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Behavioral Genetics: A Gene for Supersociality

Dispatch

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In the fire ant, the number of queens per colony is determined by the workers' Gp-9 genotype. This gene has been found to encode an odorant binding protein, which probably influences workers' abilities to recognize queens and regulate their numbers. Remarkably, the same gene seems to control social organization in three other closely related species.

Behavioral genetics is an emerging field of biology. Many biologists have been reluctant to admit that behavior is under strong genetic control, because of the significant implications this may have on human social policy [1]. There is growing evidence, however, that most behaviors, be it the level of aggressiveness in mice, the foraging propensities of bees or the cognitive abilities of humans, are at least partially influenced by genes. Generally, many genes are involved and there is a strong interaction between genes and environment. But this need not always be so, as demonstrated by a new study [2] showing that a single gene determines a complex social behavior in the fire ant *Solenopsis invicta*, as well as in several other closely related species.

The fire ant is a serious pest that has been inadvertently imported from South America to the southeastern United States and more recently to California and Australia. This species displays a fundamental social polymorphism that is under simple genetic control [3]. In the monogyne form, colonies invariably contain a single queen, whereas in the polygyne form colonies contain anywhere between 2 and 200 queens. This fundamental difference in social organization is completely associated with variation at the gene *Gp-9*. In the monogyne form, the queen and all workers invariably have the *Gp-9*^{BB} genotype; by contrast, polygyne colonies always contain both *Gp-9*^{BB} and *Gp-9*^{Bb} workers.

The queens of polygyne fire ant colonies are all heterozygotes. The lack of *Gp-9*^{BB} queens in polygyne colonies has been shown to be caused by the selfish *Gp-9*^{b} allele (or a closely linked locus) [4]. This allele induces workers carrying it selectively to kill all queens without a copy (*Gp-9*^{BB} queens) immediately after the queens initiate reproduction. Both *Gp-9*^{bb} queens and *Gp-9*^{bb} workers are absent from polygyne colonies because *Gp-9*^{b} is also a lethal recessive allele, causing the death of homozygous females soon after they eclose from the pupae stage [5]. Hence, the strong directional selection against *Gp-9*^{BB} queens is exactly compensated by inviability of *Gp-9*^{bb} queens, leading to a stable polymorphism of the two alleles in the polygyne form.

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Krieger and Ross [2] have now cloned and sequenced *Gp-9*. GenBank searches showed that the *Gp-9* product most closely resembles moth odorant binding proteins. Although the absolute level of amino acid identity is low (26%), the conservation of six cysteine sites in Gp-9 and all known odorant binding proteins strongly suggests that Gp-9 is a novel odorant binding protein. These proteins are thought to be molecular components involved in chemical recognition, strongly supporting the view that Gp-9 is directly involved in the existence of the two social forms. Previous studies showed that *Gp-9*^{Bb} queens have a distinctive odor compared to *Gp-9*^{BB} queens, allowing *Gp-9*^{Bb} workers to recognize and selectively eliminate *Gp-9*^{BB} queens. Given the hypothesized function of odorant binding proteins, it is very likely that *Gp-9*^{BB} and *Gp-9*^{Bb} workers differ in how they perceive the odor of *Gp-9*^{BB} and *Gp-9*^{Bb} queens, hence explaining the different response of workers toward monogyne and polygyne queens.

It remains to be determined why the presence of *Gp-9*^{Bb} workers in polygyne colonies influences the number of queens accepted. Previous studies showed that the number of queens is probably influenced by the level of a specific 'queen pheromone' in the colony [6]. This pheromone is produced by queens when they initiate reproduction, and the colony level is presumably proportional to the number of reproductive queens [7]. In monogyne colonies, workers apparently start destroying queens when the pheromonal level in the colony is higher than the amount produced by a single queen. *Gp-9*^{Bb} workers may have a higher pheromonal threshold than *Gp-9*^{BB} workers, so that they accept several queens. Alternatively, *Gp-9*^{Bb} queens may produce less of this pheromone than *Gp-9*^{BB} queens, allowing several queens of this genotype to be accepted in polygyne colonies.

A remarkable finding of Krieger and Ross [2] is that the same gene also influences social organization in other, closely related species. A phylogenetic analysis of *Gp-9* sequences of 10 species of the genus *Solenopsis* showed that, in the three other species of fire ants that display both monogyne and polygyne colonies, there is a perfect association between a queen genotype at *Gp-9* and whether the queen was collected from a monogyne or polygyne colony (though sample sizes are small). In the three species, queens from monogyne colonies were homozygous for a *Gp-9*^{B} allele very similar to the *Gp-9*^{B} allele identified in *S. invicta*. By contrast, queens from the polygyne colonies all had one copy of a *Gp-9*^{b}-like allele, again very similar to the *Gp-9*^{b} alleles identified in *S. invicta*.

Thus, the same gene influences social organization in four ant species. The *Gp-9*^{B}-like allele of one of these three species (*Solenopsis richteri*) is the sister sequence to all other *Gp-9*^{b}- and *Gp-9*^{B}-like alleles, leading Krieger and Ross [2] to conclude that the ancestral *Gp-9* allele for the socially polymorphic clade was of the *Gp-9*^{B} type. This would imply that

monogyny was the ancestral stage, although other scenarios are possible. For example, queen number might have been a plastic and non-genetic trait in ancestral fire ants, as probably is the case in many other ant species. Later, genes conferring both a higher fitness in polygyne colonies and a higher probability of queens to join such colonies might have become linked together. This scenario is consistent with the observation that almost no recombination occurs in a large genomic region containing *Gp-9* [5]. Conversely, selection might have favored an association of genes increasing queen fitness in monogyne colonies and the probability for queens to be in such colonies. This would set the stage for a genetic basis of social organization — the emergence of the *Gp-9*^{b}- and *Gp-9*^{B}-like clades — from an early stage where it was a plastic response to the environment.

The clustering of the *GP-9*^{b}-type and *GP-9*^{B}-type alleles into their own groups and not with respect to species has other important implications. This appears to be the same type of pattern observed at vertebrate multiple histocompatibility complex (MHC) loci, where homologous alleles across related species are frequently more closely related to each other than to other MHC alleles within species. This is thought to occur through a combination of positive selection for diversification, and selection for maintenance of specific alleles adapted for recognizing antigens common to a species group [8]. The major difference is that social environment — polygyny or monogyny — instead of disease resistance is the suggested selective force in the case of the *GP-9* polymorphism.

Krieger and Ross [2] go on to demonstrate that, as with the MHC loci, positive selection acts on the *GP-9*^{b} alleles. They demonstrate this by comparing synonymous and nonsynonymous substitution rates in the branches of their tree with socially polymorphic species. They find evidence of positive selection acting in the evolution of the *GP-9*^{b} alleles, but not of the *GP-9*^{B} alleles. Although social environment is probably the driving force, it remains to be investigated how diversification at the *GP-9* locus would affect queen fitness. This still leaves the enticing riddle of the extreme lack of synonymous changes among *GP-9*^{b}- and *GP-9*^{B}-type alleles (there is only one synonymous, but eight nonsynonymous mutations in the coding sequence). Furthermore, within the *GP-9*^{b} allele cluster, there are no synonymous differences across the four species sharing the *GP-9*^{b} type (again considering only the coding sequences).

Whatever explanation is offered must also allow for the eight amino-acid-changing mutations occurring in *GP-9*^{b} and *GP-9*^{B} types over the same time period. Possible factors might include extreme selective sweeps in both *GP-9*^{B}- and *GP-9*^{b}-type alleles associated with either very recent divergence of the four species or lateral spreading of the alleles via hybridization, and/or some other unknown mechanism reducing the synonymous variability. Thus, the extraordinary function of this first social gene is accompanied by interesting questions about its equally extraordinary evolutionary origin.

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