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EVOLUTIONARY BIOLOGY

Why reproduction often takes two

Aneil F. Agrawal

On the face of it, self-fertilization is the efficient way to breed: compared with outcrossing, there's usually much less fuss, for a start. So why isn't reproduction by selfing far more prevalent than it is?

Finding a mate can be difficult or even dangerous. Moreover, in many organisms one parent — typically the female — makes a much larger energetic contribution to offspring than the other parent, even though offspring receive an equal number of genes from both parents. Because of these costs, uni-parental forms of reproduction, such as self-fertilization and asexual reproduction, would seem a more evolutionarily sensible alternative[1,2]. Although many plants and animals are capable of self-fertilization, most species reproduce completely or partially through bi-parental reproduction or outcrossing[3,4]. The prevalence of outcrossing implies that there are advantages to this mode of reproduction that outweigh its substantial costs.

Among the hypothesized benefits of outcrossing are that it reduces the effects of deleterious mutations, or that it improves the ability to adapt to changing environmental circumstances. Relevant data that bear on these possibilities have been limited in scope. In this issue (page 350), however, Morran *et al.*[5] report an experimental study that demonstrates the existence of both advantages of outcrossing.

All populations harbour variants (alleles) of genes that are deleterious because mutation is constantly converting good alleles into bad ones ($A \rightarrow a$). Such mutations are often recessive, meaning that most of the negative effects are masked in heterozygotes (*Aa*). Self-fertilization puts these alleles into the homozygous (*aa*) state, thereby exposing them to selection and causing a reduction in fitness known as inbreeding depression. A classic explanation for the maintenance of outcrossing is the avoidance of inbreeding depression. However, when populations reproduce by selfing, recessive deleterious mutations are expressed and eliminated by selection, reducing the magnitude of future inbreeding depression. Consequently, the act of self-fertilization can make it easier for selfing to evolve in subsequent generations[6,7].

But inbreeding depression can never be completely purged, for two reasons. First, selection is ineffective at eradicating mutations of small effect, especially in smaller populations. Second, new mutations are constantly occurring. If deleterious alleles of small effect are introduced at a sufficiently high rate, then inbreeding depression will be maintained at a sufficiently high level to provide an ongoing advantage to outcrossing.

Outcrossing is also hypothesized to be advantageous by allowing for faster adaptation[8,9]. In highly selfing populations, each beneficial mutation is more or less trapped on the genetic background on which it arose. This reduces the rate of adaptation for two reasons. First, the genetic background may contain deleterious alleles at other loci, thus hampering the spread of the beneficial mutation. Second, by being trapped in its original genotype, the beneficial mutation cannot combine with other new beneficial mutations that may have occurred on other genetic backgrounds.

By contrast, when populations are outcrossing, a process of genetic recombination between different genomes occurs, which allows a new beneficial mutation to escape deleterious alleles on its original background and to combine with other beneficial alleles that arise elsewhere in the population. In selfing populations, individuals are largely homozygous, and recombination has no effect on the distribution of alleles, even though genetic crossing-over occurs. Outcrossing is advantageous because it puts different sets of chromosomes together, allowing crossing-over to result in meaningful genetic exchange.

These, then, are two potential advantages of outcrossing. Morran *et al.*[5] tested them with experiments involving populations of the nematode *Caenorhabditis elegans* (Fig. 1). This worm normally exhibits a low to moderate level of outcrossing. But by making use of some well-studied mutants, Morran *et al.* were able to create populations that were either obligately outcrossing or obligately selfing. They then subjected these populations to various evolutionary conditions to investigate how the degree of selfing affects evolutionary outcomes.

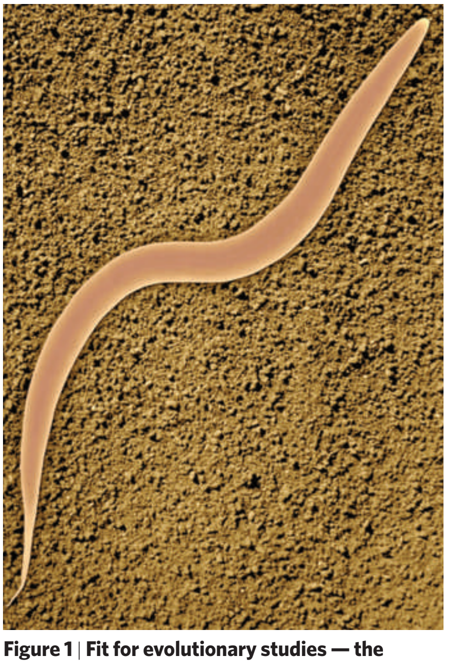

Figure 1 | Fit for evolutionary studies — the nematode *Caenorhabditis elegans*. When it comes to reproduction, one will do, but Morran *et al.*[5] find that outcrossing has evident advantages over selfing (×150).

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In the first experiment, populations were repeatedly exposed to a mutagen, artificially inflating the mutation rate to about twice the normal rate. So that more mutations would affect fitness, these populations were kept in a challenging environment that required the worms to traverse a rugged terrain, as opposed to the benign conditions typically used for rearing *C. elegans* in the lab. After 50 generations, the highly selfing populations showed substantial declines in fitness, as predicted if deleterious alleles cannot be efficiently eliminated. By contrast, obligately outcrossing populations showed no decline.

In a parallel treatment, another set of populations was allowed to evolve in the same conditions but at the normal mutation rate. At this lower mutation rate, the outcrossing populations improved in fitness over time, adapting to the rugged terrain. But the highly selfing populations showed no evidence of adaptation. To further test whether outcrossing facilitates adaptation, Morran *et al.* performed another experiment in which a set of populations evolved in environments containing a virulent bacterial pathogen. After 40 generations, the obligately outcrossing populations showed a staggering 150% increase in fitness, whereas the obligately selfing populations did not adapt at all.

These experimental studies[5] demonstrate a clear advantage of outcrossing populations over selfing populations, and they parallel previous work showing that sexual populations have advantages over asexual populations with respect to the rate of adaptation[10,11]. Although bi-parentally reproducing populations may be more fit, this does not guarantee that alleles causing uni-parental reproduction will not easily invade a population — the individual-level benefits of selfing may be much more important than the group-level costs. The work of Morran *et al.*[5] is particularly intriguing because the authors found evidence that outcrossing evolved within those of their wild-type populations that were not genetically constrained to be obligately selfing or obligately outcrossing. Outcrossing rate in wild-type populations increased in populations subjected to elevated mutation rates, and possibly also in populations adapting to the pathogen.

Experimental evolution studies such as these provide a fundamental first test of theory. However, more detailed experiments are needed to provide a clearer understanding of why reproductive strategies evolve within such populations; are short-term or long-term effects responsible for this type of evolution[12]? By being amenable to a variety of coarse- and fine-scale approaches, such experimental systems hold great promise for helping us to achieve a better understanding of the patterns we see in nature. ■

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PALAEOCLIMATE

Kink in the thermometer

David Noone

Temperature estimates derived from isotopes in polar ice cores reveal much about Earth's past climate. According to the latest analysis, interglacial periods were rather warmer than previously thought.

For the past million years or so, the transition between glaciations and warm interglacials has been dominated by a cycle of about 100,000 years. The last warm period, the Eemian, occurred around 128,000 years ago, and from various proxy measurements it is widely accepted that temperatures then were higher than those during modern pre-industrial times. The Eemian therefore offers a window on the consequences of contemporary global warming. For instance, the warmer climate was associated with significant changes in the volume of the Greenland ice sheet, and as a result sea level could have been about 4–6 metres higher than it is today[1].

In this issue, Sime and collaborators[2] (page 342) describe how they have used climate-model simulations to re-examine the temperature history recorded by the isotopic composition of three long ice cores from Antarctica. The authors conclude that previous estimates of southern-polar warmth during the Eemian and other interglacials have in fact been underestimates. They suggest that temperatures peaked at some 6 kelvin higher than at present, about double the usually accepted figure.

Climate records from polar ice cores provide arguably the best indication of global environmental change on timescales from centuries to many millennia. Like tree rings that mark each year by a season of growing, the continuous accumulation of snow on the ice sheets provides a chronology. The isotopic chemistry of the ice then provides a measure of climate at the time the snow fell. This use of the stable hydrogen- and oxygen-isotope composition of polar snow as an indicator of past temperature comes from pioneering work performed almost half a century ago[3,4]. At sites outside the tropics, a strong relationship exists between annual mean temperature and the annual mean isotopic composition of precipitation[5], which hints at the possibility of using the isotopes from a single site as a palaeothermometer. However, the question remains as to what degree this spatial information can be used to interpret the temporal variability captured in polar ice cores[6,7].

The mechanism leading to the temperature–isotope relationship at high latitudes is the preferential removal of the heavy nuclides oxygen-18 and deuterium (^{18}O and ^{2}H) during precipitation. During transport to the cold polar atmosphere, continual precipitation from an air mass originating at a lower latitude will deplete that air mass in the heavy nuclides. The isotopic composition will depend on the fraction of the original water mass remaining, which depends exponentially on temperature via the Clausius–Clapeyron relation. This gives an approximately linear relationship between the isotopic composition of precipitation and temperature, with a slope of about 8‰ per kelvin for ^{2}H (Fig. 1). Knowing this slope, one can in principle convert measured changes in isotopic composition to a temperature scale.

There are, however, various confounding factors[8]. The isotopic composition of vapour at the source region is unlikely to remain constant; and changes in the distribution of the moisture source will change the isotope–temperature slope, because less-distant sources are less depleted and lead to a reduction of the slope[9]. Further, different cloud microphysical processes dictate a different efficiency in isotopic fractionation. Also, the average isotopic composition of annual layers of snow will be biased towards that of the season in which most of the precipitation falls, so changes in the time of year when snow falls could distort the reconstruction of annual mean temperature. Such factors mean that the spatial relationship

50 & 100 YEARS AGO

NATURE

50 YEARS AGO

It has often been suggested that the dark areas of Mars consist partly of vegetation, particularly in view of the seasonal variation of the intensity of the dark regions. Tests for the high near-infra-red reflectivity characteristic of many plants have all given negative results. A few terrestrial plants, such as some lichens, do not show this characteristic, and possibly such plants are present on Mars. W. M. Sinton ... has suggested and twice carried out a new test for the presence of vegetation. All organic molecules possess strong absorption bands at wave-lengths near 3.4µ ... The radiation received from Mars was analysed theoretically into thermal radiation and reflected solar radiation. The latter shows three absorption bands at 3.43µ, 3.56µ and 3.67µ ... Although one cannot be certain that no inorganic molecule can explain these absorption bands, the observed spectrum does fit very closely that of organic compounds and plants ... Sinton's results are the best evidence yet produced for the existence of vegetation on Mars.
From *Nature* 21 November 1959.

100 YEARS AGO

With reference to the recent paper by Dr. Pocklington before the Royal Society, on the functions of the Martian canals ... I should like to suggest that these canals may perhaps be used for power-storage purposes. In Mars, possibly, there are seasons of winds or monsoons during which the upper reaches of the canals would be pumped full by innumerable windmills, and the power thus stored utilised during calm seasons, and transmitted electrically for lighting, heating, and general power purposes. For a population which had exhausted all its mineral fuel, which possessed no extensive ocean, and whose soil and climate were unsuitable for the growth of fuel, this would indeed appear to be the only means of obtaining heat and power.
From *Nature* 18 November 1909.