extinction — the quantitative reduction of an organism below a certain threshold making it non-functional in the community — and secondary extinction — the loss of a species triggered by the primary extinction of an ecologically linked species. Unravelling these microbial ecology dynamics, together with the investigation of their effects, is of crucial relevance in the effort to preserve our ancestral microbiome and defend the biodiversity that co-evolved with our body before westernization.

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Evolution: Sex Limits Adaptation

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Evolution is affected by survival of individuals and by mate choice, but how sexual selection affects adaptation remains unclear. A new study finds that sexual selection can limit adaptation by causing male-induced harm to females and thus opposing natural selection.

Darwin realized that evolutionary change is affected not only by the survival of individuals and natural selection, but also by their reproductive success under sexual selection [1,2]. Over the years, it has become clear that both processes act regularly and that natural selection is the mechanism creating adaptation to the environment [3]. In contrast, there are still debates about the role of sexual selection in adaptation. On the one hand, if healthy individuals in good condition have high reproductive success, then sexual selection might align with natural selection and promote adaptation [1,4,5]. On the other hand, sexual selection may reduce survival through the evolution of costly and exaggerated sexual traits [6], or via mating systems where the sexes harm each other [7,8]. In these scenarios, sexual selection opposes natural

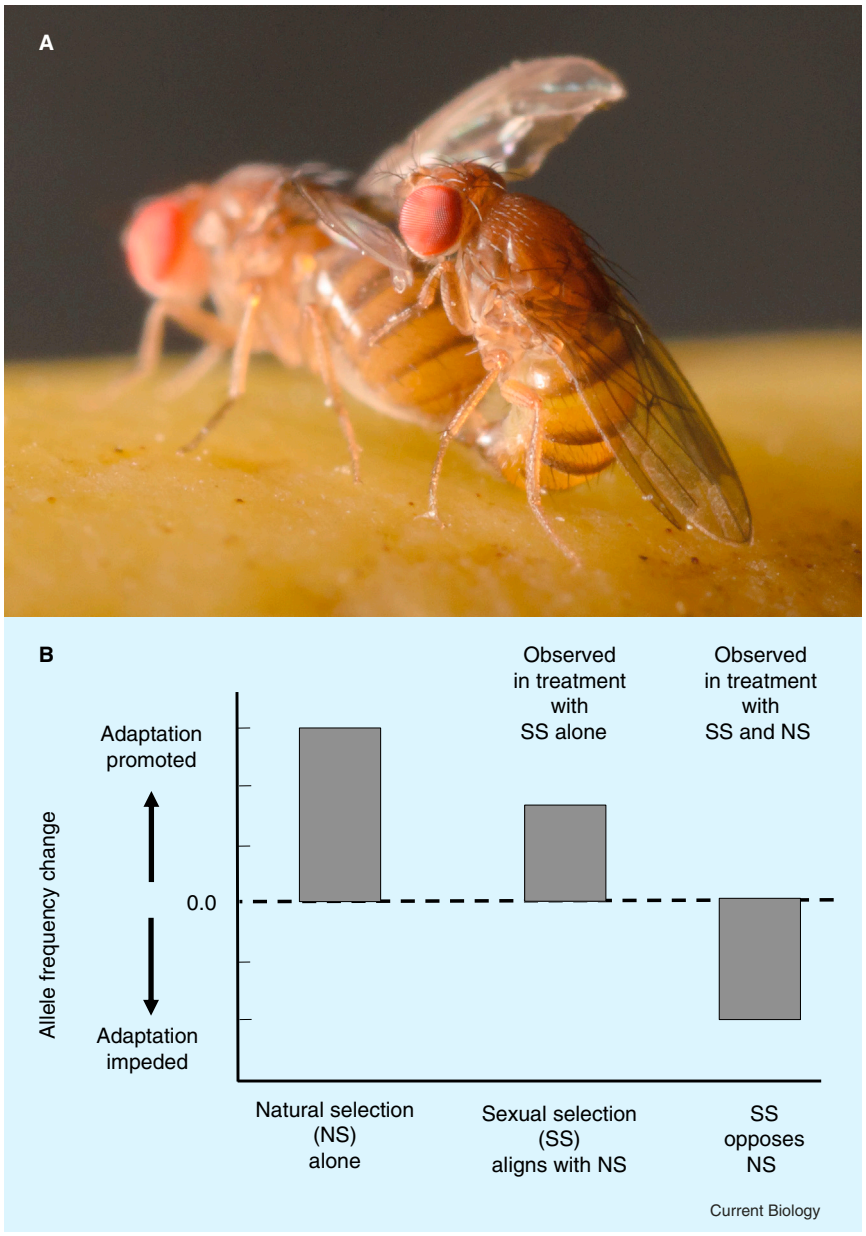

Figure 1. Natural and sexual selection.
(A) A mating pair of *Drosophila serrata*, the species used to test if sexual selection opposes natural selection by Chenoweth *et al.* [9]. Photo credit: Antoine Morin. (B) Schematic representation of the hypotheses tested by Chenoweth *et al.* [9] (below x-axis) and the general results observed in their experiment (above bars).

selection and can limit adaptation (Figure 1). These ideas are reasonable, but experiments are needed to test them. A paper by Chenoweth *et al.* [9] in this issue of *Current Biology* now shows that sexual selection opposes natural selection.

Two main approaches have been taken prior to the study by Chenoweth *et al.* [9]: first, some have manipulated the opportunity for mate choice and sexual selection and then measured the consequences for population level mean fitness [10,11]; second, other experiments have assayed the effects on male sexual fitness of deleterious mutations [5,12]. Both approaches have yielded useful insights by suggesting costs of sexual selection, but there are nonetheless shortcomings that call for further work [9]. For example, measuring mean fitness integrates genetic effects across the genome such that genomic regions with opposing effects on natural versus sexual selection cancel each other out, underestimating the gross cost of sexual selection. The other class of experiments examining individual mutations can isolate effects of individual alleles, but many of these new mutations are deleterious and thus unlikely to be involved in adaptation to the ecological environment, and inferences are restricted to one or a few loci. Thus, further experiments are required to test how multiple loci potentially involved in adaptation are affected by sexual selection.

The new study by Chenoweth *et al.* [9] provides such an experiment in *Drosophila serrata*. The authors obtain genomic data from an evolution experiment that manipulated natural and sexual selection during the early stages of adaptation to a new environment. The study thus extends previous work by examining numerous loci and naturally occurring standing genetic variation, which is more likely to be involved in adaptation than are individual deleterious mutations. Specifically, the study examined evolution at >1400 single nucleotide polymorphisms (SNPs) across the genome in fly populations evolved under three treatments: natural selection alone, sexual selection alone, or both.

The authors found that sexual selection affected many of the same genomic regions (i.e., SNPs) as natural selection, aligning with it as often as opposing it (Figure 1B). However, they found that treatment effects in their experiment, although predictable, were not necessarily straightforward. The reason for this was that roughly half of the SNPs affected by selection were affected by an interaction between natural and sexual selection — the effects of one form of selection were dependent on the other. For these SNPs affected by the interaction, sexual selection on its own (i.e., in the absence of natural selection) often caused the SNP to change in frequency in the same direction as occurred under natural selection alone. Thus, sexual selection in isolation from natural selection would not limit adaptation. Strikingly, the situation was reversed when sexual selection occurred in conjunction with natural selection: here, the effects of sexual selection were almost exclusively in opposition to

those of natural selection, reducing or even reversing the direction of genetic response relative to that expected under natural selection. In short, the study reports an antagonism between natural and sexual selection that could limit adaptation when both forms of selection occur together. How can these results be explained?

The authors went towards explaining the observed pattern by investigating the mechanisms that cause antagonism between natural and sexual selection at the genomic level [9]. Using behavioral experiments, they identified a role for the combination of male mate preference and male-induced harm to females, a hypothesis explored at the phenotypic level in a previous study by Long *et al.* [8]. Specifically, Chenoweth *et al.* [9] showed that males preferentially courted and mated with high-fitness females that would be favored by natural selection. The harm to females associated with this 'over the top' male attention eliminated the female fitness advantage. Thus, females carrying otherwise adaptive alleles suffer greater harm from males due to increased sexual attractiveness. This process can prevent the otherwise adaptive alleles from rising to high frequency in the population, thereby limiting adaptation.

Beyond increasing our understanding of adaptation, the results have implications on how genetic variation in sexually selected traits is maintained in the face of strong directional selection, which depletes variation. This issue, called 'the lek paradox', can be resolved if there is a trade-off between reproductive success and survival, as seen by Chenoweth *et al.* [9] and in some studies of natural populations [13].

Despite these advances, no study is without issues that call for further work. For example, effective population sizes were not followed by Chenoweth *et al.* [9]. Consequently, random evolution due to genetic drift could not be explicitly estimated. Although the consistent results among independent replicates observed in the experiment make chance explanations for evolution less likely, it is still possible that population sizes could have differed systematically among treatments (natural selection, sexual selection, or both) such that drift was stronger in some treatments than in others, which might partially explain the differences among them. Additionally, the approach of sequencing pools of individuals makes it difficult to estimate correlations among loci ('linkage disequilibrium'), such that the independence of responses at different loci in the experiment is unknown. This leads to the more general point that determining the role of selection acting directly on a genomic region — as opposed to effects of indirect selection on correlated regions — remains one of the largest challenges in understanding selection's role in shaping genomic variation [14,15].

The study by Chenoweth *et al.* [9] is part of a wave of recent studies combining genomic and experimental approaches to address questions in evolutionary biology. For example, 'evolve-and-sequence' studies of experimental evolution in the lab are flourishing [16]. Moreover, experiments even in natural or semi-natural conditions are emerging. For example, studies in plants, insects and marine invertebrates have combined common garden, transplant, or mesocosm experiments with next-generation sequencing to test the number, size, distribution, and types of genomic regions affected by selection [15,17–19]. We clearly are witnessing the birth of 'experimental genomics'. Despite the promise of this approach, careful study designs are required to yield strong inferences.

Finally, while genomic approaches have now examined the consequences of selection, no study preceding that of Chenoweth *et al.* [9] partitioned the contributions of natural and sexual selection during adaptation. Thus, this study represents some of the strongest evidence to date that sexual selection can impede adaptation and further provides a potential explanation why: males prefer, but harm, attractive, high-fitness females such that otherwise adaptive alleles have trouble rising to high frequency. Why some other studies have found that sexual selection aids [20], rather than hampers, adaptation is a major outstanding question, but the results of Chenoweth *et al.* [9] point to differences among species' mating systems as a potential explanation for the different results.

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Palaeontology: Clearing the Heads of Cambrian Arthropods

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Understanding the identity of segments and the evolution of their appendages is a prime concern of arthropod evolution studies. This has been challenging for long extinct stem-groups. Now, Cambrian fossils offer insights that will help further evolutionary considerations.

For well over half a billion years arthropods have been, and are still, the planet's dominant animal life-form. One reason for their evolutionary success is their versatility that has resulted in a segmental ground pattern evolving all manner of adaptive traits, such as a huge variety of limbs and modifications of the exoskeleton [1]. Such rich diversification offers a special challenge when it comes to comparative studies, not least with respect to the arthropod head. This was explicitly recognized in 1975 by the Canadian entomologist Jacob Rempel, who published a now famous — or for some infamous — paper titled "The Evolution of the Insect Head: The Endless Dispute" [2]. In it, Rempel reviewed the then current theories, and some of the personal quirks of their advocates, listing thirteen divergent opinions about which parts of the arthropod head correspond to which segments of the arthropod ground pattern. Disagreements were compounded by differences of opinion about how many segments made a head. Today, we tend to think we are in a more secure position now that such analyses no longer have to rely on morphological and embryological criteria. Today, developmental genetics and gene expression studies inform us that the heads of mandibulate arthropods (crustaceans, insects, millipedes and centipedes) comprise six segments: the ocular, antennal and antennular or intercalary segments followed by three segments providing modified limbs serving as mouth parts [3]. But how can a mandibulate head compare with that of a spider or scorpion? Indeed, what is the 'head' of a spider? The answer is that 'heads' are a distraction, because it is the segmental match-ups that inform us about homologies across the front ends of arthropods. While these correspondences can nowadays be resolved by molecular biology [3,4], for palaeontologists trying to resolve homologies of head organization across stem-group arthropods Rempel's "Endless Dispute" is very much alive and kicking. Ascribing correspondence of parts of the head across fossil species is important because if wrongly identified, structures will be incorrectly coded for cladistics and lead to false phylogenetic relationships. Now a new study in Current Biology by Javier Ortega-Hernández [5] identifies for the first time features that confidently define the most rostral head segment in fossil arthropods, an iconic group that hallmarks the expansion of metazoan life in the lower and middle Cambrian.

Deducing homologous structures across the diversity of ancient arthropods has been problematic, as illustrated by a couple of examples. Take for instance the Cambrian's pre-eminent predators, such as the well-known *Anomalocaris*, a member of a group called 'Radiodonta' comprising arthropods that had not yet evolved segmental sclerites or articulating appendages. What in radiodontans might correspond to the bivalved head shields or any other anterior structure of early euarthropods that had evolved arthrodization and jointed appendages [6]? One favoured homology is that an unpaired dorsal structure (the 'H element') extending to in front of the eyes, and flanked by two lateral plates or 'P elements', corresponds to the bivalved shield of stem euarthropods [7], which today is a familiar structure for those who enjoy shrimp. But what other structures would allow the designation of the H and P elements as belonging to the most anterior head segment when segmentation in radiodontans is not

