

Anisogamy, sexual selection, and the evolution and maintenance of sex

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Summary

In the present paper we distinguish between two aspects of sexual reproduction. Genetic recombination is a universal feature of the sexual process. It is a primitive condition found in simple, single-celled organisms, as well as in higher plants and animals. Its function is primarily to repair genetic damage and eliminate deleterious mutations. Recombination also produces new variation, however, and this can provide the basis for adaptive evolutionary change in spatially and temporally variable environments.

The other feature usually associated with sexual reproduction, differentiated male and female roles, is a derived condition, largely restricted to complex, diploid, multicellular organisms. The evolution of anisogamous gametes (small, mobile male gametes containing only genetic material, and large, relatively immobile female gametes containing both genetic material and resources for the developing offspring) not only established the fundamental basis for maleness and femaleness, it also led to an asymmetry between the sexes in the allocation of resources to mating and offspring. Whereas females allocate their resources primarily to offspring, the existence of many male gametes for each female one results in sexual selection on males to allocate their resources to traits that enhance success in competition for fertilizations. A consequence of this reproductive competition, higher variance in male than female reproductive success, results in more intense selection on males.

The greater response of males to both stabilizing and directional selection constitutes an evolutionary advantage of males that partially compensates for the cost of producing them. The increased fitness contributed by sexual selection on males will complement the advantages of genetic recombination for DNA repair and elimination of deleterious mutations in any outcrossing breeding system in which males contribute only genetic material to their offspring. Higher plants and animals tend to maintain sexual reproduction in part because of the enhanced fitness of offspring resulting from sexual selection at the level of individual organisms, and in part because of the superiority of sexual populations in competition with asexual clones.

Keywords: Evolution of sex; sexual selection.

Introduction

'Since most species retain sexual reproduction despite its seeming inefficiency, it follows that it must provide advantages great enough to be worth the enormous cost. The search for such powerful evolutionary advantages has yet to produce really convincing results. I conclude that the prevalence of sexual reproduction is a major unresolved mystery' (Williams, 1980, p. 383).

There are two main theories for the evolution of sex. The traditional theory is based on the presumed advantages of genetic variability among individuals. There are many variations on this theme. Most authors have posited an advantage to parents of producing genetically diverse

offspring in an environment where, as a consequence of either temporal or spatial variation, the offspring are not likely to experience the same conditions as their parents (Williams, 1975; Glesener and Tilman, 1978; Maynard Smith, 1978; Bell, 1982). Others have suggested that populations of genetically variable individuals have an advantage over less variable asexual clones as a result of some form of group or species selection (Lynch, 1984). 'Muller's ratchet', which proposes that sexual recombination permits populations or offspring to be purged of deleterious mutations, is a special case of the variation theory (Muller, 1932; Felsenstein, 1974; Maynard Smith, 1978; Leslie and Vrijenhoek, 1980; Shields, 1982). A more recent theory proposes that the general function of sexual reproduction is repair of damage to the genetic material (Bernstein, 1977, 1983; Bernstein *et al.*, 1981, 1985a).

Whatever the advantages of sex, they must be sufficiently great to offset two potentially serious disadvantages. First, for all individuals that engage in sex there are some costs of mating and recombination. Time, energy and other resources must be allocated to find another individual and to exchange and recombine genetic material. Second, for all organisms with differentiated sexual roles, there is an additional cost of producing males. Since an asexual parthenogenetic female could presumably produce twice as many female offspring as a sexual individual that produces equal numbers of offspring of both sexes, this has been termed the two-fold cost of males (Maynard Smith, 1958; Williams, 1975).

In the present paper we emphasize the distinction between two processes that must have occurred sequentially in the evolution of sex: first, the evolution of mating and sexual recombination, and second, the evolution of differentiated male and female sexual roles. We focus on the second process, which began with the origin of anisogamy (different-sized male and female gametes). This asymmetry, which means that females invest more resources than males in each offspring, promotes competition among male gametes and individual males for opportunities to fertilize a limited number of female gametes. It led inevitably to sexual selection for attributes of males that enhanced their competitive ability and for attributes of females that enabled them to discriminate among males. We suggest that the advantages of such non-random matings are sufficient to outweigh the costs of producing males, because those few males with the highest overall fitness tend to sire a disproportionate number of offspring in each generation.

Background: evolution of recombination and diploidy

The coming together, exchange, and reassortment of genetic information from different individuals is the universal feature of sexual reproduction. This process must be of ancient origin, because it occurs in many kinds of bacteria, protozoans and algae, in which similar sized cells of different mating types join to recombine genetic material. However, it also occurs in higher plants and animals, in which the union of anisogamous gametes characterizes the differentiation of distinctive male and female roles. Thus in considering the advantages of sexual reproduction that have been responsible for its origin and maintenance, it is important to distinguish between the initial evolution of mating and recombination, on the one hand, and the subsequent acquisition of anisogamy and associated male and female characteristics, on the other.

The argument developed below for the evolution of differentiated male and female gametes and reproductive roles does not depend on the nature and adaptive significance of the process invoked to account for the evolution of sexual recombination. Nevertheless, we find the suggestion that recombination evolved as a mechanism for repair of genetic damage and elimination of mutations compelling, and our ideas are consistent with these hypotheses. Bernstein *et al.* (1985a) made an important distinction between genetic damage and mutation. They used the term genetic damage to refer to the physical disruption of a strand of DNA that can be recognized

and repaired by a process that uses an homologous strand as a template. Because primitive single-celled organisms were presumably haploid, as are many contemporary microbes, repair of genetic damage requires exchange of homologous DNA among different individuals. As organisms became structurally and functionally more complex, and in particular when multicellular individuals evolved, the size of the genome increased and the opportunities for recombinational repair between individuals were restricted to the unicellular phase of the life cycle. If such organisms were haploid, the accumulation of DNA damage could seriously impair normal function. The evolution of diploidy, which is characteristic of some of the most complex unicellular organisms and virtually all multicellular plants and animals, reduced the consequences of genetic damage in two ways. Firstly, the redundant information provided by the two homologous strands of DNA meant that normal function was usually preserved so long as both strands were not damaged in the same place. Secondly, the possession of two homologous strands of DNA, each derived independently from a haploid gamete from a different parent, meant that the homologous strand could be used as a template to repair genetic damage without sexual recombination. Periodic exchange and recombination of DNA between individuals was still advantageous however, in order to repair double-stranded damage.

In addition, sexual recombination between individuals provided the only mechanism by which mutations could be isolated, and eliminated. Bernstein *et al.* (1985a) define mutations as changes in the sequence of bases on a DNA strand, which change function but cannot be detected and corrected by the repair mechanism. The majority of mutations are deleterious, but they can be eliminated from the population and from the offspring of an individual only by natural selection. One additional consequence of sexual recombination is not only that individual mutations are exposed, but also that several mutations may be recombined in the same offspring. Thus several deleterious mutations may be eliminated simultaneously by the death or failure to reproduce of impaired offspring (Muller, 1932), while genotypes with fewer mutations tend to be preserved because such offspring have higher fitness (Maynard Smith, 1978; Shields, 1982).

One consequence of the scenario developed by Bernstein *et al.* (1981, 1984, 1985a) is that genetic variation among offspring is viewed as a byproduct of sexual recombination. These authors argue that because such a high proportion of mutations is deleterious, the adaptive significance of sexual recombination is that it maximizes the fidelity of DNA replication and transmission. The arguments that we develop in the following sections are also based on the assumption that on average new variation is disadvantageous. This does not deny that a small proportion of mutations is beneficial, that these variants tend to increase in frequency by the action of natural selection, and that they are responsible for adaptive evolutionary change.

Evolution of differentiated sexual roles

Evolution of anisogamy

The appearance of multicellular diploid organisms with haploid gametes set the stage for the evolution of anisogamy. Once haploid cells functioned solely in sexual reproduction, they were able to specialize for functions related to mating. An important problem was for gametes to find, recognize and join with gametes of a different mating type. As multicellular organisms evolved to become larger, more complex and longer-lived, they often became rarer and acquired sedentary habits, increasing the difficulty of acquiring a mate. Thus these trends tended to increase the cost of rarity (Hopf and Hopf, 1985), which must be offset by genetic benefits if sexual reproduction is to be retained.

Once the haploid phase of the life cycle became reduced to short-lived cells that functioned only in mating, the costs associated with mating could be reduced by adopting specialized male

and female roles. The essence of maleness and femaleness is the production of either small, mobile or large, nutritive gametes, respectively. Parents contribute two kinds of materials to their offspring: the genetic information necessary to direct the development of the new individual, and the resources necessary to sustain the developing individual until it is capable of independent life. It is a constraint of the sexual process (except in unusual cases, such as haplo-diploidy) that each parent contributes approximately equally to the genome of each offspring. There is no such constraint, however, on the allocation of resources. In fact, the costs associated with mating can be minimized if one mating type, female, produces a small number of large, relatively immobile gametes that contain all of the resources required for development, while the other mating type, male, produces a large number of small, mobile gametes that contain only the genetic complement and the materials required to locate and fuse with a female gamete. Such a mating system increases the probability of encounter between gametes of different mating types and still provides the offspring with all essential resources; it is mutually advantageous for both mating types, because it tends to maximize the number of surviving offspring that each can produce. This is the essence of recent theoretical biomechanical explanations for the evolution of anisogamy (Parker *et al.*, 1972; Cox and Sethian, 1984, 1985; but see Manning, 1976; Bell, 1978; Charlesworth, 1978; Parker, 1978).

The evolution of anisogamy had two important consequences. First, it resulted in competition among male gametes to fertilize female gametes, thereby establishing the necessary conditions for sexual selection. Second, it resulted in the evolution of male gametes with insufficient resources to develop into new individuals, thereby establishing the two-fold cost of producing males. We shall consider each of these in turn.

Sexual selection

The origin of anisogamy meant that there were many small, mobile male gametes potentially available to fertilize each of the large, relatively immobile female gametes. This led inevitably to competition for limited mating opportunities among male gametes, and hence among the individuals producing them. In such a competitive environment, any attributes of male gametes or individuals that tended to enhance their access to mates and their ability to fertilize female gametes would be advantageous. Sexual selection is the process that favors the evolution of traits which confer an advantage in mating (Darwin, 1859). Thus as soon as different-sized gametes began to evolve, sexual selection began to play a central role in the evolution of distinctive male and female attributes. In fact, those features of anisogamous gametes that conferred biomechanical advantages in mating can be attributed to the operation of sexual selection.

Once in operation, sexual selection resulted in the evolution of suites of traits that characterize the different reproductive roles of males and females. The attributes that define maleness and femaleness have been emphasized in current discussions of patterns of sexual selection and parental investment (e.g. Trivers, 1972; Thornhill, 1980). Although these sexually selected traits ultimately result from competition among males for limited mating opportunities, they are not restricted to males. In males, sexual selection favors the evolution of traits (i) that enhance the fertilization success of sperm or pollen (Mulcahy *et al.*, 1983; Stephenson and Bertin, 1983; Sakaluk, 1984); (ii) that are used in aggressive encounters to increase access to females (Clutton-Brock, 1982); (iii) that are employed in courtship behaviors to attract females (Andersson, 1982a; Kodric-Brown, 1985). In females, sexual selection favors the evolution of traits that permit discrimination among competing males and their mobile gametes so that their investment in nutrient-rich eggs is realized as high-quality offspring (Bateson, 1983).

There are two main theories of sexual selection. The 'runaway' theory, first proposed by Fisher (1930) and subsequently amplified and extended (Lande, 1980; O'Donald, 1980; Kirkpatrick,

1982), holds that any trait that confers an initial mating advantage will tend to be amplified as a result of the preferences of females and the reproductive success of their sons until the trait becomes so exaggerated that its detrimental effects on survival outweigh its positive effects on reproduction. The 'good genes' theory, first proposed by Zahavi (1975, 1977) and subsequently modified (Andersson, 1982b; Hamilton and Zuk, 1982; Heisler, 1984; Kodric-Brown and Brown, 1984; Nur and Hasson, 1984; Andersson, 1986; Seger and Trivers, 1986) claims that selection favors the elaboration of traits in males that reflect overall genetic quality and favors the evolution of discrimination by females so that they mate with the most fit males. An important difference between these two theories is that 'runaway' selection will cease to operate once the disadvantage of a trait for male survival counterbalances its advantages for reproduction, whereas the 'good genes' theory predicts that directional selection for certain male traits will continue because both male and female offspring obtain superior genes.

The cost of producing males

The two-fold cost of sex, cost of meiosis, or cost of producing males, which has puzzled evolutionary biologists since Weismann (1889; see also Williams, 1975, Treisman and Dawkins, 1976; Maynard Smith, 1978), is a consequence of the evolution of anisogamous gametes. When similar-sized, single-celled organisms came together, recombined their genetic material, and then separated, the only cost of sexual reproduction was the time and resources allocated to this mating process. However, once anisogamous gametes had evolved, then any 'female' gamete that contained a complete diploid chromosome complement should be able to develop into a new individual. Therefore, a parthenogenetic female that did not undergo meiosis and produced only female offspring could potentially leave twice as many descendants in subsequent generations as a sexual female that produced both male and female offspring. We note parenthetically that it seems to be a moot point whether there would be a similar two-fold cost for a complex multicellular organism that produced isogamous gametes, because isogamy would imply that a single diploid 'gamete' possessed insufficient resources to develop into a new individual. Therefore, as Maynard Smith (1978) has pointed out, the so-called cost of sex or cost of meiosis is more properly termed the cost of producing males.

The two-fold cost of producing males suggests that a large advantage for sexual reproduction by means of anisogamous gametes is necessary to account for the evolution and maintenance of this mode of reproduction. Three additional points are relevant. First, the two-fold cost of producing males is incurred *in addition* to the costs of locating mates and exchanging genetic material, which are inherent in any sexual process. These costs of mating can also be substantial, especially for rare or sessile organisms. Second, since the two-fold cost of producing males is a consequence of anisogamous gametes, in order for the evolution of anisogamy to go to completion and produce male gametes that contribute only genetic information to the offspring, the advantages of this mode of reproduction must have been sufficiently great to outweigh this cost. This problem has not been considered in most theoretical treatments of the evolution of anisogamy (Bell, 1978; Charlesworth, 1978; Parker, 1978; Cox and Sethian, 1984). We do not consider this issue here except to note that the two-fold cost of producing males should not become a major factor until the evolution of anisogamy is nearly complete, and the female gamete contains sufficient nutrients to develop without fertilization. Third, although the cost of producing males is most easily conceptualized by considering the two-fold reproductive advantage that would accrue to a parthenogenetic female that produced diploid gametes, both this cost and the cost of mating are avoided by other forms of asexual reproduction, such as vegetative budding. The costs of sexual reproduction are also substantially reduced or eliminated in certain plant breeding systems, such as apomixis, which entail meiosis, recombination, and fertilization

but obligate selfing and little expenditure for male gametes. Fourth, the fact that many contemporary parthenogenic animal species do not enjoy a two-fold reproductive advantage over their closest sexual relatives (Lynch, 1984), does not necessarily diminish the importance of the cost of producing males in the initial evolution of anisogamy. Indeed, simply because many parthenogens presently have less than a two-fold reproductive advantage, it does not follow that the parthenogenetic lineages did not enjoy the full two-fold advantage when they first evolved from their sexual ancestors. As developed below, our explanation for the advantages of sex and for the role of males in breeding systems predicts that the reproductive advantage of parthenogenetic clones, compared to their sexual relatives, should decline with time.

The preceding points emphasize that the evolution of anisogamous gametes introduced a substantial new cost of sexual reproduction, over and above the existing costs associated with mating and genetic recombination. We suggest that two advantages unique to anisogamy outweighed this new cost and led to the evolution of differentiated sexual roles. First, the biomechanical consequences of producing large numbers of small, mobile male gametes increased the efficiency of mating for both sexes. As multicellular organisms evolved larger size, greater complexity, increased longevity and (in many cases) decreased mobility in response to other selective pressures, population density tended to decrease. The resulting cost of rarity (Hopf and Hopf, 1985) enhanced the biomechanical advantages of anisogamous gametes. Thus the advantages and disadvantages of anisogamy are not completely independent of the costs and benefits of genetic recombination in organisms with obligately outcrossing breeding systems. A second consequence of anisogamy is that through sexual selection it leads inevitably to competition among male gametes and male individuals, and thus to the evolution of male traits that promote mating success. Because of this reproductive competition and the sexual selection that it engenders, males play a unique role in the evolution of complex, multicellular organisms with anisogamous gametes.

The role of males

In species in which males contribute only genetic material and no resources or paternal care to offspring, there is a greater variance in reproductive success among males than among females. This is a consequence of the asymmetry between the sexes in the allocation of resources to offspring (Bateman, 1948; Trivers, 1972). Because females devote most of the resources available for reproduction to provisioning gametes and caring for young, variation among individuals in reproductive success tends to be directly and approximately linearly proportional to their ability to accrue resources over their lifetimes. In contrast, because males devote most of the resources available for reproduction to competing with other males for mating opportunities, the small proportion of individuals that are able to acquire the most resources usually obtain a disproportionately large share of the matings (Bateman, 1948; Le Boeuf, 1974). This asymmetry means that a smaller proportion of males than of females are the parents of the offspring produced each generation.

Because of competition for mates and the high variance in reproductive success among males, sexual selection operating on males can intensify the effect of natural selection operating on the population as a whole. This occurs when the differential success of individual males is owing in part to their overall genetic quality, not solely to some combination of chance and the expression of secondary sexual characteristics that are uncorrelated with fitness. The arguments that follow are based on the assumption that sexual selection operates entirely, or at least primarily, according to such a 'good genes' model. Elsewhere (Kodric-Brown and Brown, 1984, 1985; see also Zahavi, 1975, 1977; Andersson, 1982b, 1986; Heisler, 1984; Nur and Hasson, 1984), we have summarized the evidence favoring 'good genes' models rather than 'runaway' or Fisherian models. In essence, the 'good genes' models hold that success of males in reproductive competi-

tion is positively correlated with the degree of expression of secondary sexual traits, which in turn is positively correlated with phenotypic vigor and overall genetic quality. These correlations are maintained by sexual selection because the most fit males win competitive contests with other males, are chosen as mates by females, and pass on their superior genes to both male and female offspring.

Such a mechanism of sexual selection effectively intensifies the selection acting on the males in a population, because each generation the reproductively successful males must pass through a more selective fitness filter than females. Furthermore, the primary effect of sexual selection is to reinforce the effects of natural selection, because traits that ultimately determine male reproductive success, such as ability to acquire resources and to avoid predators and disease, are the same attributes that promote survival and reproduction of all individuals regardless of age or sex. Therefore, when a population contains males that experience a much higher variance in reproductive success than the females, it is subject to qualitatively similar, but *quantitatively* more severe selection than an otherwise identical asexual clone.

This enhanced effect of selection operating on males tends to compensate, at least in part, for the two-fold cost of producing males. Compared to asexual clones, sexual populations should be more responsive to both stabilizing and directional selection. Traditional theories that purport to explain the evolution and maintenance of sex based on the adaptive value of genetic variation, in essence have relied upon the greater capacity of sexual populations to respond to directional selection resulting from environmental variation in space or time. However, the findings of modern molecular biology support the conclusion of Muller (1932) and other early geneticists that the vast majority of new mutations are deleterious. 'Spontaneous' DNA damage appears to occur frequently in all organisms, and a significant fraction of this damage cannot be repaired without sexual recombination (Bernstein *et al.*, 1981). It follows that if most new genetic variation is disadvantageous, then the primary role of sexual reproduction must be to eliminate variation rather than to enhance it (Bernstein *et al.*, 1985a). The more intense selection acting on males can contribute importantly to eliminating variant phenotypes.

Populations with males are also more responsive to directional selection than asexual clones. We suggest, however, that the changes in gene frequency are primarily owing to the differential reproductive success of the fittest males, rather than to the adaptive variation resulting from recombination. We recognize that beneficial recombinations and mutations provide the basis for adaptive evolutionary change. The unique role of males, however, is that they enhance the rate of change in gene frequency in response to selection.

In all breeding systems (except for those with male parental care; see below) in which outcrossing sexual reproduction is favored, the advantages of anisogamy and differentiated male and female roles complement the advantages of genetic recombination to enhance fitness. This effect is achieved both through sexual selection, operating at the level of individual organisms, and through group selection, operating at the level of sexual species and asexual clones. The greater average fitness of male than of female parents that occurs as a result of male-male competition and female choice, tends to increase the genetic quality of offspring. The higher rates of adaptive evolution in sexual than in asexual lineages that occurs as a result of more intense selection on males, tends to promote the survival of sexual populations at the expense of asexual clones.

Discussion

Asexual reproduction in higher plants and animals

Williams (1975; see also Weismann, 1889; Maynard Smith, 1978; Bell, 1982) emphasized the difficulty of accounting for the maintenance of sex in higher organisms, given the two-fold cost of

producing males and the frequent occurrence of several forms of asexual reproduction. If viable asexual mutants occur with significant frequency and realize the full two-fold benefit of eliminating males, how have sexual populations been able to persist in the face of competition from related asexual clones?

Trivers (1976) attempted to answer this question by suggesting that the quality of genes contributed by males could offset the cost of producing male offspring. On the assumption that sex is maintained by selection operating solely at the level of individuals, Trivers proposed that each generation the average genetic fitness of male parents must be twice that of female parents. Most subsequent authors seem not to have taken Trivers' suggestion seriously, probably because a two-fold differential in fitness between the sexes seems unreasonably high. Although the variation and heritability of fitness within natural populations requires empirical measurement, it seems unlikely that it could be so great that reproductive competition among males could result in successful individuals having twice the average fitness of their mates.

In animals parthenogenesis, in which females produce all female offspring from some form of unreduced diploid 'gametes', is by far the most prevalent form of asexual reproduction. In theory, if sexual populations are not to be replaced by asexual clones, genetic recombination and differentiated male and female roles must confer at least a two-fold reproductive advantage. In fact, however, parthenogens produce female offspring at rates which are little, if any higher than their sexual relatives (Lynch, 1984). This much lower than expected fecundity of parthenogens can be attributed in part to their impaired capacity to repair genetic damage (Bernstein *et al.*, 1985a), their reduced ability to eliminate deleterious mutations through production of recombinant offspring (Maynard Smith, 1978; Shields, 1982), and their lower rates of response to both stabilizing and directional selection in the absence of differential selection on males. Parthenogenesis seems to be favored initially in special circumstances, such as when population densities are low and there is a high premium of producing offspring without mating or when interspecific hybridization has created genotypes that are uniquely adapted to certain environments (Bernstein *et al.*, 1985b). However, the evolutionary duration of many parthenogenetic clones is much shorter than that of related sexual species. For example, extant sexual species can reliably be identified as the ancestors of all known asexual forms of *Cnemidophorus* lizards (Cole, 1984) and *Poeciliopsis* fishes (Schultz, 1977). Thus it appears that, far from having an inherent advantage, parthenogenetic forms are usually inferior to their sexual relatives over evolutionary time.

In general, higher plants exhibit more frequent occurrence of asexual reproduction and a greater variety of asexual mechanisms than multicellular animals. We cannot consider all of this diversity in detail. Other authors (e.g. Lloyd, 1979; Willson, 1983) have discussed the distinctive features of plants that enhance the advantages and mitigate some of the costs of asexual reproduction. These include (i) the absence of a sequestered lineage of germ cells; (ii) the presence of many independent reproductive organs, often of different sexes, on the same individual; (iii) the presence of multiple undifferentiated meristems that have the capacity to give rise vegetatively to new individuals; and (iv) the prevalence of various degrees and mechanisms of self-fertilization and genetic recombination. Although the adaptive significance of the great variety of mechanisms of sexual and asexual reproduction is an area of great current research activity, we know of no special features of plant reproduction that refute the relationships between anisogamy, sexual selection, and the evolution and maintenance of sexual reproduction that we have developed above.

Use of males in artificial selection

Plant and animal breeders have long exploited the higher variance in male than in female reproductive success to maximize the effectiveness of artificial selection. By restricting breeding

to a small proportion of males bearing the most advantageous traits, they are able to achieve high intensities of either stabilizing or directional selection. Simultaneously, they can maintain high rates of reproduction by exerting much less or no restriction on the breeding of females, because they can obtain many more offspring from a male than a female. Interestingly, even when exclusively female traits, such as milk production in dairy cattle, are the targets of selection, animal breeding programs frequently rely almost exclusively on differential reproduction by fathers, brothers, or sons of females with desirable traits.

Thus, males are used to enhance the response of domesticated strains to artificial selection in a manner analogous to their role in the response of wild populations to sexual selection. Furthermore, continual selective breeding, usually involving more intense selection on males than females, is usually necessary to eliminate variation resulting from both mutation and recombination, and thereby to maintain the desirable traits of domestic species.

Male parental care

The arguments presented above are based on the assumption that the male parent contributes only genetic information to offspring, while the female parent provides not only an equal share of the genetic material but also all the resources and care required by the offspring. This is by far the most common pattern of parental investment in higher plants and animals. In some animals, however, males provide some of the resources, and some or all of the care allocated to offspring. These parental allocations, which reach their extreme form in the monogamous and polyandrous breeding systems of birds and mammals, are the exceptions that prove the rule.

When males provide parental care, a smaller proportion of the resources available for reproduction can be devoted to competing with other males for mates. Consequently, as male paternal allocations increase, the variance in reproductive success among the males in the population tends to decrease, and the fitness of the genes contributed by the male parent relative to the female parent tends to decrease. In the extreme case of monogamous species the genetic contribution to offspring fitness should be equal for both parents. In order for derived breeding systems with increased male parental care and decreased variance in reproductive success to have evolved from primitive polygynous systems, the resources and care provided by male parents had to increase offspring fitness sufficiently to compensate for the reduction in the quality of their genetic contributions. Thus, the force of sexual selection and its role in offsetting the cost of producing males diminishes as the resources allocated to offspring become more equal between the sexes.

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