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Polydomy: the organisation and adaptive function of complex nest systems in ants

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Many ant species spread their colonies between multiple spatially separated but socially connected nests, a phenomenon known as polydomy. Polydomous species are ecologically and phylogenetically diverse, and often economically significant as invasive pests. Benefits of polydomy may include risk spreading, efficient resource exploitation and ergonomic factors. Very little is known about the costs of polydomy; facultatively polydomous species are good candidates for identifying costs. Analysing polydomous colony structure provides insights into which costs and benefits are driving the colony organisation; for example, a cross-species analysis of inter-nest trail networks shows structural features related to long-distance transport efficiency. Deeper understanding of polydomy will shed light on key issues in evolutionary and behavioural ecology, and also benefit both conservation and pest control.

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Introduction: what is polydomy, and why is it important?

The idea of an ant colony as a cooperative group of closely related ants that live together in a single nest may seem appealingly obvious; however, many ants defy this paradigm for at least part of their life-cycle. Over 150 ant species, so far, are known to instead spread their colony across multiple spatially separated but socially connected nests. This phenomenon is known as polydomy (Box 1, Figure 1) and has evolved many times independently among the ants — polydomous species are phylogenetically and ecologically diverse. It is likely that different evolutionary drivers have been responsible for different origins of polydomy, especially as polydomy occurs in both polygynous and monogynous species (Box 1) [1]. The prevalence of polydomy poses a significant challenge to the traditional view of a social insect colony as a 'factory within a fortress' [2].

Studies of the organisation of behaviour in social insect colonies are important in behavioural ecology, explaining collective behaviours such as foraging, division of labour and nest construction [3]. However, the majority of these studies assume that a colony is operating from a single nest. Many processes operate differently under the spatial structure provided by multiple nests, so studying these behaviours in the context of polydomy is important to complete our understanding. Taking polydomy into account is essential also for the definition of colony boundaries [1,4–9] and this in turn is important for several reasons, both fundamental and applied. In social insects, such as ants, the colony can be seen as the reproductive unit, and thus the unit on which natural selection is operating. To understand the evolutionary ecology of these species, we need to be able to define a colony so we know at what scales we would expect to see cooperation, intra-colony reproductive conflict and inter-colony competition. For example, in populations that are highly polydomous or even unicolonial (Box 1, Figure 1), genetic variation between nests may be so low that individuals helping nestmates are no longer differentially helping their kin. Without kin-selection via differential benefits to relatives, the selection for worker traits is predicted to weaken, while selfish reproductive strategies will be selected for [10]. Together, these processes should contribute to making extreme polydomy an unstable strategy over evolutionary time [10]. Over rather shorter timescales, when individuals from polydomous species are sampled, knowing colony identity is important so that, in addition to the nest, the polydomous colony can be included as a grouping factor [11,12]. Relying on nest alone to provide independent replication may give pseudoreplicated or misleading results. For example, genetic differentiation between nests of the same polydomous colony can be low [13] and if nests such as these were sampled and assumed to be independent, then this could lead to artificially low values for within-nest relatedness.

Polydomous species are often highly ecologically successful with far-reaching ecosystem impacts, some even becoming invasive pests [14••,15–18]. All of the ant species on the list of the world's 100 worst invasive species are polydomous [19]. Polydomy poses significant challenges to pest control because of the difficulties of treating a spatially dispersed colony that can repopulate

Box 1 Glossary

Monodomy: An ant colony is housed in a single nest, that is, the nest houses all queens, all brood and at least the majority of workers (Figure 1a).

Polydomy: An ant colony simultaneously occupies at least two spatially separated but socially connected nests (Figure 1b,c).

Nest: A nest houses both workers and brood, but not necessarily a queen [1].

Social connection: Socially connected nests share or exchange resources, for example, food or workers.

Unicoloniality: A population of an ant species functions as a single large polydomous colony (Figure 1c).

Multicoloniality: A population of an ant species consists of colonies (monodomous or polydomous) that function independently and usually interact agonistically (Figure 1a,b).

Polygyny: At least two reproductively active queens are present in a colony. The colony may be monodomous or polydomous: if it is polydomous, the queens may or may not be dispersed between multiple nests.

Monogyny: Only one reproductively active queen is present in a colony; the colony may be monodomous or polydomous.

an area from a single overlooked nest [20]. These problems also apply to conservation, for the opposite reason: an ant population may seem healthy because many nests are present, but these may represent a very small number of actual colonies, leading to risks associated with small effective population size.

In conclusion, understanding polydomy is essential to understanding the evolutionary and behavioural ecology of ants, and for effectively and accurately sampling and studying polydomous colonies. This review focuses on recent developments in the study of the ecological costs and benefits of polydomy, and on how polydomous colony structure relates to function.

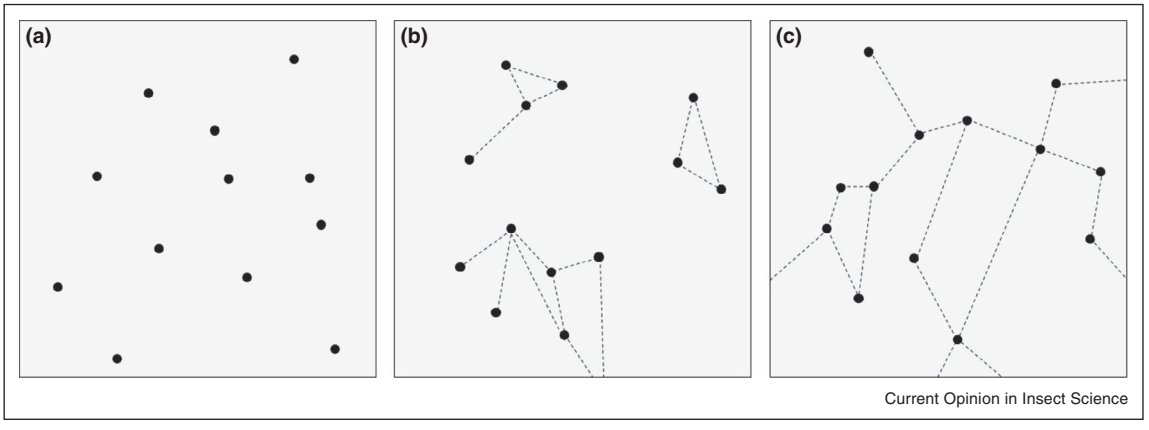
Benefits of polydomy

Polydomy allows colonies to create new nests without going through the high-risk bottleneck of single-queen nest foundation. Local foundation of socially connected nests provides a relatively low-risk way of spreading into a new area. For polygynous species, this also offers a method of colony reproduction, because a budded nest or group of nests can later become socially separated from the 'parent' colony and function independently. Indeed, polydomy is likely to have arisen from processes of incomplete budding or nest migration. Other ecological factors related to polydomy, while not necessarily having been drivers of the evolutionary origin of polydomy, may still confer current adaptive benefits. These include risk spreading, foraging advantages and ergonomic benefits (Figure 2). Below, some examples of recent advances and gaps in our knowledge regarding the adaptive function of polydomy in relation to these three areas are highlighted.

Risk spreading

It seems intuitively obvious that spreading a colony over multiple nest sites makes the colony less reliant on the survival of any particular nest. This applies most obviously to polygynous species, but even in monogynous polydomous species, sexual brood is often transported to queenless nests, making the survival of the queenright nest less critical than it would otherwise be. This has obvious potential to be beneficial if a nest suffers predation or attack by conspecifics [21,22], or indeed pest control attempts [23–25]. However, clear evidence of the adaptive benefit of polydomy in these contexts is lacking. Multiple nests may also be useful if local conditions change, because the inhabitants of a nest that becomes unsuitable can relocate [26] to other more successful nests. An additional possible risk-spreading benefit to polydomy could be the potential to isolate pathogens or parasites by cutting off contact with an

Figure 1



Schematic representation of different forms of colony organisation. • = ant nest; – = social connection: these could be inter-nest trails, or more diffuse movement of individuals between nests. **(a)** a multicolonial population of monodomous ant colonies; **(b)** a multicolonial population of polydomous ant colonies; **(c)** a unicolonial polydomous ant population.