The trouble with sex

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WHEN the 17th-century microscopist Anton van Leeuwenhoek looked down his microscope at pond water, he became the first human to see rotifers - tiny animals with thrashing cilia that flail so rapidly the rotifers spin like rotating wheels. Although van Leeuwenhoek was struck by their beauty and elegance, he did not suspect that some species of rotifer hold the world record for sexual abstinence. They have been celibate for the past 70 million years, a period of suppressed desire that even the American religious right might find daunting.

The rotifers' enduring celibacy isn't just a curiosity, it's a major biological problem. Biologists generally believe sex to be essential for species' long-term survival, because species that give it up usually disappear within a few hundred thousand years. The standard explanation for this is that **genetic recombination** is essential for purging harmful mutations and allowing new combinations of genes to arise with every generation. But the fact that the rotifers have been asexual for so long suggests that there is something wrong with this view. In spite of their asexuality they have positively thrived: more than 300 asexual species of rotifer are found throughout the world.

So if sex isn't strictly necessary, what is it for? This is one of the most intractable problems in biology. Over 30 different theories have been suggested for solving it, including the mutation-purging and generation of new gene combinations just mentioned, but most have little evidence to support them and none has yet provided a satisfactory answer.

In recent years, however, experimentalists such as myself have started to catch up with the theorists. By studying natural and artificial populations that are mixtures of sexual and asexual strains, or that cycle between the two, we are finally starting to test the theories. And the emerging story reinforces what theorists have long suspected - that there is a delicate balance between sexual and asexual reproduction, and that appropriate conditions can tip the balance in either direction.

The more you think about sex, the more problematic it becomes. Genetic recombination might well be useful for throwing up new mixtures of genes, but what if you have a terrific set of genes to begin with? Why break it up and produce a lot of downwardly mobile offspring? And this is not the only problem sexual organisms face. They have another, almost crushing, disadvantage as well: they make males.

As a male it pains me to have to say it, but we really aren't much good for anything. Imagine a population of animals in which some members reproduce sexually and others asexually. Suppose that each animal that can produce offspring has two of them. This gives the asexual animals an immediate advantage over the sexual ones. On average, the number of sexual animals will not change from one generation to the next. By contrast, the number of asexual animals will double in the first generation, quadruple in the second, and so on. The asexual animals should surely win any race for resources hands-down.

The numerical disadvantage that sexual organisms have in competition with equivalent asexual ones is known as the twofold cost of sex. If a member of a sexual population acquires a mutation that makes it asexual, its progeny should be able to take over the resources and drive the sexual members of the population to extinction. So sex looks like a losing strategy.

With this in mind it's easy to see why rotifers might have abandoned sex. If the original asexual rotifer had a great set of genes, its progeny would have thrived. But there's a problem with this strategy, too. Being asexual might be good in the short term but it is no great shakes in the long run. A set of genes that was fabulous 70 million years ago is very unlikely to be up to scratch today. The world has changed enormously during this time, but the rotifers have only been able to adapt through the slow accumulation of mutations. Which is probably why most asexual species die out in the blink of an evolutionary eye.

Hence the theorists' problems. On the one hand, sex must be advantageous because it is so common. But on the other, asexuality should always win in the short term - and is clearly no absolute barrier to long-term survival, if the rotifers are anything to go by.

Several natural systems have proved useful in testing the various possible solutions to this paradox. One is a group of **21 closely related species of freshwater minnow from the genus Poeciliopsis** that live in Mexico and the south-western US. Robert Vrijenhoek of Rutgers University in New Jersey has followed these minnows for a number of years and has found a complex interplay that illustrates the delicate balancing act between the advantages of sexual and asexual reproduction.

Vrijenhoek discovered that **the fish can move easily from sexual to asexual reproduction**. In fact asexuality arises with unusual ease and many of the asexual species turn out simply to be hybrids of two sexual species. As a result, this type of asexuality has appeared many times in different ponds and streams. Its appearance and disappearance, then, must reveal when and where the different strategies pay off.

What Vrijenhoek found is that **asexual fish often dominate in extreme environments**, such as ponds that reach high temperatures. This is because all the progeny of an asexual, temperature-tolerant fish have the same set of genes as their parent and can therefore survive in the extreme environment. A sexual fish that just happens to be adapted to high temperature will mostly produce progeny that are not well adapted - that problem of downward mobility again.

Nonetheless, sexual populations persist. The advantage they have must be substantial to overcome the twofold cost of sex. One possible advantage is the ability of sexual fish to survive in diverse environments. Where streams show strong seasonal fluctuations in temperature and flow rate, sexual species of Poeciliopsis dominate. Could this be the secret?

The appearance of asexuality in animals is usually a one-way street: Vrijenhoek's asexual fish cannot regain their sexuality. But many plants can slip between the sexual and asexual worlds and can tell us something else about when it pays to use one strategy and when the other. Egyptian lotuses (Nymphaea lotus) are weeds that run rampant in the fields of the Nile delta, and part of their success can be traced to the fact that - like many plants - they can reproduce both sexually and asexually. A lotus plant can not only release seeds, but it can also send out underground "stolons" in every direction. New plants, genetically identical to their parent, grow whenever the stolons reach the surface.

Ahmed Hegazy and his colleagues at Cairo University, Egypt, have found that in the lotus's native marshland, three-quarters of new plants grow from stolons. But when the lotuses invade farmers' fields, they shift their reproductive strategy. Now plants from stolons outnumber those from seeds ten to one.

When a new environmental opportunity opens up, that puts a premium on fast reproduction and the plants shift to a greater reliance on asexual reproduction. Other weedy plants adopt similar strategies.

In many plants, then, the balance between asexual and sexual reproduction depends on the environment. **Asexual species appear to have the advantage if the environment is uniform or at least predictable from one generation to the next, while sexual ones may have the advantage when the environment varies unpredictably in space or time.** But which kind of unpredictability - diversity across space or change over time - gives sexual species the advantage?

There is little doubt that natural environments show variation in space. **Darwin, in the final paragraph of On The Origin of Species, expresses beautifully how complex most environments are when he describes "an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth".** He goes on to claim that his theory of evolution explains such complexity. Now some biologists are using the idea of environmental complexity to explain the function of sex.

Tangled banks

According to these so called "**tangled bank" theories**, spatially complex environments give sexual reproduction the edge over asexual reproduction. This is because the progeny of sexual organisms are all different, and so no matter how numerous they are they will all be able to find somewhere to live. But because asexual organisms only produce progeny identical to themselves, most of them will get crowded out of the few places they can find to live in the tangled bank, and will be unable to live in places available to sexual progeny. And so the numerical advantage of asexual reproduction vanishes.

It's a nice idea but there is little experimental support for it. Back in 1987, Graham Bell of McGill University in Montreal, Canada, and his colleague Austin Burt, now at Imperial College in London, looked at the frequency of genetic crossovers between the chromosomes of mammals with many progeny, compared with those that have small families. They hypothesized that recombination would be greater in the animals that have large families so that their progeny would all be so different from each other that they could all find a place to live in the tangled bank. That would mean large-littered animals, such as rodents, would recombine more genes per generation than animals with small families, such as primates. But Burt and Bell found no such trend.

That suggests environmental variation across space does not give sex the edge. Perhaps, then, it is unpredictability over time that gives the advantage to sexual reproduction. A number of organisms, such as some species of the water flea Daphnia, reproduce asexually during the summer when the living is easy, filling the environment with females. But with the onset of autumn, they start to produce both male and female progeny that mate with each other. Some of the resulting eggs survive the winter, and a whole range of different genetic types of Daphnia emerge the following spring.

Perhaps sexual reproduction is advantageous because conditions change unpredictably from year to year, but this is not usually the case. The seasons tend to follow each other in a predictable fashion. A more likely advantage lies in the fact that sexual recombination produces such a wide range of eggs that some survive the winter, even though they all came from Daphnia selected for their ability to grow and reproduce rapidly in a warm and friendly environment. Daphnia, like the lotuses, reap the benefits of switching between sexual and asexual reproduction.

The picture that is emerging is that unpredictability in some future environment may hold the key to the mysterious advantage of sex. And the very latest experiments back up this picture. A study came out showing that in populations of the nematode worm Caenorhabditis elegans, which reproduces both sexually and asexually, sexually produced individuals are better able to adapt to a changing environment (Science, vol 302, p 1046).

One of the major sources of environmental unpredictability is the diseases that you and your children will encounter in the future.

The late William Hamilton proposed that because our pathogens are always evolving, we must produce a variety of progeny to ensure some will survive to reproductive age. Such environmental change over time would indeed be unpredictable and could give sex the edge. **Hamilton called the process of scrambling to keep up with our pathogens a "Red Queen race" because, like the Red Queen in Through the Looking-Glass, we must race furiously simply to stay still.** Is there any evidence that this actually happens?

Well, host-pathogen races do seem to be important to the advantage of sexuality. Results from the human genome projects show that our immune system genes have evolved more swiftly than other genes, suggesting that they have been caught up in a Red Queen race with the bacteria and viruses that attack us. In their test of recombination frequencies, Burt and Bell found that long-lived mammals such as primates show higher levels of genetic recombination than short-lived ones such as lemmings, perhaps because their progeny will be exposed to a larger range of pathogens during their lifetimes and therefore need to be more variable.

Some recent observations also support the Red Queen theory. Curtis Lively of Indiana University in Bloomington has shown that asexual populations of the New Zealand snail Potamopyrgus antipodarum are more heavily infected with parasitic worms than sexual populations of the same species. And Steven Kelley of Emory University in Atlanta, Georgia, looked at the grass Anthoxanthum odoratum, which also has asexual and sexual populations, and found that the sexual populations have lower rates of viral infection. In my lab, we have run Red Queen races between "killer" and "sensitive" strains of the brewer's yeast Saccharomyces cerevisiae. The killer strains behave like pathogens, destroying the sensitive strains and multiplying in their place. We find that the sensitive strains can fight off the killer strains more effectively if they recombine sexually, and that the killer strains too can become more effective killers through recombination. When both types of strains recombine, they often fight each other to a draw. Of all the myriad theories about sex, the Red Queen seems to be gaining the greatest experimental support.

But it's too soon to discard the other theories. How come rotifers don't need to recombine to evade pathogens? We still have no good answer to that puzzle, but Matthew Meselson of Harvard University has evidence that rotifers have few if any mobile DNA elements that can cause severe mutations. Perhaps the rotifers aren't burdened with as many harmful mutations as most organisms. And so the theory that sex is all about purging harmful sequences from the genome may yet gain strong support. Trust the rotifer to be the odd man out.