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Uncoupling Flight and Reproduction in Ants: Evolution of Ergatoid Queens in Two Lineages of *Megalomyrmex* (Hymenoptera: Formicidae)

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Abstract

*Megalomyrmex* Forel (Myrmicinae: Solenopsidini) consists of 44 species with diverse life history strategies. Most species are predatory and may also tend honeydew-producing insects. A morphologically derived group of species are social parasites that consume the brood and fungus garden within fungus-growing ant nests. The reproductive strategies of *Megalomyrmex* queens are somewhat aligned with these life-style patterns. Predatory species in the *leoninus* species group are large in body size and have ergatoid (i.e., permanently wingless) queens whereas the social parasitic species are smaller and typically have winged queens. We examined two ergatoid phenotypes of *Megalomyrmex foreli* Emery and *Megalomyrmex wallacei* Mann and compared them to winged species, one a social lestobiotic or “thief ant” parasite (*Megalomyrmex mondabora* Brandão) and the other a predator (*Megalomyrmex modestus* Emery). *Megalomyrmex foreli* colonies have a single queen with an enlarged gaster that is morphologically distinct from workers. *Megalomyrmex wallacei* colonies have several queens that are similar in body size to workers. Queens in both species showed a simplification of the thorax, but there was a dramatic difference in the number of ovarioles. *Megalomyrmex foreli* had 60–80 ovarioles compared to eight in *M. wallacei* and *M. mondabora* and *M. modestus* had 22–28. Along with flight loss in queens, there is an obligate shift to dependent colony founding (also called budding or fission) consequently influencing dispersal patterns. These constraints in life history traits may help explain the variation in nesting biology among *Megalomyrmex* species.

Key words: ovary, ergatoid, *Megalomyrmex foreli*, *Megalomyrmex wallacei*, dispersal

The evolution of strongly dimorphic queens and workers (winged vs. wingless) is a fundamental characteristic of ants. Flying queens follow the basic design of aculeate hymenopterans although the thorax in many species houses hyperdeveloped wing muscles that serve as a metabolic reserve to feed the first generation of workers during independent colony founding. Moreover, a bigger abdomen (gaster) allows enhanced fecundity (more ovarioles enable many eggs to develop simultaneously). This combination of thorax and abdomen modifications contrasts sharply with the phenotypes of workers (Peeters and Molet 2010). The lack of wings and wing muscles causes an extreme reduction in thorax volume, and fusion of sclerites in most species. The diminished thorax of workers is coupled with an abdomen that is generally much smaller than queens’, with fewer ovarioles and an almost universal loss of spermathecae.

Compared to various solitary wasps that evolved winglessness, ant workers show extreme simplification in the thorax. The same is also true for the permanently wingless (“ergatoid”) queen caste, occurring in at least 55 ant genera (Peeters 2012). Their thorax resembles that of workers, although the abdomen is often bigger with more ovarioles and a spermatheca. Ergatoid queens have evolved convergently across diverse ant lineages therefore their morphology is highly heterogeneous. Similarly, the life history characteristics of their colonies vary immensely, except that dependent colony founding (colony fission or budding) appears to be the rule (Cronin et al. 2013).

The *Megalomyrmex* genus consists of 44 described species (Boudinot et al. 2013), most of which are ground-living ants inhabiting subtropical forests in Central and South America. Species have been separated into four species groups on the basis of morphology and behavior (Brandão 1990). In a recent revision of the Central American species, new species were described and worker morphology indicates that *leoninus* and *modestus* groups, as well as the
Materials and Methods

Fieldwork was done in Costa Rica, Braulio Carrillo National Park from 21 March 2011 to 30 March 2011. Three colonies of M. foreli and three colonies of M. mondabora (thief ant parasite of Cyphomyrmex cornutus Kempf) were collected from El Ceibo station (10°20’N, 084°05’W, 450–550 m elevation, Waterline trail). Twelve colonies of M. wallacei and four colonies of M. modestus were collected from La Selva Biological Station (10°24’59”N, 084°01’12”W, 50 m elevation). Worker numbers were either counted or approximated. In M. foreli, adults and brood were counted and egg-laying was monitored. Ovaries and spermatheca were dissected in queens and workers of all species. Except for M. mondabora, queen and worker specimens were examined by SEM. Species determination was conducted by R.M.M.A. (Longino 2010, Boudinot et al. 2013) and vouchers are at The Ohio State University, Museum of Biological Diversity.

Results

Three M. foreli colonies were excavated from within a large wet log (RMMA110324-03: workers = 226; brood, excluding eggs = 130; zero males; one ergatoid queen), at the base of a Pouroumana tree (RMMA110323-01: workers = 455; brood, excluding eggs = 219; zero males; one ergatoid queen), and at the base of a small plant (RMMA110323-05: workers = 2,231; brood, excluding eggs = 134; 64 males; one ergatoid queen). Queens were strikingly distinct from workers due to their big gasters (Fig. 1). The M. wallacei ergatoid queens were much less conspicuous with a gaster only slightly larger (Fig. 3B). Several queens were inseminated in each colony, but only some had active ovaries with yolky oocytes. Other mated queens had few yolky oocytes and lacked dark “yellow bodies.” For comparison, M. modestus queens had 22–28 ovarioles (Fig. 3C), and queens of M. mondabora had eight ovarioles (n = 3) (Fig. 3D). Workers in all four species had two ovarioles (n = 3).
Megalomyrmex foreli builds shallow but large permanent nests in the soil that can be observed year after year (R. M. Adams, personal observation). The ants aggressively guard extrafloral nectaries of Cassia sp. and Inga spp. (Leguminosae) (Jones et al. 1991), riodinid butterflies (Lepidoptera) (DeVries et al. 1992), and build soil structures that cover membracids (Longino 2010, Boudinot et al. 2013). Few foragers can be seen during the day but more can be drawn out with baits (R. M. M. Adams, personal observation). They are apparently more active at night (Jones et al. 1991) therefore estimating colony size is difficult unless the entire colony is excavated. The three colonies that we dug took four researchers, large trash bags, and careful attention to collect the majority of workers and find the queen. Colonies are widely spaced suggesting that foraging territories are established and perhaps their honeydew producing associates help drive this (R. M. M. Adams, personal observation).

In contrast, M. wallacei colonies were found in dense populations within deep leaf litter. The population is stable and colonies have been retrieved from the same trails 8 years apart (2003, 2005, 2011) (R. M. M. Adams, personal observation). The nests however are temporary structures found in the litter between dead leaves and at the base of the leaves of short palms (Boudinot et al. 2013). Colonies are small and readily emigrate following the slightest disturbance. High polygyny means a high probability that at least one mated queen will be present following accidental fragmentation, thus leading to autonomous colonies (Cronin et al. 2013).

Unlike flightless insects that live and reproduce alone, flightless reproductives in most ant species have lost the ability to find new colonies independently, and they completely rely on nestmate workers during dependent colony founding (DCF) (Peeters 2012). The multiple occurrences of ergatoid queens in Megalomyrmex reveal that DCF (fission or budding) has replaced independent foundation (ICF) repeatedly. However little data on colony founding behavior are available in Megalomyrmex. As the two congeneric species studied here differ in queen number, it is evidence against the persistent belief in the literature that DCF species are always polygynous.

The mosaic nature of ergatoid queens in Megalomyrmex, (i.e., exhibiting traits specific to both workers and winged queens), suggests that morphological modules became recombined during development (Molet et al. 2012). Ergatoid queens are novel phenotypes that evolved by uncoupling the growth of the thorax and abdomen. Because they evolved convergently across the ants, the phenotypes of ergatoid queens are very heterogeneous. Molet et al. (2009) recognized two categories of ergatoid queens: (1) “single-purpose”, few are produced in each colony, they are much bigger than workers and function exclusively for reproduction and (2) “multi-purpose”, many are produced in each colony and they are similar in size to workers, only one or few reproduce while others remain virgin and function as labourers. This corresponds to the phenotypes of M. foreli and M. wallacei queens, respectively, which appear to be alternative solutions to the replacement of winged queens.

Within the modestus group, both ergatoid and winged queens have been recorded in separate populations of Megalomyrmex goeldii (Brandão 2003). Similarly, M. wallacei has winged queens in Brazil (Brandão 2003) but not in Costa Rica (this study). Molecular and/or morphological studies would help determine if Brazilian populations represent a different species or an intraspecific polymorphism. Both winged and ergatoid queens have also been described in the facultative thief ant social parasite, M. silvestrii (Boudinot et al. 2013). Although only one ergatoid was examined, it is slightly larger than workers and has a less voluminous thorax compared to the winged queens. The raiding behavior (Adams et al. 2015), nesting...
habits (Boudinot et al. 2013), and morphology suggest that the *M. silvestrii* ergatoids may be the “multi-purpose” type (Molet et al. 2009). Studies of *Megalomyrmex* species that include colony demography, ovarian development, and population genetics will advance our understanding of the evolutionary implications of queen winglessness at the ecological timescale and shed light on the plasticity of independent and dependent colony foundation. Comparative studies conducted on the variety of *Megalomyrmex* species with obligate (e.g., *M. foreli*, *M. leoninus*, and *M. staudingeri*) and facultative ergatoid queens (e.g., *M. wallacei*, *M. silvestrii*, and *M. goeldii*) will elucidate factors that influence the evolution of queen winglessness. Furthermore, future work can draw on the developmental pathways identified in worker winglessness and link these to genomic changes within the obligate ergatoid species. Finally, phylogenetic studies of *Megalomyrmex* and other genera in the tribe Solenopsidini (Ward et al. 2015) will reveal the number of independent evolutionary events of ergatoid queens (e.g., *Monomorium* and *Megalomyrmex*) for broader comparative analyses.

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Fig. 3. Developed ovaries of ergatoid queens in (A) *M. foreli* and (B) *M. wallacei* compared to winged queens (C) *M. modestus* and (D) *M. mondabora*. The large difference in ovariole numbers indicates different rates of egg-laying. Scale bar = 1 mm.
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