

FORUM Genetics

A social rearrangement

Some worker fire ants will tolerate multiple queens in their colony, but others only one. It turns out that this behaviour is governed by a gene cluster on an unusual pair of chromosomes. Two scientists describe what these findings mean to the fields of social evolution, genetics and beyond. [SEE LETTER P.664](#)

THE PAPER IN BRIEF

- The two social forms of the fire ant (*Solenopsis invicta*) are under genetic control and follow a Mendelian inheritance pattern that is associated with variants of a single gene, *Gp-9*.
- On page 664 of this issue, Wang *et al.*¹ show that *Gp-9* lies within a single gene cluster containing multiple genes*.

- This 'supergene' is located on a heteromorphic pair of chromosomes, which differ in sequence and structure, in a similar manner to the X and Y sex chromosomes.
- Recombination (the shuffling of DNA between paired chromosomes during cell replication) is suppressed at a region containing more than half of the genes on this chromosome pair.

Genes and queens

ANDREW F. G. BOURKE

One momentous day in the early 1930s, a ship bearing stowaways docked at Mobile, Alabama. On board was a party of fire ants (*Solenopsis invicta*), inadvertently transported from the species' native range in South America. The fire ant has since become a notorious invasive pest, inflicting painful stings, hampering agriculture and damaging native fauna over much of the southern United States and, more recently, reaching Australia and China². It has also provided one of the best case studies of the genetic basis of social behaviour^{3,4}. Wang and colleagues' impressive study shows that the fire ant's genome bears its own secret cargo — the first supergene known to be associated with variable social structures within any species of animal.

Like many ants, fire ants live in two social forms (Fig. 1). Monogyne and polygyne colonies contain, respectively, a single queen and multiple queens. In addition, the queens of monogyne colonies are larger and more fecund than polygyne queens. The fire ant's social polymorphism is associated with variation at a single chromosomal location, or locus, containing the gene *Gp-9*, which encodes an odorant-binding protein^{3,4}. The two forms of the gene, the alleles *B* and *b*, predict colony type by influencing worker-ant behaviour.

*This article and the paper under discussion¹ were published online on 16 January 2013.

Workers with genotype *BB* live under only a single queen, whereas *Bb* workers accept many queens, but only if these queens are *Bb*. This is because, remarkably, *Bb* workers recognize and kill any *BB* queens that they encounter.

The outcome of these behaviours is that the *B* allele occurs in both colony forms but the *b* allele is found in polygyne colonies only. Because *Bb* workers execute all queens lacking the *b* allele, the allele acts as a self-promoting 'green beard' gene (a gene that allows its bearers to discriminate behaviourally between other bearers and non-bearers through an external label)⁵. However, *b* does not spread unchecked, because, in a final twist, it is a lethal recessive allele — in *bb* individuals, the *b* allele causes early death.

Social evolution — the evolution of behaviours that have effects beyond the individual — requires genetic variation to influence social behaviour, so that natural selection has something to act on. The *Gp-9* system shows that, indeed, a multifaceted social trait can be under genetic influence. But how can a single gene have such a wide range of effects? Using next-generation sequencing and other advanced genomic methods, Wang *et al.* confirm previous suspicions⁴ that *Gp-9* sits within a supergene that also contains most of the other genes that are differentially expressed between the two colony forms. It is therefore likely that other loci among the more than 600 genes in the supergene, as well as *Gp-9*, contribute to the monogyne–polygyne distinction. But the supergene acts like a single locus because recombination is prevented between the *B* and *b* versions (see 'Chromosome mysteries' below). Wang *et al.* estimate that the fire ant's

supergene arose approximately 390,000 years ago, much more recently than the origin of the fire-ant genus. Other ants show monogyne–polygyne forms, but these need not share a similar genetic basis, because in these species new queens are often admitted to colonies if they are relatives, suggesting that acceptance is not dependent on their similarity at just one locus. The *Gp-9* system therefore seems to be a secondary arrangement that arose after the evolution of polygyny, and long after eusociality (societies with a worker caste). Other complex traits, including some that stem from self-promoting genetic elements⁶ (the mouse *t* haplotype is a good example), also involve single, non-recombining, multigenic regions. By using new tools to cast light into the dark hold of the nuclear genome, Wang *et al.* have shown that supergenes can underpin both social behaviour and social structure.

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Chromosome mysteries

JUDITH E. MANK

At first glance, it might be difficult to see what, if anything, fire-ant behaviour can tell us about the evolution of sex chromosomes. However, Wang and colleagues' study shows us that ant behavioural differences are controlled by a group of genes linked together on 'social chromosomes' that are, in many ways, similar to X and Y chromosomes. Moreover, the fire-ant social chromosomes offer interesting clues about how Y chromosomes initially form.

Y chromosomes are strange, mysterious things. Although initially identical to their X-chromosome partner, they diverge when recombination between the two chromosomes ceases. But because the Y is always paired with



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the B and b forms of the social chromosome, in much the same way as we think inversions might prevent recombination between X and Y chromosomes. It also allows for the transmission of a supergene that encodes the polygyne social structure, directly analogous to the male supergene on the Y chromosome.

The fact that bb ants do not survive long enough to reproduce means that the b social chromosome is always paired with the B chromosome, much like sex chromosomes. And, again just as in the X and Y chromosomes, when recombination is halted between the B and b chromosomes, the b chromosome stops recombining altogether within the inversion. Interestingly, the b chromosome exhibits several characteristics also observed on Y chromosomes, including the accumulation of repetitive elements and gene-function decay. So it seems that ant behaviour has a lot to tell us about sex-chromosome evolution after all. ■

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the X , halting recombination between them means that the Y stops recombining entirely, although recombination continues between pairs of X chromosomes in females. This causes all sorts of problems for the Y chromosome, such as gene-function decay and the accumulation of repetitive DNA.

However, even though sex chromosomes have been objects of scientific obsession for decades, we do not really understand how recombination between X and Y chromosomes is suppressed. There are theories, of course, the most accepted of which suggests that Y -chromosome inversions, in which a region is flipped end-to-end, are selected for when they encompass both the male sex-determining gene and a nearby gene with male-specific benefits⁷. Such beneficial changes ensure that these genes are transmitted as a single unit — a ‘male’ supergene — from father to son, as inversions cannot pair correctly during meiosis and therefore recombination is halted in the inverted region between the Y and X . Over time, a series of inversions could theoretically encompass the entire Y chromosome.

There is circumstantial evidence to support this model, namely, in the existence of ‘strata’ within sex chromosomes that seem to correspond to specific inversion events⁸. However, it has proved exceedingly difficult to identify alleles with sex-specific benefits and, without this, it is almost impossible to find direct evidence for the inversion theory of sex-chromosome evolution.

Enter the fire ants. It was previously recognized that their monogyne and polygyne social forms corresponded to their allele status at the $Gp-9$ locus. But these social forms come with an assemblage of morphological and

life-history differences, so it is probable that other genes are involved. This begs the question of how alleles at multiple genes can be transmitted as a single unit along with $Gp-9$. Wang and colleagues show that this is accomplished through at least one massive inversion on the chromosome that encompasses the $Gp-9$ locus as well as most of the other genes that show expression differences between the social forms. This inversion has, in effect, created a pair of social chromosomes. The inversion prevents recombination between

SOLAR PHYSICS

The planetary hypothesis revived

The Sun’s magnetic activity varies cyclically over a period of about 11 years. An analysis of a new, temporally extended proxy record of this activity hints at a possible planetary influence on the amplitude of the cycle.

PAUL CHARBONNEAU

Right to the end of his life, the Swiss astronomer Rudolf Wolf (1816–93) sought to establish a causal link between the 11-year cycle of the number of dark patches on the Sun (sunspots) and planetary motions. Through his relentless historical detective work, he reconstructed the time series of sunspot number all the way back to the seventeenth century. Taken quite seriously

and quantitatively elaborated upon until the end of the nineteenth century, the idea rapidly fell into disfavour following George Ellery Hale’s discovery of the magnetic nature of sunspots¹. Since then, the origin of the sunspot cycle, or solar magnetic cycle, has been sought in the Sun’s interior, where the flow of magnetized fluid can lead to self-sustained dynamo action. Rediscovered periodically ever since (pun intended), nowadays the ‘planetary hypothesis’ for the solar cycle is