



# Pathways to parasitic strategies in ants

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Evolutionary biologists find delight in tracing their study topics back to Charles Darwin, and ant researchers are no exception. The dulotic habit of many ant species was highlighted by Darwin as one of the most sophisticated adaptive outcomes of natural selection (1). Dulotic ants raid nests of other ant species for pupae, so that when workers eclose from the raided pupae they start working for their dulotic host nest. Thus, dulotic ants gain work force with little investment, whereas the captured workers are deprived of evolutionary fitness. The wonderful ways in which ant species exploit each other's behaviors to get their brood reared do not stop here, however. Some species are temporary social parasites whose queens infiltrate nests of other species and kill the resident queen, so that the host workers start rearing the parasite's young, and the colony gradually turns into a colony of the parasitic species. So-called inquilines, workerless social parasites, live permanently in colonies of their host species alongside the host queens, relying on the host workers for rearing their offspring (2). Social parasitism is found outside ants as well, in wasps, bees, and even in birds such as cuckoos and cowbirds, but the diversity of such strategies is the highest in ants. In PNAS, Borowiec et al. (3) use phylogenomics to reconstruct the evolutionary routes to parasitic strategies taken by *Formica* ants and their connections to dispersal and nest-founding strategies more generally.

*Formica* is a Holarctic ant genus that comprises the mound-building wood ants and their relatives, dominant in temperate and boreal ecosystems from coniferous forests to peat bogs to prairie. All the main types of social parasitism are found within the genus. In addition to diversity in social parasitism, *Formica* are remarkably diverse in their social ecologies: Some species live inconspicuous and submissive lives in underground nests with some hundreds of workers and one or a few queens; more dominant species build impressive mounds or thatches and may form extensive nest networks, "supercolonies," so that a single multinest colony easily spans several

hectares, with tens or hundreds of thousands of workers and hundreds of queens in each nest (4). The phylogeny constructed by Borowiec et al. (3) traces the origin of the genus to the Old World ca. 30 Ma ago, with repeated colonization of the Nearctic. They use ultraconserved elements in the genome to construct the family tree of the genus and map findings of an extensive natural history literature as well as their personal observations on variation in social parasitism, queen dispersal behaviors, and nest-founding behaviors into the family tree, which allows reconstructing ancestral states of behavior and timing of transitions in strategies.

*Formica* is not the only ant genus with all the three major types of social parasites, but the phylogenetic reconstruction suggests that the evolutionary routes *Formica* ants have taken to different parasitic strategies stand out from earlier described cases. In *Formica* both dulosis and inquiline social parasitism have evolved from ancestors with temporary parasite lifestyles. Elsewhere, as in *Acromyrmex* leafcutter ants (5) and *Myrmica* red ants (6), inquiline social parasitism has evolved independent of temporary parasitism, with inquilines occasionally parasitizing closely related species, possibly even via sympatric speciation (6). Thus, these remarkably sophisticated strategies may convergently evolve from different evolutionary backgrounds.

Mapping trait covariation into a phylogeny is a powerful method for understanding the coevolution of traits; Borowiec et al. show that parasitic strategies are strongly interconnected with variation in colony-founding and dispersal strategies of young queens (3). Evolution of these strategies is driven by competition (7). Competition against other ants, including conspecifics, is a key feature of ant ecology, and colony founding and early growth are the key stages when the risk of succumbing to competitors is at its highest. The ancestral *Formica* already had diverse solutions to this problem, each with its own pros and cons (Fig. 1). Some queens disperse on the wing and attempt to establish their own nest,

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Author contributions: H.H. wrote the paper.

The author declares no competing interest.

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See companion article, "The evolution of social parasitism in *Formica* ants revealed by a global phylogeny," [10.1073/pnas.2026029118](https://doi.org/10.1073/pnas.2026029118).

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Published October 7, 2021.

# Dispersal and reproductive strategies of an ant queen

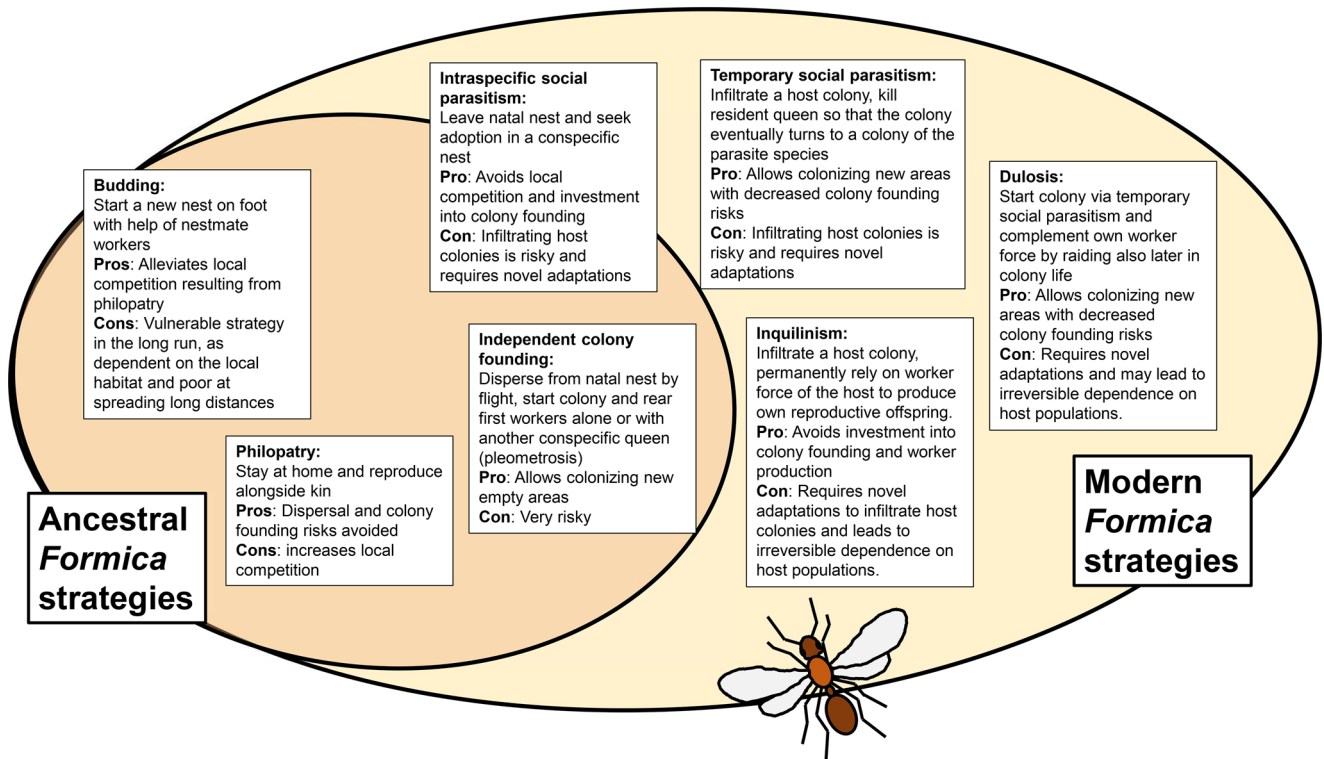


Fig. 1. The range of dispersal and reproductive strategies available for a young ant queen. Strategies on the left (darker orange shading) represent the options used by the ancestors of modern *Formica* 30 Ma. In modern *Formica* the strategies have diverged to include the parasitic strategies on the right (lighter orange shading), with intraspecific social parasitism as a likely evolutionary intermediate.

sometimes joining forces with another queen (pleometrosis), a risky strategy with potentially high payoffs if a pristine habitat devoid of competitors is found. Some stay in their natal nest with their mothers and siblings and some join nestmate workers to initiate a new satellite nest on foot nearby, leading to “polydomous” colonies that inhabit many interconnected nests, although this latter strategy was probably rare ancestrally (3).

All these strategies still exist in *Formica*, but a major evolutionary turn was taken ca. 18 Ma ago, when the ancestor of the modern *difficilis*, *integra*, *rufa*, *dakotensis*, *sanguinea*, and *exsecta* groups replaced the risky independent founding option with a temporary parasitic strategy to be used when dispersing from the natal site. Thus, the burdens of nest founding and rearing early brood were outsourced to the host species. It seems likely that parasitizing conspecific nests was an evolutionary intermediate on the way. The option of staying at home and expanding the colony via budding was retained and in some cases developed further to supercoloniality. This combination of strategies seems very successful, as in these species groups we can find the most dominant *Formica* species.

Thus, *Formica* ants have two strategies available, with very different strengths and weaknesses. One is good for local dominance but very poor in reaching new areas, and the other is good for reaching new ground but demands abilities to infiltrate host nests. Interestingly, most species are polymorphic in their strategies and thus seem to get the best of both worlds. The importance of different strategies differs between species. Species like *Formica aquilonia* seem to rely almost exclusively on budding, whereas temporary parasitism is prevalent in, e.g.,

*integra* and *difficilis* groups (3). In some species the variation is extensive. For example, *Formica truncorum* and *Formica exsecta* may live either in populations comprising many separate single queen nests founded via temporary social parasitism or form supercolonies comprising hundreds of interconnected nests founded via budding (4).

The origins and maintenance of the variation in strategies needs to be understood bottom-up, from the social evolution of dispersal decisions taken by young queens. While dispersal abilities are highly relevant for a species’ ability to colonize new ground, and thus essential for long-term success, the selective pressures still need to be looked for at an individual level. Dispersal is selected for only if the immediate fitness prospects are higher outside than at home. Success outside depends on independent founding chances or on availability of potential hosts, the success in invading them, and the competition faced after successful establishment. The payoffs of staying at home depend on the local family situation. Alongside gains through personal reproduction, effects on relatives need to be considered. Staying at home to reproduce is costly if it increases competition with relatives: Dispersal under high risks is first and foremost selected for to avoid local competition with family members (8). A multitude of things affects the payoffs of staying, including number of resident queens and their relatedness to young queens. To complicate matters further, it is not well understood who controls whether queens disperse or are allowed to stay. The young queens, resident queens, and workers may all have different evolutionary optima with respect to dispersal outcomes, bringing about kin conflicts in the nests (9).

While studies of kin conflicts in *Formica* have been very successful, the ecologically very fundamental conflict over queen dispersal and recruitment still needs careful attention.

Maintenance of dispersal polymorphism seems puzzling when the different strategies require such different adaptations. Parasites need to fly, find a mate, and locate and infiltrate host colonies, which sometimes requires remarkable precision in chemical mimicry (10). Those who stay at home can focus just on egg laying and competing for worker attention and have no use for wings, flight muscles, or chemical mimicry. In addition to understanding the heterogeneity of selection pressures through behavior and ecology, we can look into comparative and functional genomics of plasticity of life histories to solve this puzzle. Interestingly, maintenance of polymorphism in *Formica* might be facilitated by genetic linkage, as a supergene has been shown to underlie differences in queen number regulation intimately linked to dispersal behaviors, perhaps facilitating coinheritance of coadapted alleles in key genes (11). While this far this supergene has only been studied in detail in a nonparasitic species, *Formica selysi*, the same polymorphism extends throughout the genus, making *Formica* a very promising system for comparative genomics.

While flexibility and plasticity prevail in temporary parasitism, dulosis and inquiline seem to be irreversible strategies as both evolved once in *Formica* and no reversals back to a free-living life are seen. In leafcutter ants, inquiline strategies are accompanied by gene losses and genome erosion, similar to other tight interspecific relations such as obligate nonsocial parasitism and intracellular symbioses (5). *Formica* provides an

interesting group for studying possible genome erosion and host–parasite coevolution in dulotic species, both for comparisons to other ants such as *Temnothorax* acorn ants (12) but also for observing parallel genomic evolution in an unusually large group of dulotic species that share a common ancestor.

Colony-founding strategies arise from selective processes at individual and colony levels but have far-reaching consequences at the population level. They are a nexus where within-colony conflicts, morphological evolution of the queen caste, genome evolution, community dynamics, and intricate mechanisms of host–parasite coevolution combine in complex coevolutionary feedback loops (9). The work of Borowiec et al. (3) is a beautiful example of how such complex interactions can be tackled by combining genomic methods with a wealth of meticulous natural history observations into a big picture that in turn inspires and guides more detailed hypotheses and their tests.

Phylogenetic comparative work has produced some of the most compelling examples of our understanding of evolution of social traits, and *Formica* ants have the potential to offer similar insight into a complex of traits with huge ecological significance. As this text started with Darwin, it is fitting to close with him as well, hitting the nail on the head when writing about the coordinated traits underlying social parasitism, although this time in cuckoo strategies in birds (1): “It has been objected that I have not noticed other related instincts and adaptations of structure in the cuckoo, which are spoken of as necessarily co-ordinated. But in all cases, speculation on an instinct known to us only in a single species, is useless.”

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