

## COMMENTARY

# Origin, age and diversity of clones

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The origin of sexual reproduction may well have been a unique evolutionary event, or series of events, but the maintenance of taxonomically widespread sex is not: it consists of many local skirmishes between sexual lineages and their asexual offshoots. Neither sexually reproducing populations nor asexual lineages are uniform in their characteristics. They vary in many ways that might influence the outcome of their evolutionary interaction, such as their ecological role, genome size and complexity, level of genetic variation, mutation rate and, for sexual populations, freedom of recombination. Although sexual reproduction predominates in animals and plants, and asexual lineages are typically short-lived and taxonomically isolated, these general patterns should not be allowed to obscure the true diversity. There are long-lived, widespread, genetically and even taxonomically diverse asexual lineages at one extreme and sexual populations with no asexual descendants at the other. In between, there are sexual species with high levels of inbreeding and asexual lineages that hybridize with sexual relatives. A complete understanding of the evolution of reproductive modes will encompass these extremes as well as the typical pattern. It seems to us that only a pluralist approach is likely to be successful in the sense that there are complex patterns to explain, not a simple dichotomy. However, this is not equivalent to the approach advocated by West *et al.* (1999) who apparently wish to abandon the search for a single mechanism capable of explaining the predominance of sexual reproduction but at the same time ignore the variety of reproductive modes found in nature.

West *et al.* (1999) draw much needed attention to the dynamics of the interaction between sexual species and asexual lineages. Initially, a new clonal lineage is very susceptible to parasites as it becomes abundant but, as it accumulates genetic diversity, this risk declines. Although individual asexual lineages may persist for short periods of time, asexual reproduction might persist if new clones originate with sufficient frequency from the sexual population. It may be that building frequent origination of clones into the models of Howard & Lively

(1994, 1998) would increase the parameter space in which asexual reproduction displaces sexual reproduction. On the other hand, West *et al.* (1999) argue (p. 19) that maintenance of clonal diversity and maintenance of sex are 'somewhat separate issues'. While we agree that clonal diversity may be explained in part by resource partitioning, this is not readily separable from the outcome of interactions between sexual populations and asexual lineages: clonal diversity maintained by resource partitioning can make the asexual lineages more resistant to displacement by the sexual population because clones are better adapted to environmental conditions, because diversity in parasite resistance is maintained incidentally through linkage disequilibrium, and because resource partitioning allows higher population size and thus retards the ratchet.

The diversity of clones, their modes of origin and their rates of turnover are empirical issues that need to be addressed. The standing diversity of clones is clearly a product of origination and extinction rates but these are very hard to separate. In nonmarine ostracods, for example, clonal diversity is highly variable, as detected by allozyme electrophoresis: from seven clones in *Darwinula stevensoni* to 211 clones in *Eucypris virens* with comparable sampling efforts across Europe (Rossi *et al.*, 1998). However, the reasons for this variation are largely unexplored. Clonal diversity may be generated in at least three ways (Butlin *et al.*, 1998): mutation within existing clones (including autopolyploidy), separate origin of clones from a sexual ancestor, or hybridization between asexual females and males of the same or related species (usually generating triploid offspring). Only the first process is available to *D. stevensoni*, which lacks sexual relatives, but multiple origins of asexual reproduction and hybridization have both been demonstrated in ostracod species with sexual populations or closely related sexual species, including *E. virens* (Turgeon & Hebert, 1995; Schön & Butlin, 1998). It has been suggested that species with sexual congeners tend to have higher clonal diversity than those that do not (Havel & Hebert, 1989). On the other hand, very little is known about rates of turnover. Griffiths & Butlin (1995) found that asexual species were less abundant, and more variable in abundance, than sexual species in Holocene fossil sequences. Note that the term 'asexual species' here refers to a set of morpholog-

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ically similar asexual lineages. The variable abundance could reflect clonal turnover on a time-scale of thousands of years. However, clones may show DNA sequence divergence equivalent to several millions of years of separation (Chaplin & Hebert, 1997; Schön & Butlin, 1998; Schön *et al.*, 1998). Unfortunately, molecular phylogenetic data cannot distinguish multiple origins of lineages relatively recently from smaller numbers of older origins, and can only include extant lineages. Therefore, these data do not really answer the critical question.

The situation in ostracods is as well characterized as in most taxa (Martens, 1998). Only in some asexual vertebrates, derived from interspecific hybridization in all cases, is the origin, diversity and turnover of clones better documented (Avisé *et al.*, 1992). Thus, it is premature to abandon studies of 'pattern' in order to concentrate on parameter estimation and the testing of assumptions, as advocated by both Kondrashov (1993) and West *et al.* (1998). The prediction that asexual lineages persist in the face of the Red Queen through clonal turnover needs to be tested, for example by determining the distribution of parasites among clones as suggested previously by Lively (1992). An explanation is needed for the persistence of asexual lineages with low clonal diversity or without sexual relatives and therefore with limited input of new genotypes. In a species with many asexual lineages like *Eucypris virens*, we need to understand why sexual populations coexist with asexuals in only a small part of the current range. There is no evidence that this is due to parasite prevalence. Currently, the best explanation is based on climate change during the Holocene (Horne & Martens, 1999). It may be true that Red Queen models can potentially explain patterns of sexuality but the Red Queen hypothesis should not be restricted to parasites: in its original form (Van Valen, 1973), it encompassed all environmental change, biotic and abiotic, parasites, predators and competitors. We are not convinced by the claim, unsupported by references, that 'the parasite models predict the majority of within- and between-host patterns of sexuality' (West *et al.*, 1999, p. 16).

West *et al.* (1999) do not mention the so-called 'ancient asexuals' (Judson & Normark, 1996). These lineages have apparently persisted for tens of millions of years without sex (100 million years or more for the darwinulid ostracods on the basis of their excellent fossil record, Schön *et al.*, 1998), have diversified (more than 20 extant darwinulid species, all asexual; Rossetti & Martens, 1998), and in some cases are abundant and widespread (e.g. *Darwinula stevensoni*; Griffiths & Butlin, 1995). They present a real difficulty for all theories but, as arguments are made that suggest additional reasons for sexual lineages to displace asexual ones, the problem becomes ever more serious. While Howard & Lively's (1994, 1998) simulations based on the pluralist approach indicate a wider parameter space for the maintenance of sex, so they automatically imply a narrower range of conditions in

which asexual lineages can persist for long periods of time. Indeed, in their 1994 simulations where Muller's ratchet operates in the absence of epistatic effects of deleterious mutations, asexual lineages go extinct rapidly (150–500 generations) even in the 'asex wins' part of parameter space! With epistatic fitness effects, the ratchet is less effective or may cease to operate (Hurst & Peck, 1996; Howard & Lively, 1998) but the pluralist approach suggests that its effects will be augmented by the Red Queen so that again, even lineages that initially displace their sexual competitors are doomed to rapid extinction. Ancient asexuals must simultaneously escape both processes. Perhaps they achieve this by virtue of a 'general purpose genotype' (Lynch, 1984) or by efficient DNA repair (Schön & Martens, 1998). In any case, they are a part of the overall picture of reproductive modes and must be accommodated by any complete theory.

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