



Peer Community In Evolutionary Biology

Supergene Control of a Reproductive Polymorphism

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Küpper C, Stocks M, Risse JE, dos Remedios N, Farrell LL, McRae SB, Morgan TC, Karlionova N, Pinchuk P, Verkuil YI, et al. (2016) A supergene determines highly divergent male reproductive morphs in the ruff. bioRxiv, ver. 1, peer-reviewed and recommended by Peer Community in Evolutionary Biology. <https://doi.org/10.1038/ng.3443>

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Two back-to-back papers published earlier this year in *Nature Genetics* provide compelling evidence for the control of a male reproductive polymorphism in a wading bird by a "supergene", a cluster of tightly linked genes [1-2]. The bird in question, the ruff (*Philomachus pugnax*), has a rather unusual reproductive system that consists of three distinct types of males ("reproductive morphs"): aggressive "independents" who represent the majority of males; a smaller fraction of non-territorial "satellites" who are submissive towards "independents"; and "faeders" who mimic females and are rare. Previous work has shown that the male morphs differ in major aspects of mating and aggression behavior, plumage coloration and body size, and that – intriguingly – this complex multi-trait polymorphism is apparently controlled by a single autosomal Mendelian locus with three alleles [3]. To uncover the genetic control of this polymorphism two independent teams, led by Terry Burke [1] and Leif Andersson [2], have set out to analyze the genomes of male ruffs. Using a combination of genomics and genetics, both groups managed to pin down the supergene locus and map it to a non-recombining, 4.5 Mb large inversion which arose 3.8 million years ago. While "independents" are homozygous for the ancestral uninverted sequence, "satellites" and "faeders" carry evolutionarily divergent, dominant alternative haplotypes of the inversion. Thus, as in several other notable cases, for example the supergene control of disassortative mating, aggressiveness and plumage color in white-throated sparrows [4], of mimicry in *Heliconius* and *Papilio* butterflies [5-6], or of social structure in ants [7], an inversion – behaving as a single "locus" – underpins the mechanistic basis of the supergene. More generally, and beyond inversions, a growing number of studies now shows that selection can favor the evolution of suppressed recombination, thereby leading to the emergence of clusters of tightly linked loci which can then control – presumably due to polygenic gene action – a suite of complex phenotypes [8-10]. A largely unresolved question in this field concerns the identity of the causative alleles and loci within a given supergene. Recent progress on this question has been made for

example in *Papilio polytes* butterflies where a mimicry supergene has been found to involve – surprisingly – only a single but large gene: multiple mimicry alleles in the doublesex gene are maintained in strong linkage disequilibrium via an inversion. It will clearly be of great interest to see future examples of such a fine-scale genetic dissection of supergenes. In conclusion, we were impressed by the data and analyses of Küpper *et al.* [1] and Lamichhaney *et al.* [2]: both papers beautifully illustrate how genomics and evolutionary ecology can be combined to make new, exciting discoveries. Both papers will appeal to readers with an interest in supergenes, inversions, the interplay of selection and recombination, or the genetic control of complex phenotypes.

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