

Figure 1 Untangling sperm competition in *Drosophila*. To study last-male sperm precedence, Price *et al.*⁴ used genetically modified fruitflies that produce sperm with green, fluorescing tails. These sperm can easily be distinguished from non-fluorescing sperm.

lity was that sperm from the most recent insemination physically displaces previous deposits, pushing them to the back of the female's sperm store, such that successive ejaculates could become stratified. This would result in a 'last in, first out' system⁵.

But there was no direct evidence to support the idea of stratified ejaculates, and subsequent studies revealed that last-male sperm precedence might be the result of rather more subtle processes. Some researchers, for example, have found that the seminal-fluid component of a male fruitfly's ejaculate disables the sperm from previous inseminations. Not only that, but it transpires that these ejaculatory secretions are also toxic to the female herself. So, these results showed that the more often a female copulated the sooner she died, creating a serious sexual conflict over the frequency of copulation. However, not all studies found that seminal fluid incapacitates sperm, so it has been difficult for researchers to agree on the relative importance of this mechanism⁶.

Price *et al.*⁴ have now used new techniques to assess the relative importance of displacement and incapacitation in last-male sperm precedence. In their first experiment, they allowed female fruitflies to be inseminated by two different males at intervals of either two or seven days. In both cases, as in previous studies, the second male fathered most of the offspring — 87% with a two-day interval, and a huge 96% with a seven-day interval. The authors found that displacement alone was responsible for second-male sperm precedence with a two-day interval between inseminations. But with seven days between inseminations, the second mechanism, incapacitation, worked in conjunction with displacement, resulting in almost complete precedence of the second male's sperm.

How did the authors work this out? By using a pair of males, one of which was genetically modified so that the tails of its sperm fluoresced green (Fig. 1), Price *et al.* followed the fate of individual sperm from each male

in the female's reproductive tract. This was not quite as straightforward as it sounds, because the males whose sperm fluoresced green transferred many fewer sperm than other males. But, after accounting for this effect, the authors concluded that an incoming ejaculate physically displaces sperm from one of female's three sperm stores (the seminal receptacle). So, most of the stored sperm in the female are those from the second male. Based on the distinguishable sperm, Price *et al.* also state that the sperm from different males were not stratified within the sperm receptacle, although they do not provide quantitative details.

In a second set of experiments, Price *et al.* used a spermless mutant fly to show that the incapacitation effect of seminal fluid works only when the interval between the two inseminations is seven days. This result implies that sperm must remain in the female's sperm stores for at least two days before they become vulnerable to incapacitation. The authors offer a neat explanation for this effect — they state that it prevents males

from inactivating their own sperm. In the wild, female fruitflies usually re-mate to replenish their dwindling sperm supplies after two or three days⁷. So, the interval that sperm must be stored before becoming vulnerable to debilitation is probably closer to three days than to seven. This remains to be tested.

Price and colleagues' study has taken us forward both in understanding the mechanism of last-male sperm precedence, and in identifying new tools for the job. But there is still much to be discovered. We do not, for example, know how one ejaculate physically displaces another. Nor do we know what happens to incapacitated sperm — are they merely less mobile? And why does incapacitation work only on sperm that has already been stored for several days? Comparing these results with those from other studies also raises the question of why sperm-competition mechanisms vary so much between species^{8–11}. Finally, Price and colleagues' study confirms what other sperm-competition researchers have known for some time — that males and females do not readily relinquish their reproductive secrets. □

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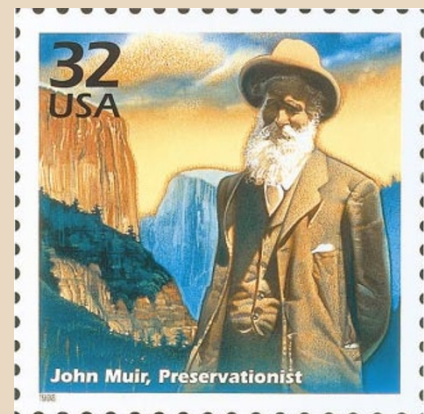
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Exhibition

Roots of a conservationist

John Muir, icon of Americans, and of conservationists world-wide, is being reclaimed by his native Scotland from 31 July to 2 October, in the form of an exhibition in Edinburgh to celebrate his life and achievements. In 1849, aged ten, Muir and some of his family left his native Dunbar, East Lothian, to emigrate to Canada. They became diverted to Wisconsin from where, after an initial career as an engineer and inventor, Muir was drawn to travel and map the wilds of North America. During this long period, 1870–1914, he became increasingly dismayed at the despoilation of the natural world and became the standard bearer in the battle to protect it. Over 200 sites bear his name, and he is here commemorated



on a US stamp. The exhibition is entitled "An infinite storm of beauty" and is at Edinburgh's City Art Centre. **Tim Lincoln**