

Outbreeding and Sexuality

Fisher (1958) established the principle upon which analyses of sex ratio selection have since been based. The essential part of his statement is this. "In organisms of all kinds the young are launched upon their careers endowed with a certain amount of biological capital derived from their parents. . . . If we consider the aggregate of an entire generation of such offspring. . . at the moment when. . . parental expenditure on their behalf has just ceased. . . it is clear that the total reproductive value of the males in this group is exactly equal to the total value of all the females, because each sex must supply half the ancestry of all future generations of the species. From this it follows that the sex ratio will so adjust itself, under the influence of Natural Selection, that the total parental expenditure incurred in respect of children of each sex, shall be equal. . ."

We will consider the problem of sex ratio selection in detail later. In connection with our interpretations of the functions of sexuality and reasons for its maintenance, however, it is essential to consider the fact that Fisher's principle does not hold when siblings of the sex in which sexual competition is more severe interfere with one another's mating success (Hamilton, 1967). For most species this limitation can be stated more simply, that brothers devalue the parental effort invested in them when they compete for the same mates. In the extreme case, if a female produced in her brood two sons which competed solely with each other for every mate secured by either of them, the two sons would be of no more value to her than a single son. If they competed solely with one another for half the mates secured by both of them, they would be worth three-fourths as much as two sons which never competed. This quantification could be continued. When brothers simultaneously compete for a female also being competed for by nonsibling males, whether or not they are devalued for their simultaneous participation depends upon their effect on the likelihood that one of their mother's sons will secure the copulation: if their simultaneous presence doubles the chances, they are not devalued. If they cooperate in some fashion so as to more than double the chances of one of their mother's sons being successful, their individual values to their mother will be enhanced. I believe that similar reasoning will eventually be used to account for the large numbers of sperm produced by males, and for variations in numbers of sperm produced by males evolving in different kinds of breeding systems

It is commonly assumed that Fisher's explanation of sex ratio selection holds in outbreeding populations but does not hold when inbreeding occurs. The reasons for this confusion of inbreeding with local competition for mates maybe that when matings are frequent between siblings, brothers are likely to compete for copulations with their sisters. If all matings are between siblings, a mother will partition her parental investment optimally between the sexes when she produces the minimal number of males necessary to inseminate all her daughters fully, and when the investment in those males is barely sufficient to enable them to accomplish this insemination (assuming males show us parental effort).

On the other hand if siblings do not mate with one another there is an implication that some dispersal occurs before mating*. Most of the time this dispersal will reduce the likelihood of brothers competing for mates. This is not necessarily true, for example, in species in which males gather in crowded leks within which most females in the vicinity are inseminated.

Now we may ask a question about matings between siblings which I believe bears on the problem of whether or not sexuality is favored in vertebrates. I am not aware of any exceptions to the rule that in vertebrate species studied in this regard, if sibling matings are likely as an incidental result of the circumstances

* If, however, brothers disperse so thoroughly as never to interact in sexual competition, one wonders how the loss of one or another can increase the value of the others in the fashion required in Fisher's hypothesis that mortality following termination of parental care cannot affect the primary sex ratio.

of family and social life, one or both sexes show strong tendencies to avoid them. In other words, vertebrates tend to outbreed. Earlier we cast the problem of the cost of meiosis in terms of misdirected parental effort, noting that in a species in which males do not invest, a female suffers a 50% loss in genetic reproduction if she is forced to invest in zygotes only 50% derived from her own genotype. Such females can recover some of the loss incurred as a result of sexuality by mating with their brothers unless (1) there are other disadvantages to such matings (2) sexuality is actually favored because of its effect on the genetic environments of gametes, or (3) such mating severely reduces their brothers' opportunity to pass on the cost of meiosis to nonrelatives (i.e., a ♀ should mate with a brother who is nonparental if he has only one mating to give and there is a unrelated ♀ available). There are two other disadvantages -- or barriers -- to inbreeding that must be considered. First, when inbreeding follows outbreeding it exposes recessive alleles deleterious in the homozygous condition. Although breeders of plants or animals inbreed in order to eliminate such alleles, they do so at great cost, by discarding the offspring with deleterious alleles and no longer using their parents or, in some cases, other relatives, as breeding individuals. Such practices can pay because sterile individuals are useful in various ways to humans (e.g., as pets, riding horses, or sources of meat); they are unprofitable, however, for reproductively competitive organisms under most natural conditions.

The second barrier to inbreeding derives from the fact that a female whose offspring are inbreeding (mating with one another) for the first time will suffer a loss because she will have invested heavily in superfluous males. This is a cost to the parent and to males who do not invest parentally, and who, by mating with their sisters, are passing the cost of meiosis on to their closest relatives. Likewise, females should gain from having their brothers outbred if other mates are available.

These last two inbreeding disadvantages are temporary. If a population is forced to inbreed for a time, compensation of each kind of loss will tend to evolve. The number of generations required for significant alteration of sex ratios or weeding out of deleterious recessive alleles presumably could be calculated.

Evidently, then, in a species in which sexuality is maladaptive, long periods of forced inbreeding, should lead to continued inbreeding for the following reasons:

1. Costs of sexuality that derive from diverted parental effort will be reduced, particularly in species in which the male does not invest parentally (This hypothesis predicts that inbreeding is less likely to continue in monogamous species in which male and female invest parentally to the same extent than in promiscuous-polygynous species when inbreeding is forced for the same number of generations).
2. Mating with a sibling will generally reduce the costs of mating for both sexes. If females allow their brothers to inseminate them often, the convenience of this arrangement will cause few matings to be available to males outside of sibling groups.
3. The inbreeding barriers of deleterious homozygosity and uncompensated sex ratios are both temporary.

Unless vertebrates have not been subjected to sufficiently long periods of inbreeding or an undiscovered prevalence of inbreeders exists among them, we are led to the conclusion that aversions to matings with siblings remain because they tend to increase recombination and genetic heterozygosity. Particularly in promiscuous vertebrates with little or no male investment in offspring, such reasoning argues that sexuality is maintained because even the environments of low fecundity vertebrates are too uncertain for the combination of increased parental care and

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phenotypic plasticity through extensive learning to render genetic recombination disadvantageous. This would mean that inbreeding should continue in a sexual organism only when outbreeding is impossible or very expensive. Perhaps long histories of outbreeding are the reason for overdominance rather than vice versa. In other words, long-term tendencies of organisms to combine their gametes with unlike gametes may have favored genes which tend to produce unusually vigorous heterozygous individuals. This might explain the general phenomenon of heterozygote superiority.

One way to test the above arguments about maintenance of sexuality in vertebrates may be to look for vertebrate populations in which the sex ratio is skewed in favor of females. This would imply forced inbreeding leading to sex ratio adjustment. If sex is disadvantageous in vertebrates such populations should not show tendencies to outbreed. Absence of such populations might suggest that the barriers to inbreeding, have not been overcome in vertebrates by periods of forced inbreeding, and this would weaken or destroy my argument. Because my conclusion here differs from that of Williams (1975), and the required uncertainty in the environments of complexly social vertebrates like ourselves does not seem easy to identify with confidence, you should regard my arguments with an appropriate skepticism.