The evolution and maintenance of gene clusters must involve recombination events. Studies on the segregation of *MAT* during meiosis in *C. neoformans* reveal that this locus is flanked by activators that increase recombination 10 to 50-fold above the genomic average [19]. These regions of activated recombination correlate with sequences with an increased G+C content, similar to γ class recombinational activators. These *MAT*-associated hotspots may play a central role in the evolutionary events outlined above that fashioned this unique genomic region [19]. Similar recombinational activators — γ, α or β hotspots, which recruit transcription factors or alter nucleosome positioning — may have played analogous roles in the evolution of biosynthetic, metabolic, and virulence-associated gene clusters. Thus, in addition to comparative genomics to understand gene cluster evolution, analysis of meiotic segregation patterns and DNA sequences near clusters provides a fertile avenue for investigation in *U. maydis* and other fungi.

In closing, the *U. maydis* genome sequence, associated expression patterns, and functional analysis of the 12 gene clusters [1] highlight the fact that novel host-microbe paradigms remain to be discovered and explored. These tools can reveal general principles by which hosts are subject to invasion and infection, and how gene clusters evolved and function as unique genomic structures.

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[1]School of Botany, The University of Melbourne, Victoria 3010, Australia.
[2]Department of Molecular Genetics and Microbiology, Duke University Medical Center, Durham, North Carolina 27710, USA.
E-mail: bhowlett@unimelb.edu.au, heitm001@duke.edu

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Evolution: Lending a Helping Hand in Sperm Competition?

Most females mate with many males. This can be costly, but the benefits to females are often unclear. A new study raises the possibility that females could benefit through an unconventional genetic pathway, while also showing that males can inadvertently increase rival males' fitness in surprising ways.

Clarissa M. House, John Hunt and David J. Hosken

It has become increasingly clear that, in contrast with traditional views, females of most species mate with many males [1]. Understanding why they do this has become a mini-industry — mating is costly after all — and the consequences of female multiple-mating (polyandry) are often unclear. Explanations for polyandry are varied and range from the production of higher quality offspring — polyandry allows females to choose superior fathers for their offspring — to male sexual-coercion — females mate multiply because males force them to. While the female benefits of polyandry remain hotly debated, one undisputed consequence of mating with multiple males is sperm competition, where the sperm of different males compete to fertilize a female's ova. Females could benefit by allowing sperm to compete if, for example, good sperm competitors father higher quality offspring [2], or produce sons that are themselves good at sperm competition [3].

Regardless of the female benefit, the male–male interactions that occur during this form of competition are viewed as unconditionally antagonistic: if one male does better, the other does worse. This fundamental premise is exemplified by the kamikaze-sperm hypothesis, which suggests males produce sperm especially designed to attack rival males' gametes [4], or by the idea that seminal fluid somehow recognises rival sperm and damages them [5], although there is little evidence for either of these scenarios [6,7]. The idea that competing males' ejaculates could interact in more synergistic ways, and that this also benefits females, is not one that has received any great attention, although this may change with recent findings published in *Current Biology* [8].

Working on the Australian field cricket (*Teleogryllus oceanicus*; Figure 1), a species already known for the positive effects of polyandry on embryo viability [9], García-Gonzáles and Simmons [8] found that males can enhance the viability of embryos sired by rivals. The protocol employed to come to this conclusion involved batches of six full-sisters that were grouped with two males unrelated to each other or the females. Each male mated twice to two females in a monogamous setting, so that there was no sperm competition; and then both males mated once each to the remaining two female — polyandrous matings, with sperm competition. Using a neutral morphological marker (eye colour) that enabled the paternity and survival of embryos to be assessed, the authors first documented embryo viability

Figure 1. Male (bottom) and female (top) Australian field crickets (*Teleogryllus oceanicus*) just after mating.
Photo courtesy of Francisco García-González.

differences between males in the monogamously mated sisters. Then, in the sperm competition experiment — where the females mated with the two males in succession — males with higher embryo viability competed against males producing embryos with lower viability.

If purely genetic effects determined embryo survival, males with low offspring viability in non-competitive matings should always produce low-viability embryos. What García-Gonzáles and Simmons [8] found in the competitive matings, however, was that males inducing high embryo viability in the non-competitive setting increased the viability of embryos sired by males previously shown to be poor embryo-viability enhancers. Furthermore, this effect was greatest when the difference in viability enhancement between the two males was greatest: when the viability enhancement of the two males was similar, embryo survival was occasionally reduced. The authors suggest that the females did not influence this pattern, as no significant female effects were detected. Furthermore, the proportion of eggs fertilized by a male was independent of his effect on embryo viability, indicating that females were not biasing paternity toward superior males. It therefore appears that the rescuing effect was not due to the mothers or to the direct action of the superior sires' genes, but instead rescue resulted from the quality of the environment provided by the male inducing high embryo viability. This opens up a whole new can of worms, raising the possibility that the benefits of polyandry may not necessarily have to be transmitted through conventional (additive) genetic pathways.

So how could this work? García-Gonzáles and Simmons [8] raise one intriguing possibility: indirect genetic effects. Individuals often have a strong impact on the environment for others, whether they be related, as in the case of mothers and offspring [10], or unrelated, as with sexual partners [11]. If there is variation in the quality of this environment and if this variation reflects genetic differences among individuals, then indirect genetic effects will exist and the environment will be heritable [12]. Previous work by García-Gonzáles and Simmons [13] has shown heritable differences between males in their ability to induce embryo viability. Moreover, a role for accessory gland products was implicated in this process through a positive genetic correlation between hatching