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E-mail: [1]timothy.bayne@monash.edu (T.B.), [2]brainard@psych.upenn.edu (D.B.), [3]rwb@st-andrews.ac.uk (R.W.B.), [4]l.chittka@qmul.ac.uk (L.C.), [5]nsc22@cam.ac.uk (N.C.), [6]cecilia.heyes@all-souls.ox.ac.uk (C.H.), [7]mather@uleth.ca (j.M.), [8]olveczky@fas.harvard.edu (B.Ö.), [9]shadlen@columbia.edu (M.S.), [10]t.suddendorf@psy.uq.edu.au (T.S.), [11]B.Webb@ed.ac.uk (B.W.)

Quick guide
Supergenes

Daniella Black and David M. Shuker*

What are supergenes? Supergenes are clusters of physically linked genes inherited as a single unit. Supergenes are often involved in the control of common complex phenotypes, such as body coloration or reproductive strategy (Figure 1). For alleles to stay together and co-segregate, recombination must be suppressed or absent within the supergene cluster.

How do supergenes come about? If alleles at two or more genes work together to produce an advantageous phenotype, whilst different allelic combinations at these loci are less advantageous, selection is expected to reduce recombination between these loci, keeping beneficial allelic combinations together. When this occurs, a supergene may be created. Some supergenes span large stretches of the chromosome and can include many hundreds of genes. The expansion of a supergene can occur when a further favourable allele arises near the original locus and is recruited to the supergene (under the increasing umbrella of reduced recombination).

How is recombination suppressed? Recombination among linked genes can be reduced in a number of ways: chromosomal inversions, the distance from the centromere and structural differences between homologous chromosomes can all influence recombination rates. In general, the closer a gene is located to the centromere, the lower is the recombination rate it will experience. The best studied recombination suppressors are chromosomal inversions. In these cases, suppression typically occurs via mechanical complications arising during crossover, followed by selection against recombinant inversion heterozygotes, which tend to have low fitness. For instance, inversion loops may form during recombination in an attempt to maximize base pairing, creating abnormal chromatids.

Aren't supergenes a bit old fashioned? The supergene concept does indeed have a long history, and in some cases hypotheses proposed almost a century ago have only recently been tested. Ronald Fisher first described a recognizable supergene concept (which he termed co-adapted gene complexes) in 1930, as part of the debate in evolutionary biology between gradualism and mutationism. Fisher hypothesized that the polymorphic wing-pattern of the butterfly *Papilio polytes* was under the control of a supergene (as opposed to the monogenic control hypothesis proposed by mutationists). Fisher's long-suspected prediction has only recently been shown to be true (Figure 1). Of course, the idea of a single locus controlling traits harkens back to the birth of Mendelian genetics, in contrast to the contemporary view that many traits are polygenic in nature.

Which traits are associated with supergenes? Complex balanced polymorphisms are the classic kind of trait controlled by supergenes. The lack of recombination allows the maintenance of more than one morph in a population, as a lack of recombination keeps the different forms of the supergene intact, while also preventing the production of low-fitness recombinants with a mix of alleles from different co-adapted gene complexes. The control of numerous such balanced polymorphisms has now been attributed to supergenes. For example, alongside the famous case of the wing patterns of *Papilio polytes*, the wing patterns of some *Heliconius* butterflies that form the basis of classic Müllerian mimicry rings are also controlled by sugergenes. Communication signals such as these often experience antagonistic selection pressures because of their simultaneous roles as signals to predators and conspecifics. Despite involvement in Müllerian mimicry rings, for which convergence of signals is thought to be advantageous, seven distinct colour morphs controlled by supergenes are maintained in populations of *Heliconius numata*. Each morph closely resembles an unpalatable butterfly species from the genus *Melinaea.* The supergene
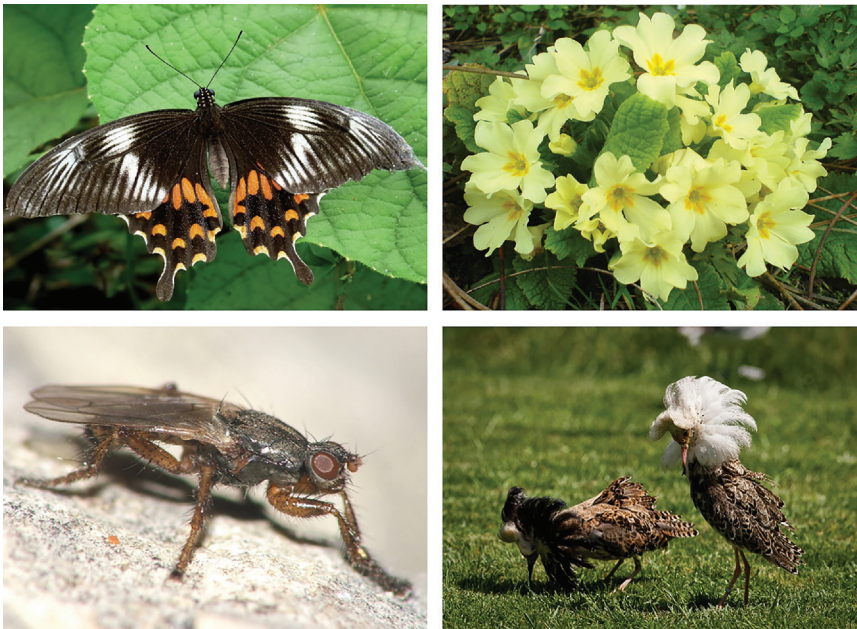
Figure 1. Supergenes underlie a variety of complex traits.
Top left: *Papilio polytes* butterfly females engage in Batesian mimicry of the poisonous species *Pachliopta aristolochiae* to evade predation. The development of mimetic and wild-type wing patterns is controlled by a supergene complex, as predicted by Fisher (photo: © 2010 Jee & Rani Nature Photography (CC BY-SA 4.0)). Top right: Distyly promotes outbreeding in numerous flowering plants including *Primula vulgaris*. In distylous systems, two morphs with reciprocal anther and stigma heights are maintained by a supergene complex (photo: Pokrajac (CC BY-SA 3.0)). Bottom left: The seaweed fly, *Coelopa frigida*, harbours a large (10% of genome) polymorphic chromosomal inversion system made up of three over-lapping inversions. This inversion influences, among other traits, body size, development time, and viability. The frequencies of the different inversion karyotypes vary along environmental clines (photo: Arjan Haverkamp (CC BY 2.0)). Bottom right: Supergenes control development of three male morphs with alternative mating strategies in the lek-breeding ruff, *Philomachus pugnax* (photo: © Rui Andrade (CC BY 3.0)).

controlling this polymorphism spans 400 kilobases, and within this region there are three breakpoints creating multiple alternative inversion arrangements. Different arrangements segregate in each morph, for which there are strict dominance relationships. Another example is the polymorphic social behaviour of the invasive fire ant, *Solenopsis invicta*. Once thought to be associated with a single gene, this behavioural phenotype is now known to be the product of many genes lying together on two inversions that make up a supergene complex. The non-recombining region spans 55% of the chromosome (approximately 13 megabases) and contains over 600 identified genes. The supergene controls the formation of either a monogyne colony (headed by a single queen) or a polygyne colony (headed by multiple queens, including up into the hundreds). Monogyne and polygyne colonies vary in multiple life history traits including the reproductive strategies of queens.

Are supergenes always adaptive?
Not always. For instance, the T-haplotype meiotic drive system in mice (*Mus musculus*) is a selfish genetic element controlled by a supergene spanning more than one third of chromosome 17. 'Meiotic drive' means that a locus is transmitted to more than the expected 50% of offspring, and the T-haplotype's primary function is to link the drive locus to a gene that confers resistance to drive. T-haplotypes are characterized by the recessive lethal mutations they carry. When T-haplotypes occur in the homozygous state individuals perish *in utero.* Sixteen complementing T-haplotypes (haplotypes with different recessive lethal mutations) have been described. Finally, we can even think

of sex chromosomes, which lack recombination between them, as being one long supergene system.

Wait a minute, sex chromosomes are supergenes? Yes! The ability to produce the two sexes can be viewed as a complex phenotype. When sex is genetically controlled, reduced recombination has repeatedly evolved between proto-sex chromosomes, making sex chromosomes supergenes. The evolution of sex chromosomes could begin by the emergence of a male sterility mutation creating genetically-determined females. This locus will remain polymorphic, as females cannot become fixed in a sexual population. Following this, a female suppressor/male enhancer mutation could occur on the homologous chromosome, creating genetically-determined males. There would be strong selection against sterile heterozygotes with both a female suppressor and male sterility mutation, with linkage disequilibrium generating selection for reduced recombination at this locus. Further mutations, favouring one sex over the other, could then occur, generating selection for further reductions in recombination, increasing the length of the supergene.

How are stable polymorphisms maintained in a population? Specific selection regimes are required to maintain multiple forms of a supergene in a population. Such patterns of selection often involve a reduction in the fitness of one form of the supergene under certain conditions, preventing it from becoming fixed in the population and eliminating other forms. For example, spatial heterogeneity can result in the varying fitness of an allele in different environments, and this can lead to clines of inversion frequency as habitat changes (Figure 1). The supergene complex controlling the polymorphic wing-pattern (mimetic and wild-type morphs) of *P. polytes* is maintained by negative frequency-dependent selection. As the mimetic morph increases in frequency, predators learn that the mimics are likely to be safe to eat. The increased death rate of the mimic at high frequencies prevents the supergene from becoming monomorphic.

Alternatively, the presence of recessive lethal mutations linked to supergenes can maintain polymorphisms. If a recessive lethal mutation is linked to a supergene, it is unlikely to be purged because the lack of recombination reduces the efficacy of natural selection. The production of low or zero fitness homozygotes therefore opposes the karyotype with the high-fitness allele from going to fixation. In the case of the large supergene system in *Solenopsis invicta*, the majority of the chromosome does not recombine. Without occasional recombination events, recessive deleterious mutations accumulate which can lead to degeneration (as is well documented in the case of Y-chromosomes). For this reason, supergene complexes occasionally exist in the homozygous state, allowing recombination and purging of the genetic load (a notable exception being supergenes associated with self-incompatibility; Figure 1).

How common are supergenes? It is difficult to tell, but supergenes are probably more common than currently thought. The renewed interest in recent years has uncovered a supergene basis for many complex adaptations in a wide range of taxa. However, further research is required to determine whether these examples are isolated cases or emblematic of what may prove to be a rather common form of adaptive genomic architecture.

Where can I find out more?

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School of Biology, University of St Andrews, UK.
*E-mail: david.shuker@st-andrews.ac.uk

Remarkably loud snaps during mouth-fighting by a sponge-dwelling worm

Ryutaro Goto[1,3,*], Isao Hirabayashi[2,3], and A. Richard Palmer[4,5]

Many aquatic animals, including mammals, fishes, crustaceans and insects, produce loud sounds underwater [1–6]. Soft-bodied worms would seem unlikely to produce a loud snap or pop because such brief, intense sounds normally require extreme movements and sophisticated energy storage and release mechanisms [5]. Surprisingly, we discovered a segmented marine worm that makes loud popping sounds during a highly stereotyped intraspecific agonistic behavior we call 'mouth fighting'. These sounds — sound pressures up to 157 dB re 1 μPa at 1 m, with frequencies in the 1–100 kHz range and a strong signal at ~6.9 kHz — are comparable to those made by snapping shrimps, which are among the most intense biological sounds that have been measured in the sea [6]. We suggest a novel mechanism for generating ultrafast movements and loud sounds in a soft-bodied animal: thick, muscular pharyngeal walls appear to allow energy storage and cocking; this permits extremely rapid expansion of the pharynx within the worm's body during the strike, which yields an intense popping sound (likely via cavitation) and a rapid influx of water. Clearly, even soft-bodied marine invertebrates can produce remarkably loud sounds underwater. How they do so remains an intriguing biomechanical puzzle that hints at a new type of extreme biology.

Leocratides kimuraorum (Annelida: Hesionidae: Hesioninae) is a polychaete worm (to 29 mm long) that lives inside hexactinellid sponges at 85–169 m depth off the coast of Japan [7]. Its nearly transparent body bears numerous long tentacles and a large, circular mouth (Figures 1A, S1A). We collected *L. kimuraorum* and its host glass sponge *Aphrocallistes* sp. (Aphrocallistidae) (Figure S1B–D) by trawling at 110–130 m depth off Kii Peninsula (see Supplemental Experimental Procedures). Several individuals typically occurred in one sponge. Worm behavior was digitally recorded in aquaria. Individuals placed close together approached each other headfirst with mouths open (Figure 1A; Video S1). During 'mouth fighting', a short proboscis extended slightly followed by extremely rapid expansion of the posterior pharynx (dashed region, Figure 1B,C). This rapid strike included a single loud popping sound and rapid influx of water that drew both opponents towards each other and sometimes caused one to bounce away after impact (see Video S1). 'Mouth attacks' were often mutual (clips three and four, Video S1). All 13 individuals (likely both sexes) examined showed this behavior. Also, loud pops occurred only during mouth fighting and never when simply disturbed. *Leocratides kimuraorum* live in narrow passageways in the host sponge (Figure S1B–D) and may use mouth fighting to defend territory or living chambers from other worms.

We recorded 15 pops emitted from three individuals with a hydrophone (see Supplemental Experimental Procedures). One pop lasted 0.41 ± 0.022 s (Figure 1E). The dominant frequency was 6912.7 ± 256.11 Hz, but frequencies extended from close to zero to over 90 kHz (Figure 1F). Sound pressure was 150.0 ± 1.41 dB re 1 μPa at 1 m (range 140.8 to 157.0).

Snapping shrimp snaps include some of the most intense sounds produced by aquatic organisms [6]. Remarkably, sound pressures and frequencies produced by *L. kimuraorum* are comparable to those of snapping shrimps. Furthermore, although invertebrates usually generate sounds with hard structures [2,4–6,8], *L. kumuraorum* lacks hard parts in its pharynx. So even a soft-bodied organism can produce loud sounds. To our knowledge, this is the first report of a loud underwater sound produced by any soft-bodied worm or any mollusc [8], so *L. kimuraorum* is the loudest known lophotrochozoan. A loud pop may be a byproduct of the rapid mouth attack, but it may also aid intraspecific communication. For example, sound intensity may affect the outcome of