## THE COST OF MATING

The existence of sexual reproduction presents a paradox for the theory of natural selection. A female who leaves $n$ sexually produced offspring transmits only half as many of her genes to the next generation as does a female who produces $n$ offspring asexually. This 50% penalty imposed upon the sexual reproducer is commonly called the "cost of meiosis." A second penalty of sexual reproduction, less readily quantified than the first, is that imposed by recombinational load.

Taken together, these two costs have been quite enough to challenge theoreticians concerned to understand the adaptive significance of sex. Despite important differences, serious students of the problem (notably Muller 1932; Crow and Kimura 1965; Maynard Smith 1971; Williams 1975) are apparently unanimous on these points: (1) The value of sex must lie in some aspect of increased diversification of offspring; and (2) in species of very low fecundity, such as most vertebrates, the costs of sexual reproduction are too great to be paid by any conceivable gain in individual genetic transmission. Williams concludes that sexual reproduction is therefore "maladaptive" in such low-fecundity organisms, in the sense that sexual reproduction would be at a selective disadvantage if placed in intrapopulational competition with parthenogenesis, and he reviews a few cases where the emergence of parthenogenesis in a vertebrate species has indeed led to a loss of sexuality.

I submit that these conclusions about the costliness of sex have been reached even while overlooking some important further costs, which may be subsumed under the label *cost of mating.*

The costs in question arise from the fact that sexual reproduction requires an orchestration of the activities of two organisms, while asexual reproduction does not, and furthermore from the fact that the mates' interests are not identical (see Trivers 1972). There are costs involved in locating mates, in courtship, in competition with rival suitors, and in copulation or other means of fertilization.

These costs fall mainly upon the male, but this greater portion we may disregard. In considering the cost of mating as part of the cost of sexual reproduction, we are concerned to contrast the costs incurred by a sexually reproducing female with those incurred by a hypothetical asexual reproducer. The female's share of the costs, although the lesser, is substantial.

Discussion of these costs is hindered by the lack of a general currency in which to express them. Ideally, we would refer to the abstract quantities "reproductive effort" and "residual reproductive value," but the costs in question presently defy measurement in these terms. As Pianka and Parker (1975) remark, for example, attempts to quantify reproductive effort have yet to deal adequately with mortality risk. I will therefore simply mention some of the costs of mating, without attempting to quantify them. Such a list must include at least these six: the energetic costs of (1) sexual mechanisms, (2) sexual behavior, and (3) escape from unwanted sexual attentions, as well as risks of (4) predation, (5) disease transmission, and (6) injury inflicted by the male. I will draw my examples primarily from the mammals, but similar considerations presumably apply widely among animals, and some will apply to sexually reproducing plants.

1. Mechanisms directly subserving sexual union are constructed at a cost in energy. This is certainly true of physical structures such as the devices by which flowering plants lure insect pollinators and the display organs by which animals lure mates. Furthermore, animal courtship and mating behavior are often elaborate. This may well be a sort of cost, though I am unsure how sound is the notion of "burdening the germ plasm" with a complex behavioral repertoire. Moynihan (1970) has argued that the manageable size of a species' repertoire of social signals is limited, so that the addition of one display may demand the loss of another.

2. Besides the costs of producing structures (including behavioral substrates), the actual performance of behavior costs time and energy too. I am not aware of any attempts to measure the energetic costs of courtship and mating. In mammals, females are much more active in courtship than has generally been appreciated (Beach 1976). In many studies of small mammals, females have been found to travel more extensively when in estrus, behavior which presumably functions to increase their likelihood of encountering a male but which also costs energy (and may heighten predation risk).

3. Pursuit by sexually interested males can cost females much time and energy. Ewes of the mountain sheep are chased, kicked, mounted, pushed, and butted until they "give up" and are mated (Geist 1971). Yearling rams attempt rape and must be fought off. The ewes apparently suffer some restriction of their possibilities for energy intake, since mating chases drive them into nonpreferred habitats and guarding by dominant rams restricts their movements. The ewes may even suffer a mortality risk: They regularly jump to narrow footholds on cliff faces to escape sexual pursuit.

The costs incurred by females as a result of male attentions are probably heaviest in highly polygynous species. In monogamous species, the males' reproductive interests more nearly coincide with those of their mates, so we would not expect the evolution of male reproductive strategies that actually penalize the females. Nevertheless, substantial costs of male attentions are sometimes incurred by females even under a relatively monogamous mating system. A coyote bitch, for example, endures more than 2 mo of mounting attempts before she is receptive. The male's attentions repeatedly demand that she threaten him or flee from him (Bekoff and Diamond 1976).

4. Sexual mating may heighten predation risks. I am unaware of data directly confirming this, but it is a testable hypothesis. Female fireflies are obliged to flash back at passing males if they are to be fertilized (Lloyd 1966). In so doing, they risk exposing themselves to other animals too. A female guppy, even when already inseminated and in no need of a male, is pursued by brightly colored conspicuous males who must increase her own conspicuousness. During the mating season, female garter snakes are sometimes enveloped by a writhing ball of competing males, and the snakes are often preyed upon under these circumstances (Gibson and Falls 1975).

5. The risk of disease transmission is another cost of mating. This is most obvious in the case of venereal diseases, but the proximity necessary for mating must facilitate the transmission of other infectious diseases as well. In times of plague, the relative advantage of asexual reproduction could be enormous.

6. A final penalty upon the sexually reproducing female lies in the risk of injury (or other direct interference with her fitness) by the male. The ethological analysis of courtship (e.g., Bastock 1967) leads to the conclusion that aggressive elements are often involved. This is not surprising in view of the fact that the courting of females and aggressing toward other males are often seasonally simultaneous male functions which share proximate causal factors such as androgenic facilitation. This fact entails risks for females. Males are often less than perfect in inhibiting their aggressiveness to females. Among the Carnivora, courtship commonly involves elements of combat, and fatalities, while rare, are not unheard of (Ewer 1973). In rhesus monkeys, wounds are incurred at a significantly higher rate during the mating season than at other times of year; this is specially true of males, but it applies to females too (Vandenbergh and Vessey 1968). Carpenter (1942, p. 141) observed several instances in which estrous females were severely wounded at the hands of males and wrote, "The process by which a male possesses a female ('courtship') involves vigorous, aggressive attacks by the male. During these attacks, many of the females are wounded and all are driven into a state of submissive 'rapport' and responsiveness to the male."

Again, such costs of mating are likely to be particularly severe in highly polygynous species, but misdirected male aggression can penalize the female in monogamous species

too. Snow (1958), for example, observed European blackbird pairs in which the males were breeding for the first time, having just won their territories from established males at considerable aggressive effort. Such males persisted in aggressing against their mates too, and in so doing they obstructed and delayed the females' nest building.

Male attacks also cost the female if they are directed against her young rather than herself. Carpenter noted one case where an infant rhesus monkey was killed as a result of a male's attacks on the estrous mother. In langurs, infants are commonly killed by males whenever one polygynous male deposes another and takes over his females (Sugiyama 1965; Yoshiba 1968; Mohnot 1971; Rudran 1973; Hrdy 1974). This startling behavior may be selectively advantageous to the murderous male, but it is unquestionably costly to the female. Hrdy (1974) reviews a number of other observations of infanticide by males in several primate species.

The cost of mating varies according to the systems of mating and parental care. In polygynous species with minimal paternal investment and much male competitiveness, the very devices by which males compete may penalize the females, as for example in prolonged mating and other burdensome methods by which male insects protect themselves against sperm competition (Parker 1970). Disease transmission risk should also be lower in monogamous species.

In species with considerable paternal investment in the young, not only are the costs of sexual reproduction lower, but the benefits are greater. In birds, Lack (1968) argues that parental feeding capacity commonly sets the limit on clutch size. If this is so, a pair of birds can fledge twice as many young as could a single parent alone, and the cost of meiosis is redressed, as Maynard Smith (1971) and Williams (1975) have noted. (Or at least virtually redressed, since there is evidence, reviewed by Trivers [1972], that male songbirds seldom quite match the females' investment.) The costs of recombination and mating remain to be paid, but it is conceivable that they are adequately compensated by biparental efficiencies, such as the capacity for uninterrupted incubation.

In a species lacking such paternal investment however, it is hard to imagine that the costs of sexual reproduction are paid. A hypothetical asexual could dispense with all the costs of mating mentioned above, as well as those of meiosis and recombination, while losing nothing in male aid, since there is none to lose. These considerations make the existence of sex all the more paradoxical. I believe they strengthen Williams's suggestion that sex is a maladaptive but inflexible evolutionary vestige in organisms of low fecundity and low paternal investment and that it should be supplanted by parthenogenesis if ever the latter arises. Once a population becomes exclusively sexual, mating competition becomes part of the selective milieu in which males evolve strategies to maximize their own fitness, and these male strategies may be quite at odds with the females' optima.

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# A NOTE ON THE TIMING OF SEX IN ASEXUAL/SEXUAL ORGANISMS

It has been observed in asexual/sexual organisms that the sexual phase of reproduction is often associated with dormancy (Bonner 1958). This has underpinned the hypothesis that sex is an adaptation to changed environments in that parents create a diverse array of offspring and so increase the likelihood that one will be particularly suited (Bonner [1958] and recently given theoretical backing by Williams [1975]). The question I would raise, however, is whether the timing of sex can inform us about the adaptive significance of sex, or is there a possible adaptive significance to the timing of sex independent of the best time for the creation of genetic diversity?

What are some factors potentially important in influencing the timing of sex? Any particular species will have a set of actual cues consisting of physiological and environmental interactions that coordinate the sexuality of its members. In an environ-