Heterogony and the Problem of Vertebrate Sexuality

There are certain problems in explaining the proportionate representation of sexuality and asexuality in low-fecundity groups such as most vertebrates, on the basis that only long-term disadvantages, accruing over several or many generations, account for the paucity of asexuality, and that there are insufficient short-term advantages, accruing, say, across one or two generations, to maintain sexuality (e.g., Fisher, 1930; see Alexander and Borgia, ms).

First, this explanation requires a low level of shifts to asexuality; otherwise, much asexuality should be in evidence, since it would be repeatedly favored for several to many generations, in lines in which it was initiated.

On the other hand, if changes to asexuality are commonly irreversible, then in every population in which asexual lines could not entirely extinguish the sexual lines, sexuality would persist, and tendencies by sexual lines to produce asexual lines would continually be downselected. Even if sexuality were always disadvantageous on a short-term basis, it would persist, and sexual lines would produce asexual lines with increasing rarity.

Williams (1975) notes that there are no heterogonic vertebrates, and he argues that this is so because vertebrates are generally unable to gain sufficiently in fecundity by asexuality during a single year to make temporary changes to asexuality profitable. In effect, he is arguing that vertebrate environments contain no multi-generational environmental switches between (a) stable and (b) changing, unpredictable environments favoring, respectively, asexual and sexual reproduction, such as are common for multivoltine invertebrates.

In regard to heterogony, Williams refers specifically to the requirement of "environmental cues to synchronize sexual reproduction at the optimal moment" (p.105). A periodically or facultatively sexual genotype could, however, feasibly cue on changes in its own evident fitness in the population, becoming sexual when its fitness was deteriorating. Only sudden and unpredictable causes of extinction would be unavoidable by this strategy.

But Williams refers to the synchronizing of sexuality, raising the question of the detriments of different clones becoming sexual at different times. Such clones might be forced to inbreed, once facultative asexuality became prevalent, severely reducing but not necessarily eliminating the advantages of recombination. On the other hand, facultatively sexual lines still in a decided minority would be able to outbreed with the prevalent sexual lines. At the very least, if asexuality is always favored on a short-term basis, this would imply that many such facultatively sexual lines should be generating continually. Such lines would be rare, then, only (1) if facultative sexuality quickly replaced obligate sexuality (leaving no obligately sexual lines to mate with), (2) if even brief facultative asexuality were disadvantageous (as compared to obligate asexuality), or (3) if for physiological or genetic reasons vertebrates are specialized beyond ability to generate facultative sexuality.

To my knowledge there is no actual evidence that any vertebrate sexual line has been extinguished, even locally, by an asexual line generating from it. The other two alternatives are (1) the asexual line quickly disappears or (2) the two lines persist and diverge, occupying different ecological niches, each failing to extinguish the other. Presence of only pure sexual and asexual lines, as in vertebrates, is not evidence for extinction of sexual lines by asexual lines, but only for temporary survival of asexual lines in the presence of sexual competitors.

Total absence of facultative sexuality, or heterogony, in vertebrates is, on the basis of the above reasoning, evidence against the argument that sexuality is not maintained because of short-term advantages. If short-term advantages did not outweigh disadvantages, some facultatively sexual lines would be expected within sexual species even if such lines characteristically outcompeted wholly sexual lines. The only defense against this reasoning appears to be that vertebrates remain maladaptively incapable of generating heterogonous lines.

Diploid parthenogenetic forms closely resembling sexual forms appear to be rare, or virtually absent in vertebrates; if prevalent they should have been detected in many common species. The parthenogenesis found in domestic turkeys and chickens seems insufficient to imply an undetected commonness of parthenogenesis among vertebrates in general (and produces only males).

Of 27 "species" of parthenogenetic vertebrates 11 are diploid, 16 are triploid, and probably all are products of interspecific hybridization (Cuellar, 1974), supporting the idea that heterogony is difficult for vertebrates. Their genotypes and phenotypes are evidently unlike those of their parental sexual forms for reasons other than slow, gradual competitive divergence or extinction of their sexual progenitors.

Regardless whether heterogony is not favored or not possible, its absence in vertebrates means that tendencies to produce asexual lines would be disfavored whether or not short-range benefits of sexuality existed. Because asexual offspring become, in Fisher's terms, threats to the descendants of the sexual line, the tendency to produce them is a disadvantageous trait of sexual individuals. This means that the paucity of diploid parthenogenesis is not evidence that the vertebrates are somehow incidentally specialized beyond the capability of producing advantageous asexual forms, but that they are adaptively unlikely to do so. Moreover, the virtual restriction of parthenogenesis in vertebrates to triploid or polyploid forms produced by hybridization implies that parthenogenetic vertebrates survive long enough to be observed only when they are so different from their progenitors as to fail to compete so completely that they are quickly extinguished by their superior sexual relatives. They survive, in other words, as peculiar species, to be extinguished over the long run in a process of group selection completely parallel to that responsible for the extinction of most sexual species during phylogenetic history.

A Caution: The above essay on costs of sexuality may seem to disagree with all other published arguments, which are illustrated by Williams (1975). The argument on sexuality in vertebrates definitely reaches a conclusion different from that of Williams. I urge you to read Williams' arguments if you are at all interested in this difficult problem.