

## **Sex: a pluralist approach includes species selection. (One step beyond and it's good.)**

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In their paper, West *et al.* (1999) propose the idea that instead of trying to oppose two hypothetical forces (fluctuating ecology and DNA repair), concerning the evolution of sex, it could be of interest to try to explore the idea that they can act simultaneously and that the interaction between them could provide interesting mechanisms. The aim of the present commentary is to try to demonstrate two points.

**1** This is a good idea; however, it suffers a handicap: namely because it tends to decrease the level of conflict between individuals (and/or 'schools'), it might be ignored by people who think that it is more fun to compete.

**2** Instead of remaining stuck to individual selection alone, one could go even further and stop opposing short-term and long-term selection but explore the possibilities offered by the simultaneous action of these two forces. This has been tried by a few of us but, perhaps because it suffers the handicap stated above, it has been forgotten in most reference lists.

G. Bachelard stated that it is not sufficient for humans to be right, they must be right against somebody. The need for such fightings has already caused great trouble in evolutionary biology. In the beginning of the 19th century, Cuvier stated that all species went extinct; Lamarck answered that no species ever went extinct. Had they accepted the idea that some species could go extinct while others would not, long and sterile fights would have been avoided. Similarly, at the beginning of the 20th century, Darwinians (Pearson) stated that natural selection was the driving force of evolution while geneticists (Bateson) were putting mutation forward

(see Provine, 1971). Thirty years of conflict would have been avoided if scientists had tried to assemble these two forces (as proposed by Yule, whom nobody seems to have listened to) instead of fighting.

This Bachelard-effect has probably contributed to the complexity of the debates about the maintenance of sex. In allogamous anisogamous species, a two-fold disadvantage (or 'cost') to sexual reproduction has been demonstrated by Williams (1975) and Maynard Smith (1978). This discovery seemed to imply that a two-fold advantage to sex had to exist to compensate for this cost. Moreover, because sex is a general phenomenon throughout the living world, this advantage had to be of a general nature. Consequently, numerous authors have desperately tortured their models and/or data in order to reach the magic value of 2. A list of some of them is provided in West *et al.* who state that most models and hypotheses fall into two categories. (i) Sexual reproduction, by producing variable offspring, is advantaged through sib competition and diverse sorts of variable environments, an idea starting with Williams & Mitton (1973) and later rendered more sexy by the involvement of parasites and the Red Queen by Hamilton (1980) and colleagues. (ii) By allowing repair of damages and/or mutations, sex is advantaged when the genome is large enough (Michod & Levin, 1988). West *et al.* quite rightly show that combining these two forces can provide interesting results.

However, they do not include the fact that these forces certainly act in the short term and in the long term. The observation that most asexual species appeared recently (see Judson & Normark, 1996, for the scandalous exceptions) shows that most of those which appeared earlier have gone extinct. It constitutes therefore a good proof that species selection is active on this trait (Maynard Smith, 1986).

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Indeed, in the real world, experiments and observations show that sex is usually not maintained by short-term selection. One can actually wonder how could asexual species even exist for more than a couple of generations if asexual reproduction implied a cost larger than 2 per generation (a point raised by Stearns, 1987). In aphid *Rhopalosiphum padi*, sex is maintained by the need for producing eggs (parthenogenesis is viviparous and winter frost kills all animals but not eggs) as shown by Rispe *et al.* (1999). The same kind of mechanism could be involved in *Chlamydomonas* (G. Bell, personal communication). In the fruit fly, *Drosophila mercatorum*, sex is maintained by an unexplained low fertility of parthenogenetic females (Templeton, 1982). Most plants cannot produce dispersal or resistance structures without undergoing sexual reproduction. Most animals do not use asexual reproduction simply because they cannot (for complex developmental reasons, including genomic imprinting). While a mixture of sexual and asexual reproduction constitutes probably an optimal strategy, species are, for most of them, either sexual or asexual ('the big theoretical problem' according to Hurst & Peck, 1996). Those which are sexual seem to keep this reproductive system for a variety of reasons. Moreover, in most of them, sex seems to be mainly maintained by constraints. All these features remain incomprehensible as long as multilevel selection is not taken into account.

The idea of multilevel selection in that context is that, everything being equal, individual selection is unable to resist the two-fold cost of sex but that species selection sorts out as extant those species which, for whatever reason, are unable to become asexual (i.e. are unable to produce 'good' asexual progenies). The others become asexual and then go extinct. From this point of view, species selection has favoured diverse mechanisms acting in the short term (e.g. constraints or other short-term forces including selection). It is thus not surprising to find that different studies provide divergent results. This idea was proposed by Gouyon & Gliddon (1988) and Gliddon & Gouyon (1989), and Nunney (1989) who formalized it. In this context, it is important to realize that evolutionists are used to forget that questions asked at different levels may ask for answers at different levels. In the present case, the questions 'Why are most species reproducing specially?' and 'Why are aphids *R. padi* reproducing sexually?' do not deserve the same treatment. The answer to the latter can be 'Because they need sex to produce eggs which resist to frost' while the answer to the former will be 'Because those which could evolve asexual reproduction eventually went extinct'. As stated earlier, the generality of sexual reproduction implies that there must be a general explanation but this general explanation can be found at the interspecific level while short-term reasons need not be general. Restricting the research to a general short-term reason has thus been misleading.

The multilevel explanation is an extension of the idea proposed by West *et al.* It is in perfect agreement with their statement that 'the factors maintaining sexual reproduction may be different from those which led to its evolution'. It is probably one of the major challenges for evolutionary theory of the next century to try to put together the different bits and pieces produced by different 'schools', particularly concerning levels of selection, chance, necessity and contingency (or constraints). Only if we are able to play this game, instead of systematically opposing the different possible hypotheses, shall we make significant progresses and avoid endless and sterile debates.

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### References

- Gliddon, C.J. & Gouyon, P.H. 1989. The units of selection. *Trends Ecol. Evol.* **4**: 204–208.
- Gouyon, P.H. & Gliddon, C.J. 1988. The evolution of reproductive systems: a hierarchy of causes. In: *Plant Population Ecology* (A. J. Davy, M. J. Hutchings and A. R. Watkinson, eds), pp. 23–33. Blackwell scientific publications, Oxford, UK.
- Hamilton, W.D. 1980. Sex versus non-sex versus parasites. *Oikos* **35**: 282–290.
- Hurst, L.D. & Peck, J.R. 1996. Recent advances in understanding of the evolution and maintenance of sex. *Trends Ecol. Evol.* **11**: 46–52.
- Judson, O.P. & Normark, B.B. 1996. Ancient asexual scandals. *Trends Ecol. Evol.* **11**: 41–46.
- Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge, UK.
- Maynard Smith, J. 1986. Contemplating life without sex. *Nature* **324**: 300–301.
- Michod, R.E. & Levin, B.R. 1988. *The Evolution of Sex*. Sinauer, USA.
- Nunney, L. 1989. The maintenance of sex by group selection. *Evolution* **43**: 245–257.
- Provine, W.B. 1971. *The Origins of Theoretical Population Genetics*. The University of Chicago Press, USA.
- Rispe, Cl., Pierre, J.S., Simon, J.-C. & Gouyon, P.H. 1998. Models of sexual and asexual coexistence in aphids based on constraints. *J. Evol. Biol.* **11**: 685–701.
- Stearns, S.C. 1987. *The Evolution of Sex and its Consequences*. Birkhäuser Verlag, Basel, CH.
- Templeton, A.R. 1982. The prophecies of parthenogenesis. In: *The Evolution and Genetics of Life-History Strategies* (H. Dingle and J. P. Hegman, eds), pp. 75–101. Springer Verlag, Berlin.
- West, S.A., Lively, C.M. & Read, A.F. 1999. A pluralist approach to sex and recombination. *J. Evol. Biol.* **12**: 1003–1012.
- Williams, G.C. 1975. *Sex and Evolution*. Princeton University Press, Princeton, USA.
- Williams, G.C. & Mitton, J.B. 1973. Why reproduce sexually? *J. Theor. Biol.* **39**: 545–554.