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## INTERSPECIFIC HYBRIDIZATION IN ANTS: AT THE INTERSECTION OF ECOLOGY, EVOLUTION, AND BEHAVIOR

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**Abstract.** Ants are social and are haplodiploid. This combination may allow the evolution of a variety of unusual genetic pathways to achieve reproductive success. These include hybridizing across species, differential use of sperm to create a hybrid worker population, and reproductively isolated gene pools that depend on each other for their survival. Although there are demonstrable costs for colony development and reproduction, these phenomena may nevertheless be relatively common in nature. The specific ecological advantages that favor the evolution of these reproductive modes remain to be discovered.

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

### INTRODUCTION

The evolution of new species is generally believed to be most often a many-generational process where natural selection and demographic processes like drift and bottlenecks change gene frequencies. When sufficient genetic differences arise between populations, reproductive isolation follows and two “species” now exist instead of one. Speciation, however, can also result from an evolutionary shortcut such as hybridization across species. This appears to be a relatively common occurrence in plants, with estimates of 6–22% of species in a biosystematic flora resulting from hybridization (Rieseberg 1997).

There are several requirements for hybridization to produce viable species (reviewed in Rieseberg 1997). First, haploid genomes from the two parental species must be able to interact in ways to produce developmentally viable individuals. Second, these individuals must be capable of producing viable gametes of their own. Third, hybrid individuals must be both reproductively isolated from the parental species, and yet able to find appropriate breeding partners. Nevertheless, these three conditions merely create the potential for a viable species. An evolutionarily stable population is only possible if hybrid individuals are also competitively successful in their environment. This usually means either outcompeting one or both of their parental species in their habitat, or being able to survive where the parents cannot.

In contrast with plants, the above barriers within animals have been thought to be much more significant, thus making speciation by hybridization relatively much rarer. Recently, however, a number of interesting cases

have been described in ants that may change this perception. This special feature brings together a number of leading individuals and research groups to explore the ramifications of the hybridization phenomena. The outcome illustrates the importance of connecting a variety of approaches: understanding the entirety of the evolutionary processes will require integrating genetics, behavior and ecology.

It is useful to first briefly review haplodiploid sex determination in Hymenoptera such as ants (see Table 1 for a glossary of terms). Females are produced from fertilized eggs and males result from unfertilized eggs (Fig. 1). A fertilized egg can have one of two developmental fates: becoming a reproductive female or a sterile worker. In most ant species, these different developmental tracks follow from different larval experiences in feeding regimes, seasonal effects, or pulses of hormones. This is known as environmental caste determination, ECD. As an example, in many species, well-fed females develop a reproductive morphology (e.g., as gynes, which are large, winged, and with considerable energy reserves for initiating colonies on their own). Less well-fed females develop with a worker morphology (e.g., smaller with stunted or nonfunctional ovaries, no wings, and no ability to initiate a new colony).

One important consequence of haplodiploidy is that several potential costs of interspecific mating may be minimized or absent. For example, hybrid offspring may be reproductively sterile. In a social insect colony, however, workers do not normally reproduce (Bourke and Franks 1995) and thus a “loss” of this capability in workers would have a minimal fitness cost (Umphrey 2006). It is true that such colonies would also lose the capacity to produce fertile gynes, but they could still produce non-hybrid and viable sons from the queen’s haploid eggs. Therefore, behavioral mating barriers in ants can be considered at least somewhat forgiving in

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TABLE 1. A summary of terms as used in this special feature.

| Term                              | Definition  |
|-----------------------------------|---|
| Caste                             | A fixed behavioral or morphological role for an individual ant in a colony.   |
| Gyne                              | A diploid female capable of reproducing. Gynes disperse from their natal colonies, mate, and begin new colonies. A successful gyne will become the queen of the colony.   |
| Worker                            | Diploid and nominally female. Workers do not mate (and thus cannot make female eggs) and differ morphologically from gynes in being smaller and lacking wings. Workers do all the colony tasks of foraging, defense, and brood care. Colonies without workers cannot survive to reproductive maturity.  |
| Male                              | Haploid individuals arising from unfertilized eggs. Males perform no significant colony tasks, and their only real function is to mate with gynes.  |
| Caste determination               | Diploid eggs potentially can become either gynes or workers. Their developmental future is determined either by environmental determination (ECD) or genetic determination (GCD).   |
| Environmental determination (ECD) | Fate can be determined by experiences such as the amount or type of food a developing female larva receives. Larval genotype does not significantly predict caste. The vast majority of ant species appear to have ECD.   |
| Genetic determination (GCD)       | Fate is determined by the genotype of a female larva. The genotype itself may preclude a particular developmental pathway, or workers may differentially raise certain genotypes as workers or gynes.   |
| Dependent lineages (DLs)          | In some <i>Pogonomyrmex</i> populations, gynes must mate with males from two distinct genetic lineages. Diploid eggs fertilized by sperm from a male of the same lineage as the female develop into gynes. Eggs fertilized by sperm from a male of the other lineage develop as workers. Although the gene pools of the lineages do not appear to mix, each lineage is dependent on the other lineage's sperm to produce workers. Thus, neither lineage can maintain a viable population in the absence of the other lineage. |
| Intralineage                      | Diploid eggs that arise from being fertilized by sperm from the same DL. Such eggs become gynes through GCD.  |
| Interlineage                      | Diploid eggs that arise from being fertilized by sperm from the other DL. Such eggs become workers through GCD.   |

that a female that mates with a male from another species has not necessarily sacrificed all chances of future reproductive success.

Furthermore, the loss in fitness from not producing gynes can be offset in one of two ways (Julian and Helms Cahan 2006, Umphrey 2006). First, having hybrid workers may allow colonies to survive and prosper in microhabitats that are inimical to pure

species' worker phenotypes, or make colonies competitively superior to the parental species. An ability and willingness to hybridize is particularly relevant in times of environmental change. As new ecological circumstances appear, hybrid colonies may be best suited to exploit them. Second, if population densities are low, females may not always be able to encounter conspecific males. Hence, a willingness to hybridize may be a "best

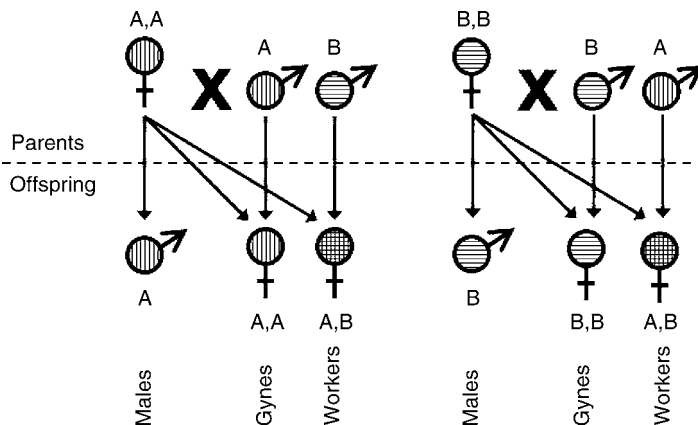


FIG. 1. Sex and caste determination in a haplodiploid species with genetic caste determination. Two dependent lineages (A and B) are shown. For a fully functional colony, a female must mate with males of both her own lineage and the other lineage. All males come from unfertilized eggs, are haploid, and are of their mother's lineage. Diploid females that result from sperm of the same lineage develop as reproductive gynes. Females arising from sperm of the other lineage develop into sterile workers. Thus, the workers across all colonies from both lineages are genotypically similar, but the males and gynes reflect the genetics of their colony's queen.

of a bad situation” strategy to gain some reproductive success rather than none. These potential positive aspects of interspecific mating demonstrate the importance of mate choice behavior and the competitive ecology of ant populations. Hybrid colonies may not simply reflect nonadaptive mating mistakes.

Umphrey (2006) further considers whether the advantages of interspecific mating are asymmetric across species. Interestingly, having hybrid workers may allow one species to expand its ecological niche, but provide no such benefit to the other (e.g., in species of the subgenus *Acanthomyops*). Umphrey defines such a situation as sperm parasitism by one species of another, and this may lead to a coevolutionary race between a sperm host and its parasite. In *Acanthomyops*, the unidirectional sperm parasitism may selectively favor delaying mating flights until later in the season in the host species and flying at temperatures that are unsuitable for the parasitic species. In response the parasite species may evolutionarily chase the host through time and temperature. Sperm parasitism, such as in *Acanthomyops*, is not a speciation event because there is still gene flow with the parental species. In the hybrid *Acanthomyops* colonies, only viable males are produced and they must mate with females produced by non-hybrid colonies. It is possible, however, that the ecology of parasitism may set the evolutionary stage for eventual speciation. Indeed, another variation in hybridization in the American southwest between two harvester ant species (*Pogonomyrmex barbatus* and *P. rugosus*) does appear to have created new, reproductively isolated species.

Many *Pogonomyrmex* colonies are found with workers that are morphologically similar, but genetically quite distinct from either *P. barbatus* or *P. rugosus*. The presence of alleles in the workers specific to both species suggests interspecific hybridization. Complicating this diagnosis, however, is that alleles strictly segregate across queens in these colonies (Helms Cahan et al. 2002, Julian et al. 2002, Volny and Gordon 2002, Helms Cahan and Keller 2003). Thus, a single “hybrid” population is actually composed of two interdependent lineages. All gynes mate with multiple males, but all the mates cannot come from just one lineage. Interlineage sperm is needed to produce all the workers, which results in all hybrid colonies have genetically and morphologically similar workers. Only eggs fertilized by intralinear sperm, however, appear to be raised as gynes. Thus, caste determination in this system is genetic: GCD rather than ECD (Fig. 1). The absence of backcrosses by the dependent lineages with either *P. barbatus* or *P. rugosus* argues that they are reproductively isolated species.

A case that appears intermediate between the *Acanthomyops* and *Pogonomyrmex* situations occurs in *Solenopsis* fire ants. Queens of a parasitizing species (*S. xyloni*) mate with males of their own species and males of a host species (*S. geminata*). GCD is present as all the

workers appear to result from the interspecific mating and all the gynes from the intraspecific mating (Helms Cahan and Vinson 2003). Differing from *Pogonomyrmex* situation, however, the *Solenopsis* hybrid colonies do not appear to be reproductively isolated from the *S. xyloni* parental species.

A strong correlation between caste and genotype has been rarely found in social Hymenoptera, although Linksvayer et al. (2006) and Anderson et al. (2006) argue it may be more common than previously believed. Furthermore, the biology of the *Pogonomyrmex* dependent lineages raises a number of very interesting questions in evolutionary biology and ecology. The lineages are dependent on each other, but their gene pools are kept separate by GCD (Helms Cahan and Keller 2003, Anderson et al. 2006). Thus, pairs of dependent lineages could be considered one species that is composed of two distinct gene pools (and three sexes, Parker 2004). Additionally, I would argue that the phenomenon of hybridization within ants raises at least six questions of broad interest within evolutionary, population, and behavioral ecology. These are:

1) Evolutionary stability of hybrid “species.” In the *Pogonomyrmex* system, each set of dependent lineages (DLs) is arguably a unique and reproductively isolated species. Anderson et al. (2006) reject the previous view that the lineages arose through several separate *P. rugosus* × *P. barbatus* crosses (Helms Cahan and Keller 2003) and instead argue that GCD is a relatively old phenomenon that initially arose within *P. barbatus* and then introgressed into *P. rugosus*. Linksvayer et al. (2006) raise the interesting speculation that if GCD initially arises within a species, the usual evolutionary progression may be to a workerless, parasitic species (i.e., an inquiline). Thus, introgression/hybridization events may be required to evolutionarily stabilize an alternative state with two mutually dependent, but genetically separate, lineages.

2) Developmental and ecological costs of GCD. DL colonies appear to suffer a substantial cost in that intralinear eggs are produced early in the colony founding cycle. These eggs apparently do not readily develop into workers. They either die, are eliminated (Helms Cahan et al. 2005, Volny et al. 2006), or at best mature as nonviable gynes (Clark et al. 2006). There is no evidence that females selectively choose sperm in fertilizing eggs. This apparent wasting of resources in same lineage eggs would seem to reduce ergonomic efficiency and place the immature hybrid colony at a severe competitive disadvantage relative to other colonies where all female eggs can become workers. Furthermore, mating is complicated for DL females because they must mate with males of both lineages in order to rear reproductives of both sexes. This, however, may not be that significant of a cost for two reasons. First, Volny et al. (2006) demonstrate that DL males have different cuticular chemical signatures, which at least provides a template for females to choose their

mating partners. This would also give females the ability to preferentially mate with males from the other lineage and therefore reduce the proportion of intralinear eggs in the total number of eggs laid. Second, DL females that mate only with males from the other lineage may actually benefit in a fitness tradeoff. Mature colonies would produce only male reproductives, but growing colonies would not suffer the ergonomic costs (Umphrey 2006).

3) Developmental and ecological benefits of GCD. The cost of producing intralinear eggs early in colony development could be offset if the hybrid workers develop more rapidly or require less investment. There is no current evidence for such advantages in *Pogonomyrmex*. Moreover, it is difficult to imagine that hybrid workers could be physiologically so much less costly to their mother that it would offset perhaps a 50% reduction in production rate of workers. Instead the more intuitively logical assumption is that hybrids have a competitive advantage in some environments because particularly advantageous heterozygote combinations are locked in place with separate gene pools (Umphrey 2006). However, Julian and Helms Cahan (2006) find that transition zones are extremely narrow between populations of pure *P. rugosus* and pure DLs (also with *P. rugosus* external morphology). There is no noticeable microgeographic habitat change in the transition zone and in one important ecological measure (the ability to dominant food piles); *P. rugosus* colonies strongly outcompete DL colonies. Therefore, to date, we have no robust explanation for how DL populations continue to exist and competitively exclude pure species colonies of *P. rugosus* and *P. barbatus*.

4) Levels of selection. The DLs must coexist in the same place to provide mates for each other. Mature colonies of seed harvesters, however, are highly competitive with each other and effectively eliminate small, founding colonies within their territories (Gordon 1999). Intense intraspecific competition normally has no ramification on mating success: successful colonies can always interbreed with other successful colonies. With two DLs, however, the ecology of competition becomes critical. If one of the two DLs is differentially successful in establishing and maintaining colonies, then it can eliminate its partner lineage, and shortly thereafter, itself as well. Furthermore, DL populations are often sympatric or parapatric to the parental species. Hence, both lineages must simultaneously have competitive advantages (as given in #3 above) over their parental species. Interestingly, Helms Cahan et al. (2006) find a pattern suggestive that one of the two *rugosus*-morph DLs is excluded by *P. rugosus*, proper. Therefore, the distribution and population biology of DL hybrids may very well reflect a complex competitive balance both across the dependent lineages themselves and simultaneously with one or both parental species. We do not know how selection at a colony level within a lineage to effectively compete against other non-lineage colonies is

resolved with selection at the individual female level to be able to find suitable mates.

5) Coevolution of gene pools. A social insect's phenotype is not only a function of its genotype, but also indirectly the genotypes of those who rear it (Linksvayer and Wade 2005). Parker (2004) noted that the *Pogonomyrmex* system is a unique example where three sexes are required for sexual reproduction. A female must mate with two different male "sexes" in order to be able to produce a colony and later to produce female offspring (Fig. 1). This complicates the coevolution of gene expression with environment in larval development because interacting genes may come from distinct lineages. We have no theoretical treatment as to how two such dependent, but isolated gene pools would further evolve through time. The best analogy would be to a pair of species locked in an obligately symbiotic relationship. Do hybrids have an intrinsic advantage because two gene pools would have higher total allelic diversity than one and could lock in heterozygous combinations at key gene loci (Umphrey 2006)? Do hybrids have an intrinsic disadvantage because a beneficial mutation in one lineage cannot be transferred into the other? Clearly, indirect genetic effects where the social environment created by one set genes affects the phenotypic expression and fitness of another genotype (e.g., Wolf et al. 1998, Linksvayer and Wade 2005) are likely to be very strong within DL hybrids.

6) Genetic chimaeras and kin nepotism. If one views a DL colony as a single superorganism, the reproductive tissues (females and males) are genetically different from the somatic tissues (the workers). Because in mature ant colonies workers are primarily responsible for brood care, this is a definitive example of reverse nepotism. Workers are favoring half sibs over full sibs in terms of creating sexualized females. Linksvayer et al. (2006) suggest that workers could gain fitness through laying unfertilized eggs and producing their own sons. There is little evidence, however, that males in harvester ant colonies are worker-derived (Helms Cahan et al. 2002). Thus questions can arise as to what extent maternally imprinted genes and intergenomic conflict may be responsible for workers apparently acting in opposition to their best genetic interests (Haig 2000, Anderson et al. 2006).

In summary, this special feature provides a great deal of new information on hybridization in ants. Nevertheless, the questions these papers raise are perhaps even more interesting than the answers they provide. Ants have historically been a fertile taxonomic group for a wide variety of ecological, behavioral, and evolutionary questions. I hope these papers will convince that ants are again a wonderful model taxonomic group for questions of the ecology of speciation through hybridization.

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## LITERATURE CITED

- Anderson, K. E., J. Gadau, B. M. Mott, R. A. Johnson, A. Altamirano, C. Strehl, and J. H. Fewell. 2006. Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology* **87**:2171–2184.
- Bourke, A. F. G., and N. R. Franks. 1995. *Social evolution in ants*. Princeton University Press, Princeton, New Jersey, USA.
- Clark, R. M., K. E. Anderson, J. Gadau, and J. H. Fewell. 2006. Behavioral regulation of genetic caste determination in a *Pogonomyrmex* population with dependent lineages. *Ecology* **87**:2201–2206.
- Gordon, D. M. 1999. *Ants at work*. Free Press, New York, New York, USA.
- Haig, D. 2000. The kinship theory of genomic imprinting. *Annual Review of Ecology and Systematics* **31**:9–32.
- Helms Cahan, S., G. E. Julian, S. W. Rissing, T. Schwander, J. D. Parker, and L. Keller. 2005. Loss of phenotypic plasticity generates genotype-caste association in harvester ants. *Current Biology* **14**:2277–2282.
- Helms Cahan, S., G. E. Julian, T. Schwander, and L. Keller. 2006. Reproductive isolation between *Pogonomyrmex rugosus* and two lineages with genetic caste determination. *Ecology* **87**:2160–2170.
- Helms Cahan, S., and L. Keller. 2003. Complex hybrid origin of genetic caste determination in harvester ants. *Nature* **424**:306–309.
- Helms Cahan, S., J. D. Parker, S. W. Rissing, R. A. Johnson, T. S. Polony, M. D. Weiser, and D. R. Smith. 2002. Extreme genetic differences between queens and workers in hybridizing *Pogonomyrmex* harvester ants. *Proceedings of the Royal Society Biological Sciences Series B* **269**:1871–1877.
- Helms Cahan, S., and S. B. Vinson. 2003. Reproductive division of labor between hybrid and nonhybrid offspring in a fire ant hybrid zone. *Evolution* **57**:1562–1570.
- Julian, G. E., J. H. Fewell, J. Gadau, R. A. Johnson, and D. Larrabee. 2002. Genetic determination of the queen caste in an ant hybrid zone. *Proceedings of the National Academy of Sciences (USA)* **99**:8157–8160.
- Julian, G. E., and S. Helms Cahan. 2006. Behavioral differences between *Pogonomyrmex rugosus* and dependent lineage (H1/H2) harvester ants. *Ecology* **87**:2207–2214.
- Linksvayer, T. A., and M. J. Wade. 2005. The evolutionary origin and elaboration of sociality in the aculeate hymenoptera: Maternal effects, sib-social effects, and heterochrony. *Quarterly Review of Biology* **80**:317–336.
- Linksvayer, T. A., M. J. Wade, and D. M. Gordon. 2006. Genetic caste determination in harvester ants: possible origin and maintenance by cyto-nuclear epistasis. *Ecology* **87**:2185–2193.
- Parker, J. D. 2004. A major evolutionary transition to more than two sexes? *Trends in Ecology and Evolution* **19**:83–86.
- Rieseberg, L. H. 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics* **28**:359–389.
- Umphrey, G. J. 2006. Sperm parasitism in ants: selection for interspecific mating and hybridization. *Ecology* **87**:2148–2159.
- Volny, V. P., and D. M. Gordon. 2002. Genetic basis for queen-worker dimorphism in a social insect. *Proceedings of the National Academy of Sciences (USA)* **99**:6108–6111.
- Volny, V. P., M. J. Greene, and D. M. Gordon. 2006. Brood production and lineage discrimination in the red harvester ant (*Pogonomyrmex barbatus*). *Ecology* **87**:2194–2200.
- Wolf, J. B., E. D. Brodie, III, J. M. Cheverud, A. J. Moore, and M. J. Wade. 1998. Evolutionary consequences of indirect genetic effects. *Trends in Ecology and Evolution* **13**:64–69.