communications biology

A Nature Portfolio journal

Article

https://doi.org/10.1038/s42003-025-08438-5

Supergene regulation of ant social organization: a *P* haplotype in workers shifts colony ontogeny towards multiple queens

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Supergenes are large clusters of linked genes that control complex phenotypes. In several ant clades, supergenes determine whether one or multiple queens reproduce in mature colonies, but how supergenes affect colony social structure has been inferred indirectly. We show experimentally that a supergene in *Formica* ant workers alters the social structure (single- or multi-queen) of developing colonies. We crossed queens and males carrying alternative social supergene genotypes, and let the queens establish single-queen colonies, which we paired in the laboratory. The presence of a paternally-inherited *P* haplotype in workers was sufficient to make the colonies more likely to fuse and become multi-queened, regardless of the genotype of their mother. The dominant effect of the *P* haplotype on colony social structure likely contributes to the spread of multi-queen colonies. This controlled experiment provides direct evidence that the *P* haplotype in workers steers social organization towards multiple queens during early colony ontogeny.

Ant societies vary widely in size and organization. They can host up to several million individuals, with many non-breeding workers helping one to many breeding queens[1–3]. The ontogenetic specialization of castes in ants resembles the ontogenetic differentiation of cell lineages in metazoans, with the term 'superorganism' used to highlight the fundamental differences between most ant species and other animal societies (where individuals remain reproductively and behaviorally totipotent)[4,5]. The ancestral life cycle of ants, present in species that have a single queen per colony (monogyne), starts with a young queen that has flown away from her maternal nest, mated in a swarm, and founded her new colony alone[1,6]. The queen raises a first cohort of daughter-workers that forage and help raise sister-workers. As the incipient colony grows, the new workers produced are physically, behaviorally, and physiologically different from the first cohort of workers[1,7]. These individual-level phenotypic differences lead to colony-level phenotypic changes, such as colonies switching from producing workers to raising young queens and males.

Some ant species harbor two types of colonies, with either one or multiple reproducing queens per colony[1,8,9]. In at least five independent ant lineages, this intraspecific variation in colony social structure (one or multiple queens per colony) is controlled by large genomic regions of low recombination, called supergenes[10,11]. The best-studied cases are the *Solenopsis* and *Formica* genera, which harbor independently evolved 'social supergenes' (supergenes that underlie queen number and other traits associated with ant social organization)[12–14]. In both systems, all individuals living in mature single-queen colonies exclusively carry the ancestral, non-inverted supergene haplotype (*B* and *M*, respectively). In contrast, some or all of the ants living in mature multi-queen colonies carry one or two copies of the derived, inverted haplotype (*b* and *P*, respectively)[10–12,15]. In both clades, mature monogyne and polygyne colonies differ in many aspects, including colony size, lifespan, and sex allocation[8,9,16], as well as in individual body size and behavior[17–21].

The way by which the derived haplotype of the supergene affects queen and worker behavior to promote polygyny remains little understood. In fire ants, *S. invicta*, workers that lack the haplotype associated with polygyny kill supernumerary queens, while workers carrying this haplotype accept extra queens if they also carry this haplotype[22,23]. Moreover, it has been suggested that monogyne queens mating with polygyne males can spread the polygyne social organization[24]. In Alpine silver ants, *F. selysi*, most young queens disperse on the wing, join mating swarms[25], and are rejected by unrelated colonies[26,27]. Queens originating from polygyne colonies, which carry the derived supergene haplotype, occasionally mate with males of monogyne origin, but the majority mate assortatively, with males of polygyne origin[25,28].

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