

Evolution

The battle between the sexes

Tom Tregenza

Male–female conflict over mating rate can drive rapid evolution and lead to female refusal to mate with males from other populations, so implicating sexual conflict in the generation of biodiversity.

Sexual conflict is a pervasive feature of the living world. Although the sexes need one another, they rarely have exactly the same priorities. Males can often increase their reproductive success — the number of offspring they sire — simply by mating with as many females as possible. Females, on the other hand, are limited by their ability to produce offspring, and unnecessary matings may be costly. This difference sets the stage for an evolutionary arms race in which males are continually evolving new adaptations to get females to mate with them rather than with other males, and females are striving to resist this manipulation.

On page 979 of this issue¹, Martin and Hosken provide evidence that sexual conflict can indeed drive very rapid evolution of female willingness to mate and of male traits that promote matings. They show that this process can lead to females being less ready to mate with males from other populations. This type of reduction in matings between populations could eventually lead to a complete lack of interbreeding, at which point the two groups would have become separate species.

Martin and Hosken took the dung fly *Sepsis cynipsea*, males of which can be seen harassing females on cowpats throughout Europe, and set up three types of laboratory populations. Monogamous populations had

females kept with only one male, eliminating conflicts of interest altogether. 'Conflict' populations had either 50 or 500 flies in the same-sized plastic box, with equal numbers of males and females. Flies kept at higher densities mate more frequently, and the females lay fewer eggs, presumably because they are continually having to fend off amorous males. After two-and-a-half years and 35 generations, females were tested for their willingness to mate, both with males from their own population and with males from an independent population of the same type. As predicted, females from monogamous populations (having been under no selection for avoiding males) were the most willing to mate. Females from conflict populations were not only generally less willing to mate, they were also even more reluctant to mate with males from a different population than they were with males from their own population.

There were also differences between the two types of conflict population. At the larger population size, females evolved even greater discrimination against males from populations other than their own. This is particularly interesting because it is exactly the opposite of what is predicted by theories of speciation that are based on the idea that smaller populations diverge rapidly. When populations are small, the frequency of different genes can change very rapidly — each

type of gene is found only in a few individuals and so the prevalence of particular genes is strongly affected by chance events that happen to their carriers. The faster progress towards speciation in the larger populations seen in Martin and Hosken's study is, however, exactly what is predicted by speciation theories based on selection that include sexual conflict². In large populations, selection will be more effective at finding genes in females that can counteract manipulative genes in males, because there will be more genetic variation available and because selection is not swamped by chance events.

But there is an alternative explanation for the pattern seen. The important thing might not be the fact that some populations were larger, but that they were at higher density, and hence experienced greater levels of conflict. This will have increased the pressure on females to be more reluctant to mate, which could have similar effects — evolution is faster because selection is stronger, while in the previous case evolution is faster because there is more variability for it to work with.

The study of the evolutionary role of sexual conflict is still in its infancy and, as might be expected, Martin and Hosken's study raises as many questions as it answers. In particular, the finding that females are more resistant to males from populations other than their own runs counter to several studies³ that have found females with lower resistance to foreign males. These previous results have been taken as support for the idea that sexual conflict is characterized by males continually evolving new ways to manipulate females, who in turn evolve new methods of resistance⁴ — that is, females are poor at resisting male tactics they have not evolved with. Perhaps the explanation for Martin and Hosken's different results is that by artificially increasing the level of conflict, they have created a situation where, instead of following male adaptations, females are leading the evolutionary dance, evolving new criteria that males must meet in order to be granted a mating. Hence, males that have been able to adapt to the preferences of females from their own population are at an advantage over foreign males.

This view has similarities to the type of argument used in models that examine the potential for differences in female mate preferences to drive speciation⁵, and highlights a second issue. Although there is clearly a lot of sexual conflict in Martin and Hosken's system, it is possible that there is also sexual selection of the more familiar type in which females are choosing the 'best' males. The laboratory is very different from the wild, and females might simply be picking males better at dealing with this new environment, with chance differences between populations in the male traits that females use for mate choice.

This study shows that simply changing

the size and density of populations provokes rapid evolution in mating traits. A powerful approach to examining the factors that may be important in determining whether conflict creates diversity will be to conduct similar experiments using a range of animals and independently changing factors such as the number of individuals and the environment they experience. We also need to start examining the nature of the signals that males use to persuade females to mate, and how these are received by females. Combining these

approaches will provide new insights into how conflict can create diversity. ■

*Tom Tregenza is in the Ecology and Evolution Group, School of Biology, University of Leeds, Leeds LS2 9JT, UK.
e-mail: t.tregenza@leeds.ac.uk*
