

# Invited Commentary

## Ecological and evolutionary perspectives on “supercolonies”: a commentary on Moffett

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Moffett provides a very thorough review of the “supercolony” concept, focusing on the biology of the Argentine ant (*Linepithema humile*). The term supercolony is being used more and more frequently in the social insect literature, however, not always to describe the same colony structure. Despite invoking an almost science fiction-like quality, we agree with Moffett that the concept of the supercolony has been valuable, providing considerable insight from both an ecological and an evolutionary perspective.

Ecologically, the term supercolony is often used to describe a polydomous colony that occupies such a large number of nests that it is impossible for all members of the colony to interact in their lifetime (Pedersen et al. 2006). That is, the society occupies many nest sites over such a large area that queens and workers who live on one side of the supercolony will never meet individuals from the other side. As Moffett points out, this is likely true for many social insects, even those that occupy relatively few nest sites over smaller areas. Moffett suggests that we restrict the definition of supercolony to societies with at least 1 million workers. However, this seems a bit arbitrary; a number of ant species are known to have more than 1 million workers yet occupy a single nest site. Are these supercolonies in the same sense that a spatially extensive polydomous Argentine ant colony is? Species that form supercolonies are also often ecologically dominant where they occur, both outcompeting other species for resources and overwhelming species through numerical superiority (Holway et al. 2002). However, as pointed out by Hölldobler and Wilson (1977), research is still needed to determine if ants become ecologically dominant because they form supercolonies or if ecologically dominant ants monopolize resources and subsequently form supercolonies as a result.

From an evolutionary perspective, a supercolony can be defined as the aggregation of ants across many nests that share a common genotype (usually inferred using microsatellites or mitochondrial DNA) and phenotype (e.g., cuticular hydrocarbon profile). This is likely due to having a shared common ancestry. Subsequently, this approach has been used to examine the source and introduction history of invasive ants. Recent holistic work combining behavior, chemistry, and genetics has provided incredible insight into the worldwide spread of Argentine ants (Wilgenburg et al. 2010), and supercolony identity has been used to infer recent exchange of ants between different introduced populations (Tsutsui et al. 2001; Corin et al. 2007; Sunamura et al. 2009; Vogel et al. 2010; Suhr et al. 2011). As Moffett points out, genetic work on both native and introduced populations of Argentine ants suggests little to know gene flow among supercolonies. However, we disagree that each supercolony should be considered its own species (much as each individual is not considered its own species in

clonal organisms). More work is needed to determine the spatial extent of gene flow in species that form supercolonies.

We agree with Moffett that we need to move past semantic arguments when discussing supercolonies. However, we believe that both ecological and evolutionary examinations of supercolonies need to be conducted from the perspective of the population. A population can be defined as a group of colonies that have the potential to exchange genes or compete for resources. A population can therefore have many colonies, even many supercolonies. However, the term unicolonial, which is often considered synonymous with supercolony (Pedersen et al. 2006), should be restricted to describe situations in which the entire population consists of only one supercolony (a “unicolonial population” Hölldobler and Wilson 1977; Suarez et al. 2008).

Research is still clearly needed on the biology of species that form supercolonies as many unanswered questions remain. For example, how do supercolonies arise and how long do they last? How much variation in social parameters exists in native populations of species that can form supercolonies (e.g., colony size, queen number, intra- vs. intercolony genetic diversity, gene flow among colonies)? Is there conflict over reproduction within supercolonies or are they as harmonious as Moffett implies? Over what spatial scales are food and information exchanged (Heller et al. 2008)? These last 2 questions in particular address whether or not supercolonies are effectively made up of aggregations of smaller colonies. Despite being one of the best-studied social insects, we still know surprisingly little about the biology of Argentine ants, particularly in their native range. From an evolutionary perspective, we often know even less about species closely related to those that form supercolonies. For example, what characteristics are shared among sibling species in the *humile* complex or are unique to the widespread *L. humile*?

**Key words:** Argentine ant, supercolony, unicolonial.

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