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SPECIAL FEATURE

The Ecology and Evolution of Hybridization in Ants¹

Interspecific mating is generally considered a poor route to enhancing fitness. Not only must gametes surmount numerous potential pre- and postzygotic mating barriers, but any resulting offspring must also successfully compete for space, food, and water. Further, all of this goes for naught if the hybrid offspring are themselves sterile or cannot find suitable mates. Nevertheless, all manner of species appear to indulge in what seems likely to be a futile endeavor. Is it just that the world is difficult and complex, and thus mistakes are made?

Recent work across several species of ants strongly argues for method to this madness. Ants are haplodiploid hymenopterans. Females result from fertilized eggs, and males arise from unfertilized ones, and this creates some unique twists in the costs and benefits of hybridization. Therefore, I begin this Special Feature with a review of the nuances of ants and haplodiploidy, along with a glossary of terms for the uninitiated. I close my introduction with a brief overview of how observing ants connects many levels of investigation from behavior through ecology and evolution. The Special Feature begins in earnest with Umphrey presenting the concept of sperm parasitism. Hymenopteran females can use the sperm of nonconspecific males to create hybrid workers. Umphrey models the conditions under which such behavior can increase the fitness of the parasitizing female, in spite of possibly severe costs in reproductive productivity. Indeed, sperm parasitism may drive the evolution of several aspects of the reproductive biology of sympatric species in *Acanthomyops* and may be relatively common in nature.

The two papers by Helms Cahan et al. and Anderson et al. describe a very different situation in which pairs of lineages of *Pogonomymex* seed-harvesting ants mutually depend upon each other for survival. Females must mate with males of their own lineage to produce future reproductive females. However, they must also mate with males from another lineage in order to produce hybrid workers. Helms Cahan et al. show that one pair of dependent lineages is parapatric with one of the putative parental species, *P. rugosus*. Most surprisingly, the transition from populations of pure *P. rugosus* to pure dependent lineages can occur on a scale of meters, and across no obvious environmental gradient. Anderson et al. confirm the findings of earlier studies that dependent lineages appear to be reproductively isolated from each other and the parental species. However, their data add a new twist in that dependent lineages may not have arisen through hybridization. Instead, Anderson et al.'s phylogeny supports a within-species origin, followed by genetic introgression. Linksvayer et al. then take up the problem of how such dependent lineages could initially evolve. Their intriguing hypothesis is that caste determination may involve interactions between nuclear and mitochondrial genes. This possibility suggests several experiments that could rework the existing paradigms of caste ontogeny.

The papers by Volny et al. and Clark et al. show that dependent lineages in *Pogonomyrmex* have developmental costs. Queens do not select sperm and thus produce eggs fertilized by males from their own lineage at the wrong time (i.e., when the colony should be making only workers). Volny et al. suggest that queens may minimize this problem by preferentially mating with other lineage males, and that cuticular differences across males are available for mate choice. Given these complications in mating and the developmental costs, how do dependent lineages successfully compete with the parental species? Umphrey suggests that hybrid workers can provide competitive advantages. However, the last paper by Julian and Helms Cahan fails to find any significant ecological advantage for the dependent lineages. Indeed for the seemingly important trait of being able to monopolize a food resource, hybrid workers are at a competitive disadvantage. Therefore, the fascinating question of how the dependent lineages maintain viable populations remains unanswered.

¹ Reprints of this 74-page Special Feature are available for \$11.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, D.C. 20006 (esaHQ@esa.org).

Across all the papers, a significant message comes through: Hybridization may be far more common in ants than previously thought. It may be often missed as in the case of *Acanthomyops*, because hybrid offspring are misidentified as alternative reproductive morphs. Or, it may be unnoticed in species such as *Pogonomyrmex*, because the hybrid workers are not morphologically distinct. If this is indeed true, then the papers here are literally the tip of the iceberg. The mating behavior, ecological advantages, and evolutionary processes that favor hybridization in ants will remain fertile fields of inquiry. In this way, ants may open up a wider consideration of the adaptiveness of interspecific mating throughout nature.

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Key words: Acanthomyops; aggression; ants; caste determination; competition; hybridization; mate choice; phylogeny; Pogonomyrmex; sperm parasitism.

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