 Short-lived workers but long-lived colonies

In many poneroid ants, queens have a relatively short lifespan (e.g. 1.8 years in *H. saltator*; Liebig and Poethke 2004), whereas several formicoid taxa have evolved queens that can live much longer (up to 20 years or more) than conspecific workers (Keller 1998). These variations in the queen's lifespan lead to major differences in colony life expectancy, because they are often directly connected. In various monogynous ants, death of the original foundress is commonly thought to be followed by rapid extinction of the colony (after a brief period of male production from worker-laid eggs). This is surprising, considering the high value of the nest and worker force (Myles and Nutting 1988), as well as the generally poor success of new queens at founding colonies. In *Nothomyrmecia macrops*, or-

phaned workers accept that one daughter queen (sister to them) takes over reproduction following the queen's death; this is likely the best reproductive option for newly mated queens, considering that ICF is so risky (Sanetra and Crozier 2001).

Such colony inheritance by a related secondary reproductive may be more common than currently perceived. The short lifespan of workers relative to queens may be responsible for the failure to detect successive queen replacements (serial polygyny), because the workers produced by a previous queen quickly disappear, making the colony appear monogynous in genetic studies (e.g. André *et al.* 2001). Colony lifespan can also be extended by adoption of unrelated queens in species where the dead queen's sexual brood could not otherwise be raised to adulthood. In *Camponotus ligniperdus*, sexuals overwinter twice in the colony before leaving on their mating flight, and workers benefit from accepting unrelated queens that will produce additional workers and ensure that the previous queen's sexuals survive (Gadau *et al.* 1998). More studies are required on this topic. One outstanding question is whether queen replacement can influence the occurrence of DCF events. Indeed, as long as the mother queen is alive, workers who leave their natal colony give up raising sisters because they start raising nieces produced by a sister queen that mates with a foreign male. However, once the mother queen has died and been replaced by a sister queen, workers face no additional cost if they leave the colony with another sister queen.

Polygynous species probably have colonies with higher longevity because multiple queens succeed each other in time, and there are no gaps in brood production (Frederickson *et al.* 2005). For instance, the lifespan of *Formica montana* colonies can exceed 33 years (Henderson *et al.* 1989). Polygyny can result either from pleometrotic associations that persist beyond the founding phase (primary polygyny, rare), or from adoption of daughter queens (secondary polygyny, common). Stuart *et al.* (1993) showed that in *Leptothorax curvispinosus*, daughter queens are adopted in 60% of laboratory colonies. In a substantial number of species, the original queen is replaced by secondary reproductives that differ in morphology. For instance, in *Technomyrmex brunneus*, many ergatoid queens mate with brothers and

reproduce after the death of the founding (dealate) queen (Yamauchi *et al.* 1991). In the relatively few species in which workers have retained the capacity for sexual reproduction, one or several gamergates reproduce in the colony after the founding queen dies (Monnin and Peeters 2008).

9.6 Causes and consequences of the shift from ICF to DCF

Irrespective of whether ICF is claustral or non-claustral, natural selection led to its replacement by DCF in many unrelated ant taxa. Evidence for this shift comes from comparing congeneric species (e.g. in *Mystrium* and *Odontomachus*, Molet *et al.* 2007a, 2009). In a minority of species, both strategies occur as alternatives (e.g. Briese 1983), but in others, DCF has become obligate. Indeed, selection has frequently eliminated winged queens because they give no benefits if they disperse together with wingless workers. Loss of dispersal has often led to the evolution of flightlessness in solitary insects as well (Roff 1990).

9.6.1 What ecological pressures favour DCF?

Several environmental factors cause difficulties for solitary foundresses (Heinze and Tsuji 1995). First, there can be a strong cost associated with long-range dispersal; for example, habitat patchiness limits the chances for a flying queen to find a suitable habitat. Second, limitation of food or nesting sites increases competition between solitary foundresses and established colonies. This competition is decreased in claustral species because incipient colonies are 'hidden' until the first workers begin to forage. However, in non-claustral species, foundresses come in direct contact with the foragers of established colonies. Last, if incipient nests are disturbed before there are adult workers, it is difficult for a lone foundress to carry all of her first brood to a new nest site. All these parameters lead to a high failure rate of ICF: Less than 1% of queens are thought to succeed (e.g. *Pogonomyrmex*; Gordon and Kulig 1996). Alternative ICF strategies such as pleometrosis or parasitism can limit this failure.

However, there are also selective pressures against DCF. In species with obligate DCF, the fate of colonies is entirely dependent on the quality of the local habitat. When environments become patchy or unstable, there can be no 'escape' by flight, since winged queens are generally absent. Lack of aerial dispersal also increases local competition for resources when a habitat is saturated. Accordingly, even if obligate DCF facilitates the colonization of local habitats over a short period, it may be costly over a longer timescale because of the loss of long-range dispersal by flight, raising the question of whether this strategy turns out to be an evolutionary dead end in many taxa. This could explain why most species exhibiting obligate DCF are nested among clusters of species that retain ICF. DCF only seems to be evolutionarily stable in taxa with a very specific life history (e.g. nomadic behaviour). It should be noted that dispersal on foot does not limit geographic range (e.g. the wide distribution of *Neivamyrmex nigrescens*) unless there are barriers; the time needed to colonize a habitat is simply increased.

These opposing selective pressures on ICF and DCF are probably responsible for the coexistence of both strategies in various species. When winged queens perform both ICF and DCF, there is often morphological variability in these queens, i.e., normal winged queens specialized in ICF coexist with microgynes (dwarf winged queens found for instance in *Ectatomma ruidum*; Lachaud *et al.* 1999) or brachypterous queens (queens with short wings unsuitable for flying found for instance in *Temnothorax longispinosus*; Howard 2006). In all other species, either winged or permanently wingless reproductives are specialized for ICF and DCF, respectively. In the *Rhytidoponera impressa*-group, the relative frequency of colonies reproducing by ICF decreases over a 3,000 km gradient from tropical rainforests to temperate forests (Molet *et al.* 2008). Founding queens need to hunt outside, so they have decreased success in a harsher and less predictable temperate environment. Instead, gamergate colonies exhibiting DCF become the predominant colonial strategy once the long-range dispersal benefit of ICF is exceeded by the enhanced survival rate of incipient DCF colonies.

There is a paucity of field studies that investigate the processes of either ICF or DCF, as well as their relative benefits. Monitoring of solitary foundresses over several weeks is laborious, and human observers can have a negative impact on success itself. DCF is often an unpredictable event in time, thus even harder to monitor. Hence, the assessment of success rates is difficult (but see Wiernasz and Cole 2003). In addition, empirical measurements of the link between environmental parameters and colony reproduction can only lead to correlative results. For a direct assessment of the effect of environment on colonial reproduction, one should transfer colonies from one habitat to another, but such a manipulation would interfere with colony performance and only give an insight into phenotypic plasticity, not evolution. Alternatively, mathematical modelling can reveal causal relationships between environmental conditions and colonial reproductive strategy. Environmental parameters together with individual and colonial traits of ants can be measured experimentally, and models can be developed to explore the underlying mechanisms that could connect them together. Using this approach, Molet *et al.* (2008) developed a population dynamical model to predict the effect of environment on the coexistence between ICF and DCF in *Rhytidoponera*. A system of two differential equations describes the dynamics of the two types of colonies: (a) queenright colonies reproduce by ICF, and following the queen's death, they turn into (b) gamergate colonies that reproduce by DCF. This model showed that fluctuations in environmental parameters (notably food availability) are responsible for the shift from ICF to DCF along a gradient from tropical to temperate forests. Empirical field data not only confirmed this prediction, but also indicated that ICF can be retained in harsh conditions due to gynes being provisioned with more fat reserves. Since the model did not take into account the benefits of long-range dispersal, the increased quality (and thus cost) of gynes suggests that retention of aerial dispersal is strongly selected. Geographic information system (GIS) maps of environmental variables can be used in the near future to study the causes of transitions in colonial reproductive strategies in ants (Kozak *et al.* 2008).

9.6.2 Investment in queen or worker castes in species with DCF

In contrast to the high mortality of winged queens during ICF, mortality of queens engaging in DCF is much lower. Accordingly, investment in queens can be much reduced, especially since there can be only one or a few DCF propagules each year. In *Myrmica rubra*, a large polydomous colony produced over 2,000 males and only five new queens in one year (Walin *et al.* 2001). Thus, in DCF, colonial resources are redirected from sexuals towards workers (Pamilo 1991). Indeed workers contribute to colonial reproduction by helping nestmate queens found daughter colonies. Their performance in non-reproductive labour determines the success of DCF. Hence, it is very difficult to quantify reproductive investment in species reproducing by DCF, unlike species that reproduce by ICF.

9.6.3 Loss of pre-mating dispersal and shift to DCF

Aerial dispersal prior to mating (see Section 9.2) dictates the subsequent behaviour of founding queens; it is very unlikely that they can return to their natal nest after mating away from it (Bourke and Franks 1995), so DCF is not an option. We suggest that changes in mating behaviour precede any evolutionary shift to DCF. In several species having winged queens, mating flights have never been observed (e.g. *Lasius neglectus*), and intra-nidal mating is probably the rule. It is then a short step for such queens to be selected to forgo ICF. We conceive that winged queens are initially involved in DCF, but that they do not fly to find sexual partners. Since mating close to the natal nest leads to a sharp drop in mortality, fewer gynes need to be produced annually, and this is entirely consistent with DCF strategy (see Section 9.6.2). A further morphological adaptation can then follow in many species (see Section 9.6.4).

9.6.4 Evolution of wingless reproductive phenotypes

The phenotype of winged queens is mostly shaped by the strong selective pressures linked to ICF. In

particular, the bulky flight muscles in many formicoid ants represent essential metabolic reserves used to feed the first generation of workers. Constraints on flying ability are relaxed with the shift to DCF, except in species where it continues to alternate with ICF (Heinze and Tsuji 1995). When DCF is obligate, flight is no longer needed since queens walk together with workers; similarly, storage of metabolic reserves becomes useless since queens are never alone, and workers feed all offspring. Therefore, in thousands of species belonging to 66 genera at least, winged queens have been replaced by wingless reproductives (Plate 7) that have a simplified thorax as in workers (i.e. flight muscles are lost, and sclerites become fused). Ergatoid queens always have functional ovaries and spermatheca; they are a caste distinct from workers, which are unable to mate and store sperm in most ants. It is only in 200–300 species (mostly Ponerinae) that ergatoid queens did not need to evolve; the workers have a functional spermatheca, hence gamergates can reproduce instead of winged queens. Intermediate stages in the elimination of winged queens still exist. In *Cardiocondyla batesii*, winged queens exhibit a large variation in body volume, one in five of them having smaller thoraces and short wings (=brachypterous) ineffective for flying, whereas the others retain normal wings, although they do not actively fly (Heinze *et al.* 2002a). This suggests that once flying is no longer adaptive, stabilizing selection on the flight thorax stops.

The evolution of ergatoid queens corresponds to a strategy of colonial economy, because per capita costs of gynes are reduced at two levels: before and after adult emergence. Thus, (a) modifications in larval development result in gynes emerging without wing muscles and with a simplified thorax; (b) adult gynes no longer need to accumulate additional metabolic reserves (fat, glucose, and storage proteins) prior to dispersal. Indeed, the continuous presence of workers ensures that there is food available to sustain egg production and feed larvae. This reduction in energy investment associated with DCF has been shown in species with winged queens (Keller and Passera 1989), but it is even more pronounced in species with ergatoid queens. Ergatoid queens appear incapable of performing claustral ICF, because the lack of wing muscles as

a metabolic store strongly reduces their chance of succeeding as would-be foundresses. Nonetheless, if ergatoid queens can predictably obtain nourishment outside, they succeed in non-claustral ICF. In *Pogonomyrmex cunicularius* (R. Johnson, personal communication), ergatoid foundresses are able to forage for seeds similarly to dealate queens of congeneric species, and thus be independent of nestmate workers. Similarly in *Plectroctena mandibularis*, ergatoid foundresses can hunt insect prey like their winged counterparts in other species (Villet 1991).

Ergatoid queens exhibit an extremely wide range of phenotypes across ants, making them much more diverse than winged queens (Plate 7). This great heterogeneity is due to independent evolution from numerous unrelated ancestors having winged queens. In many species, ergatoid queens are morphologically closer to the winged queens of congeneric species than to their workers. They are produced in very small numbers, and colonies are monogynous. Such 'sole-purpose' ergatoid queens are found across taxonomic groups (e.g. *Leptogenys*, *Myrmecia*, *Monomorium*, *Dolichoderus cuspidatus*-group; references in Table 9.2). In army ants, they are very fertile and called 'dichthadiiform'; their gaster becomes physogastric to accommodate extensive ovarian development. However, in other species (mostly Myrmicinae) 'multi-purpose' ergatoid queens are morphologically closer to the workers than to winged queens of congeneric species, and they are produced in greater numbers than sole-purpose ergatoid queens. Only some reproduce, while the others perform worker tasks. Infertile ergatoid queens do not disperse from the natal nest, and can be involved in brood care, grooming of nestmates, nest maintenance, and even foraging (e.g. *Ocymyrmex*, *Myrmecina*; references in Table 9.2).

9.6.5 DCF leads to changes in colonial life cycle

ICF species exhibit high seasonality (Figure 9.2) because sexuals of both sexes must disperse at the same time for mating to succeed. Moreover, mating is immediately followed by colony founding. Indeed, after long-range dispersal by flight, queens

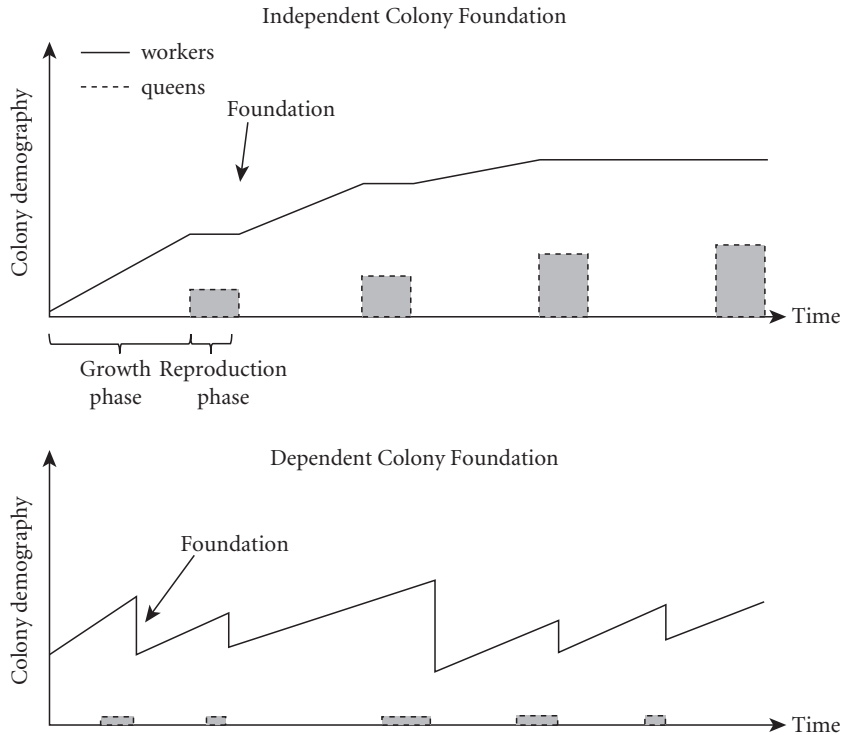


Figure 9.2 Changes in colony demography over time relative to the reproductive strategy. In ICF (*top*), colonies start with a single queen and need to grow for some time before being able to produce new gynes. These disperse during a nuptial flight. In contrast, colonies started by DCF (*bottom*) consist of a group of nestmate workers that help the new queen. Such colonies can start producing sexuals earlier; seasonality is not always selected for since mating and colony foundation can be disconnected. Only few gynes are produced as only one or a few propagules are possible, but their success rate is high.

cannot return to their natal colony and wait. In contrast, in DCF species, seasonality is less adaptive because mating and founding of new colonies can be disconnected (Figure 9.2). Males can be produced during many months of the year, not only in gamergate species, but also in species where ergatoid gynes are reared (e.g. in *Aphaenogaster senilis*, from May to January with a peak in July to August; R. Boulay, personal communication). Once mated, young queens can wait until conditions are optimal to leave the maternal nest with a group of workers. When seasons are marked, there are temporal constraints on excavation of new nests and survival of small colonies. When gynes emerge seasonally, this may provide a trigger for DCF if only one functional reproductive is tolerated per colony (e.g. *Cataglyphis cursor*; Lenoir *et al.* 1988; *A. senilis*; Boulay *et al.* 2007b).

Another important difference between the two modes of reproduction is the size of daughter colonies. ICF results in colonies that can take several years to produce enough workers, before they can rear the first pulse of sexuals (Figure 9.2). In contrast, new colonies founded by DCF start with a worker force that is already sufficient, and they can start producing sexuals much earlier. This shorter generation time is a strong advantage in growing populations (Roff 1992).

9.7 Future directions

The prevalence of DCF has been underestimated in ants. Although very few studies have described it in the field, the existence of wingless reproductives in a large number of species is strong evidence that ICF is very unlikely. Morphological adaptations in

ergatoid queens need to be studied in a wider taxonomic range of species, and followed up by focusing on colony-founding behaviour. The ability of ants to readily produce reproductive phenotypes that are wingless and hence cheaper (impossible in social wasps and bees) probably contributed to the evolution of DCF as an efficient alternative to ICF. There are also unanswered questions about the evolutionary factors selecting for different modes of ICF, and these are best studied in genera (e.g. *Pogonomyrmex*) that exhibit variations in the levels of foraging by founding queens (i.e. obligate, facultative, or absent).

9.7.1 Finding more evidence for DCF

Field studies are hindered by the unpredictability in time of DCF events in various species (especially in the tropics, see Section 9.6.5), unlike ICF which always immediately follows seasonal mating flights. Moreover, many species that exhibit DCF are prone to regular nest relocation (discussed for Ponerinae in Peeters 1997), so emigrations must be distinguished from DCF events. Brood and adult exchanges between nests sometimes need to be monitored over a few days. In polydomous species, new nests can either remain connected with an existing colony, or they can become autonomous. Accordingly, describing DCF not only implies studying the behaviours during the division itself, but also the fate of the two nests over several days. It is important to excavate both nests involved to compare their demography and reproductive structure (using ovarian dissections and/or DNA markers).

It is commonly thought that molecular markers are powerful tools to confirm the occurrence of DCF. For instance, Liautard and Keller (2001) showed that nests of *Formica exacta* are very similar genetically within pastures, but different among pastures, suggesting that queens do not disperse far from their natal nest, probably because colonies are founded dependently. Ross *et al.* (1997) found that in the native range of *Solenopsis invicta*, queens produced by polygynous colonies do not disperse far (hence DCF is likely to occur), whereas queens from monogynous colonies perform long-range dispersal by flight (hence ICF). Sympatric monogy-

nous and polygynous forms were genetically differentiated, so there was no queen exchange between colonies of different types and assortative mating may occur. In other species, complex patterns of intra-colonial relatedness linked to polygyny and/or polyandry can complicate analyses. Furthermore, a very fine-scale approach is required, i.e., analysis of neighbouring nests for which recent DCF is suspected. Nevertheless, population genetic data have shown extremely short ranges of female dispersal, as opposed to the contributions of flying males (e.g. Doums *et al.* 2002; Giraud *et al.* 2000). Such data corroborate the occurrence of DCF, but cannot unambiguously exclude ICF close to the nest of origin.

9.7.2 Understanding the behavioural processes in DCF

Diverse questions remain about the mechanisms of DCF. First, a few gynes are produced annually, but these may vary in size, potential fertility, and level of relatedness with respect to workers. Conflicts for the choice of the new queen are expected when more gynes are produced than the number of future daughter colonies (in *Aphaenogaster senilis*, Chéron *et al.* 2008). Queens compete for survival, and all workers may not prefer the same queen. Individual interactions must be studied, and relatedness between individuals as well as queen quality (e.g. cuticular hydrocarbons signaling levels of fertility) can be assessed. In a polyandrous and polygynous *Proformica* species, daughter colonies produced by DCF exhibited a higher intra-colonial relatedness than the mother colonies from which they originated (Seppä *et al.* 2008). Since workers are carried from the mother nest to the daughter nest, kin discrimination can be involved at this step. However, evidence for kinship-based DCF has not been found in other species. This may be linked to the need for an efficient daughter colony to include workers of all ages (i.e. nurses as well as foragers). Age is probably a factor that overrides genetic relatedness during the organization of DCF. In addition, workers may be unable to distinguish which nestmates they are more related to.

Second, contrary to ICF, where the winged queens land in an unknown environment and

must quickly find a nesting site, DCF allows for preliminary exploration by the workers of the neighbourhood of the mother colony in order to find a suitable new nest. Some recent studies have focused on nest emigration to assess which characteristics of the nests are most important to workers (reviewed by Visscher 2007). It must be investigated whether such choices are also made before DCF in ants and involve similar mechanisms as those found in swarming honeybees, e.g., existence of a worker quorum that triggers emigration behaviour.

Third, the dynamics of DCF are unknown. Is division triggered once colonies exceed a certain size threshold? Or simply because physical space becomes limiting in the nest? Across species, is there an effect of colony size on dispersal distance? Are behavioural mechanisms affected by colony size across species? Group decisions may be hindered below a critical colony size, and individual decisions may then be more important. During nest emigration, the queen and brood are transported at specific times, and one should study whether these parameters are similar during DCF. Testing as to whether solitary ergatoid queens can succeed in ICF by foraging outside, and how the help of workers increases founding success, is also necessary. Although this has been done under laboratory conditions (e.g. Schrempf and Heinze 2006), experiments in the field are needed and must be generalized to more taxa.

Finally, we do not know how many propagules are produced at each DCF event (this is likely to vary across species), and how frequent DCF events are. The role of parasites also warrants more attention because in infected colonies parasites could be a strong selective pressure against DCF (assuming that founding queens dispersing for ICF are not infected).

9.7.3 Morphological adaptations for more efficient DCF

Future studies need to quantify per capita costs of either winged or wingless reproductives that occur in the same species or genera. This will test the selective advantages involved in replacing the an-

cestral winged queens. In *Myrmium*, interspecific comparisons revealed that ergatoid queens (5.95 mg) are cheaper to produce than winged queens (14.5 mg) (Molet *et al.* 2007b). Similar data are needed across all subfamilies of ants.

DCF is associated with a substantial increase in the success rate of incipient colonies, because it eliminates the dangerous solitary stage. Hence, the advantages of social life are retained throughout the colonial life cycle. One could almost expect that ICF would be completely lost in ants, were it not that dispersal on the ground introduces severe constraints, i.e. no colonization of new territories, no escape from deteriorating habitats. ICF continues to exist in a majority of ants, despite DCF being an efficient strategy. This is a powerful evidence for the benefits of aerial dispersal (Hamilton and May 1977).

9.8 Summary

All ants live in perennial colonies that exhibit three phases: foundation (initiation of new colonies), growth (production of more workers), and reproduction (production of sexuals). Colony foundation can be independent or dependent, and this dichotomy has important consequences on all phases of the life history. During independent colony foundation (ICF), winged queens are alone while they disperse by flight, mate, and raise the first generation of workers. Queens feed the larvae using energy provided by degradation of their wing muscles, but the queens of various species also need to forage. Both morphological (queens become much bigger than workers and no longer forage) and behavioural (cooperation with other queens; invasion of conspecific or heterospecific colonies; mutualism with different organisms or ant species) adaptations have evolved to improve the success rate of solitary foundresses. However mortality of foundresses often remains high (especially during aerial dispersal and mating), and colonies must invest a large proportion of their resources in the annual production of numerous winged queens. Hence, colonies must grow to a large size before being able to reproduce, which may take several years. Sexuals generally mate in aggregations that require their synchronous release from many

colonies, but high predation can select against these aggregations.

Dependent colony foundation (DCF, also termed 'fission' or 'budding') is a fundamentally different strategy because young queens are continuously helped by a group of nestmate workers. Hence, reproductive investment is redirected towards the production of more workers, inasmuch as these determine the success rate of daughter colonies. Only a few gynes are reared annually, because only one or few propagules are possible. Given that colonies start at a bigger size, sexuals can be produced sooner. Males search for foreign sexual partners, who remain inside or near their natal nest. Depending on the species, mating of new gynes occurs before or after colony division. All ant workers are wingless, and thus queen dispersal occurs on the ground over short distances. Accordingly wingless 'ergatoid' queens evolved in many species (at least 66 genera, both poneroid and formicoid), and aerial dispersal is then restricted to males.

Contrary to widespread thinking, DCF occurs irrespective of monogyny or polygyny. In species founding independently, colonies can go extinct after the death of the original foundress, although queens have exceptional longevities in some species. Colony lifespan can be extended with second-

ary reproductives, and these are sometimes morphologically different from the normal winged queens (e.g. gynes of reduced size, mated workers). In polygynous species, the continuous turnover of queens also results in longer-lived colonies.

DCF is very efficient in ants as a result of adaptations in the morphology of reproductives, with ergatoid queens being cheaper to produce compared to the ancestral winged queens; ergatoid queens did not evolve in social wasps and bees. Shifts from ICF to DCF occurred many times in unrelated ant genera. Current research explores the causes and consequences of these shifts. It is likely that the loss of long-range dispersal by queens increases the chance of species extinction. DCF remains poorly known relative to ICF. Species where both strategies coexist are interesting material for future research.

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