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The American Naturalist, Vol. 117, No. 5. (May, 1981), pp. 810-813.

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IMPLICATIONS OF SEX FOR THE ANALYSIS
OF LIFE HISTORIES

Stearns (1976, 1977) criticized theoretical treatments of the evolution of life history traits for not considering the effects of sexual reproduction. He explained this lacuna by claiming that "the alternative of dealing with sexual recombination explicitly is overwhelmingly complex" (1976, p. 6).

Actually, sexual reproduction introduces two distinct complications to the analysis of life histories. First, the genotypes are constantly being reshuffled, making calculations of intrinsic rates of increase for particular genotypes impossible. This difficulty can be avoided only by assuming that the genes affecting life history traits all have additive average effects (i.e., no epistasis). The other complication arises from the fact that sexual offspring transmit only a subset of the genome of their maternal parent. Here we make the simplifying assumptions necessary to remove the first complication and then explore how the second complication affects predictions made by life history theory. By doing so, we hope both to resolve some of the ambiguity recognized by Stearns and to illuminate the general relationship between generation time and the genetic cost associated with sex.

Our point of departure is Hamilton's (1964) notion of inclusive fitness. According to this viewpoint, natural selection will tend to maximize the combined fitnesses of an individual and all of its relatives, discounted by their coefficients of relationship. Since sexually derived offspring have a relatedness of less than one, sexual fecundity should be discounted by this fraction in life history analyses. (Actually the discount includes both the degree of relatedness and the reproductive value of all relatives. In the models we consider, however, all individuals have the same reproductive value.) Another way of stating this is to consider inclusive fitness as a measure of the rate of increase of an individual's genome (genes identical by descent). Sexual reproduction reduces this rate of increase by diluting an individual's genome with genetic material from other individuals. This consequence of sexual reproduction has been termed the "cost of meiosis" by Williams (1975) and the "cost of producing males" by Maynard Smith (1978).

With sex, Cole's (1954) classic comparison between a hypothetical annual and an immortal perennial becomes modified in a simple yet profound way. Instead of adding one to the litter size of the annual to match the population growth rate of the perennial, a sexual annual must add two to the annual fecundity of a sexual and immortal perennial to match genome growth rates. This is clear, since two sexually produced offspring would be genetically equivalent in this situation to the survival of the adult to the next breeding season. If the population were somewhat inbred, the hypothetical annual would need to add somewhere between one and two offspring to match genome growth rates.

Charnov and Schaffer's (1973) generalization of Cole's result is modified similarly. They deduced that if the juvenile's probability of surviving through the first year were c , and the survivorship of the perennial adult were p for each year after

the first, then the annual would need a fecundity of p/c plus the annual fecundity of the perennial in order to have equal population growth rates. With sexual offspring discounted by their relatedness, the additional fecundity needed to match genome growth rates would be $2p/c$ in the absence of inbreeding. Whenever fecundity is limited by energetic constraints, this additional fecundity may be difficult to attain. As in the previous case, sexual reproduction favors the perennial habit.

For biennials, both Schaffer and Gadgil (1975) and Hart (1977) derived the minimum biennial fecundity (b_2) necessary to match the population growth rate of an otherwise similar annual:

$$b_2 = \frac{c}{p} b_1^2 \quad (1)$$

where b_1 is the annual's fecundity, and c and p are the first and second year survivorships, respectively. Explicitly accounting for sex and equating the genome growth rates of the annual and biennial, the relation becomes:

$$b_2 = \frac{c}{2p} b_1^2. \quad (2)$$

Here, the effect of genetic dilution is even more obvious: By postponing reproduction one year, the biennial increases its effective fecundity by a factor of two.

We are using "fecundity" here in a broad sense to include reproductive investment in both male and female functions for a hermaphrodite, or both male and female offspring for a dioecious species. It should be noted, however, that if fecundity is interpreted strictly as the number of offspring accruing through the female functions of a hermaphrodite or the number of female offspring per female in a dioecious species, then the original growth rate comparisons of Cole, Charnov and Schaffer, etc., still apply (Charnov et al. 1981). The factor of 2 can thus be incorporated either by defining fecundity in this strict sense or by modifying the life history equations in the way we propose here. In the asexual models, this problem does not arise because the definitions of fecundity are equivalent. For sexual life histories, we prefer modifying the formulation since the total change in reproductive resources needed to alter the life history indicates the difficulty of the transition and is more obvious with this approach. Also, empirical comparisons of life histories are most often based on total reproductive allocation rather than investment in female function.

Until now, we have assumed that asexual and selfed offspring are equivalent to sexually produced offspring in every respect except relatedness. If, instead, the sexually produced offspring have superior mean fitness of an extent just sufficient to compensate for their lack of relatedness, then the "cost of meiosis" would be repaid in every generation. In this case, reproductive mode would have no net effect on the optimal pattern of age-specific reproductive investment.

There are two reasons why we expect that the costs of sex cannot be repaid when the generation time becomes very short. Under conditions of high selection intensity and sibling competition, sex may be favored for its ability to produce diversity within competing sibling groups (Williams 1975; Maynard Smith 1978). High fecundity and/or local dispersal are necessary to generate these conditions.

Short-lived species, however, will generally be small (Bonner 1965), and, other things being equal, will have a lower fecundity per generation than longer-lived species. In addition, short generation time is often associated with ability to disperse widely and colonize unexploited habitats (MacArthur and Wilson 1967; Horn 1978), situations with low levels of sibling, and intraspecific competition. Thus, relatively low fecundity and occasionally wide dispersal may restrict the number of situations favoring sexuality in organisms with short generation times.

A second set of circumstances favoring sexual recombination occurs when small effective population sizes produce random linkage disequilibrium that slows adaptation that is occurring at different loci (the "Hill-Robertson effect," Felsenstein and Yokoyama 1976). Arguing again from the general correlation between lifespan and size, we expect small, short-lived species to have larger effective population sizes. Additionally, the rate of decay of linkage disequilibrium depends on the number of generations per unit time. We therefore expect less linkage disequilibrium and reduced selection for sex and recombination in short-lived organisms.

Both arguments rely on broad associations between generation time and other demographic characters. Such generalizations may seem unwarranted, given the number of possible extenuating biological details. Nevertheless, we feel justified in making them since we are interested in making only very general predictions over a wide range of generation times.

We have now turned the question around from, How does sex modify the analysis of life histories? to, How does an organism's generation time affect its probability of adopting sex? As sexual generation time shortens, the rate of gene dilution per unit time increases while the potential benefits accompanying sexual reproduction probably decrease. We therefore predict on a priori grounds that sex should be more common among long-lived perennials than among short-lived species. Without pushing the interpretation too far, there does appear to be a general pattern of a reduced sexuality among species with short generation times. At the microscopic extreme, yeast, algae, and protozoa utilize asexual fission extensively. Invertebrates, such as aphids, rotifers, and *Daphnia*, which are capable of several generations in a year, frequently restrict sexual episodes to once per year. (Williams [1975] anticipated our result by suggesting that in these organisms fecundity per generation and the number of generations per sexual life cycle should be inversely correlated because some minimum total sexual fecundity was needed to generate enough sibling competition to favor sex.) Finally, among the higher plants, annuals self more frequently than perennials, thereby restricting their rate of gene dilution (Stebbins 1950; G. Muenchow, unpublished tabulation). Baker (1955), however, has interpreted this as an adaptation for colonization by single plants. A more comprehensive comparison would be a better test of our hypothesis.

ACKNOWLEDGMENTS

We thank H. S. Horn and R. M. May for early discussion of this topic. J. J. Bull and E. L. Charnov helped us recognize how the term fecundity can be interpreted in different ways.

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Submitted January 9, 1979; Accepted October 1, 1979