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ON THE ORIGIN AND BASIS OF THE MALE-FEMALE PHENOMENON

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INTRODUCTION

The terms "male" and "female" refer to alternative and complementary lifetime strategies in gonochorists or reproductive functions in hermaphrodites. In order to discuss male and female differences and similarities, therefore, it is useful first to consider certain general features of life histories which we believe require clarification.

In evolutionary terms the lifetimes of individual organisms can be viewed as comprising two kinds of "effort" appropriately termed somatic effort and reproductive effort (Williams, 1966a, b, 1971; Hamilton, 1967; Hirshfield and Tinkle, 1975; others). These two kinds of striving include, respectively, the garnering of resources and their subsequent redistribution in the interests of the reproduction of the organism's genes. With increasing tendencies to be semelparous (to breed only once or only during one very restricted period), somatic and reproductive effort come to be represented by separate periods in the organism's life, approximately corresponding to juvenile and adult. With iteroparity (repeated breeding), the periods necessarily overlap so that resource garnering and redistribution are best described as different kinds of activities that may be engaged in either alternately or simultaneously. By these usages both somatic and reproductive effort increase the likelihood of mortality, because each involves risk taking. Somatic effort, however, evolves to increase the reproductive value of the individual by rendering subsequent reproductive effort more effective, while reproductive effort evolves to increase actual reproduction, thereby incidentally reducing the reproductive value of the individual. If senescence results from unavoidable pleiotropic gene effects (Williams, 1957), the onsets of reproductive effort

and senescence will therefore tend to coincide.¹

An organism's reproductive effort can obviously be subdivided into seasonal or annual effort for long-lived, iteroparous organisms, and there are good reasons for such division since what is expended during one period is likely to affect what is available during subsequent periods. One expects iteroparous organisms to evolve to divide their reproductive effort among reproductive periods or seasons, using environmental signs indicating the relative value or appropriateness of each period, so as to maximize the returns from the lifetime of reproductive effort (Williams, 1966a, b). In all such considerations the concept of effort, or striving, avoids the erroneous view that the amounts to be expended are predetermined and unchangeable for each individual.

Detailed comparisons of male and female activities require further subdivisions of reproductive effort for the purpose of analyzing mating and parental activities, gamete dimorphism, sexual selection, and the costs and benefits of sexuality. These further subdivisions are even more difficult, and the reasons are worth a careful review.

PARENTAL INVESTMENT AND REPRODUCTIVE EFFORT

Darwin (1871) noted that "The only check to a continued augmentation of fertility in each organism seems to be either the expenditure of power and the greater risks run by parents that produce a more numerous progeny, or the contingency of very numerous eggs and young being produced of smaller size or less vigorous, or subsequently not so well nurtured."

¹ Our distinction between reproductive and somatic effort may at first seem not entirely consistent with the discussion of reproductive effort by Williams (1966a, b). He exemplified reproductive effort by the gathering of food for offspring (i.e., the garnering of resources), an act which automatically reduces residual reproductive value. Williams' example of a robin deciding whether or not to forage for one more worm, however, requires explication. Even if the worm could not possibly be used by the parent robin except as food for its offspring, whether or not the act of foraging for worms actually reduces reproductive value could depend upon the particular time of measurement. Thus, if one measured the reproductive value of all parents just before the act of foraging, and then again upon the return of those successful after delivery of the worms to their offspring, the residual reproductive value of the aggregate of parents would be reduced. But if the second (continued on facing page)

Fisher (1958) continued the discussion, referring to an additional factor, parental care, which includes "... all expenditure in the form of nutriment, effort, or exposure to danger, incurred in the production and nurture of the young. In organisms in which that degree of parental expenditure, which yields the highest proportionate probability of survival, is large compared to the resources available, the optimal fertility will be low." Trivers (1972) attempted to make the concept of expenditures on progeny more operational by defining "parental investment" as "any investment by the parent in an individual offspring that increases the offspring's chances of surviving (and hence reproductive success)..." This parental contribution, Trivers noted, is made at a cost--the ability of the parents to make an investment in other progeny. In the next sentence, however, Trivers exposed the problem in relating these discussions to the subdivision of reproductive effort when he excluded from parental investment "effort expended in finding a member of the opposite sex or in subduing members of one's own sex in order to mate with a member of the opposite sex..." (italics added).

Low (1978) considered the arguments of Darwin, Fisher, and Trivers, and divided reproductive effort into parental effort and mating effort; she also noted that for many species a third category involving nepotism to relatives other than offspring would be necessary (see also Alexander, 1977). Low evidently meant that parental effort is altered by changing

measurement was made while the parents were still carrying their worms, just before the act of feeding them to the offspring, the residual reproductive value of the parents would show an increase, unless the decision to make the last foraging trip was a reproductive mistake. The whole act of foraging for offspring would thus reduce reproductive value, but the food gathering itself would temporarily raise it, thus representing somatic effort even if the food could not be used by the parent itself. Since ordinarily a food-gathering act would predictably be embarked upon either to feed one's young or one's self, we would not usually have to consider measurements of residual reproductive value midway in the act. But especially because, as in Williams' example, worms are food for both parents and offspring, and also because robins are iteroparous, the distinction we are making seems worthwhile. We have purposely chosen for somatic effort the word "garnering" because it means to gather and store: a robin obviously gathers and temporarily "stores" (in its beak) even worms that will inevitably be fed to its offspring, and such a robin may have greater reproductive value than another one which did not make the trip and therefore lacks a worm.

the proportion of reproductive effort devoted to care of the progeny as a whole (i.e., as opposed to mating effort), while parental investment is altered by changing the distribution of parental effort among individual offspring (i.e., by distributing it among greater or lesser numbers of offspring or by furnishing different amounts to different offspring). Theoretically, at least, variations in the proportion of reproductive effort allocated to particular aspects of mating effort could allow some individuals both to produce more gametes than others and to invest more heavily in each. In other words, parental effort is the sum of reproductive effort devoted to parental investment without regard to which offspring, or how many, received benefits. Fisher did not clearly distinguish these two concepts in his use of parental "expenditures" (see above), and Trivers, despite his careful definition of parental investment, subsequently used the term to mean either parental effort or parental investment by the definitions suggested here.

PRE- AND POSTZYGOTIC EFFORT

Low defined mating effort essentially as Trivers (1972) used it. As such it is always prezygotic. But not all prezygotic effort is a direct means of securing matings. Indeed, what Low called parental effort, some of Trivers' usages of parental investment, and Darwin's and Fisher's "expenditures" on progeny all represent provision of resources such as nutrition or protection to *either* offspring or gametes. Since females in all animal species and nearly all plant species prezygotically couple to the gamete resources which contribute to the success of the zygote, much prezygotic effort in females is properly regarded as parental effort (see also Trivers, 1972). By contrast, all of the prezygotic effort of most males, including investment in the locomotory and other devices of sperm, and even gifts later used by the females in parental care, are appropriately identified as mating effort (see below). Moreover, in most species mating effort represents most or all of the male's reproductive effort, while this is never true for females. The reason is that the female has prezygotic control over the fates of her individual gametes, hence of any investment in them. As a consequence, she can optimize the pattern of expenditure on her offspring by extending the period of investment back into the gametic stage. The male, lacking control over the fates of his individual gametes, is not in a position to realize gain from investing in them in ways designed to increase their success should they succeed in becoming part of a zygote. To some degree, then, females may be characterized as the sex which

has retained greater control over the fates of individual gametes, partly by holding the investment-rich eggs before mating, sometimes by internalizing the sperm as well prior to fertilization, and sometimes by internalizing or tending the zygote itself after mating. This retention by females of control over the success of individual gametes, and sometimes zygotes, accounts for three distinctively female attributes among modern species: (1) greater immediate control over the process of sexual selection than the male, (2) greater ability to regain resources from terminated gametes or zygotes through resorption or cannibalism, and (3) (usually) greater confidence of parenthood than the male.

Our concepts of male and female, then, actually return to the different ways in which the individuals in a sexual species invest in their gametes. Females are, by definition, those individuals in any gonochoristic (or dioecious) species which have specialized to produce a smaller number of larger and usually less motile gametes. The few exceptions are all secondarily evolved and involve only the relative motility of male and female gametes (Baccetti, 1970). We are aware of no exception to the rule that females produce fewer gametes than males and invest more heavily in each, nor to the rule that in either gonochorists or hermaphrodites with meiotic oögenesis, polar bodies are always formed, with most of their cytoplasm being given over to the sister cell destined to become a viable gamete. Assuming widespread homology of femaleness and maleness, respectively, what is indicated is the antiquity of the divergence between the sexes in the relative proportions of parental and mating effort, leading to an apparently universal male-female asymmetry in the arrangement of prezygotic effort--the only universal asymmetry in regard to the exerting of reproductive effort by males and females.

With regard to gametes, then, our attention tends to focus on how the reproductive expenditures of either sex are divided among them or on how numerous and how large are the gametes. With regard to zygotes, on the other hand, because there are two parents, we tend to be concerned with the relative amounts of effort exerted by the two parents or with the proportions of parental effort diverted from mating effort by males and females, respectively (Fig. 1).

SUBDIVISIONS OF MATING EFFORT

Mating effort may be subdivided into three categories:

- (1) competitive interactions with other individuals of the same sex, (2) transfer of benefits to members of the other sex as a part of securing matings, and (3) evidence of commitment to parental effort to be directed at the offspring resulting

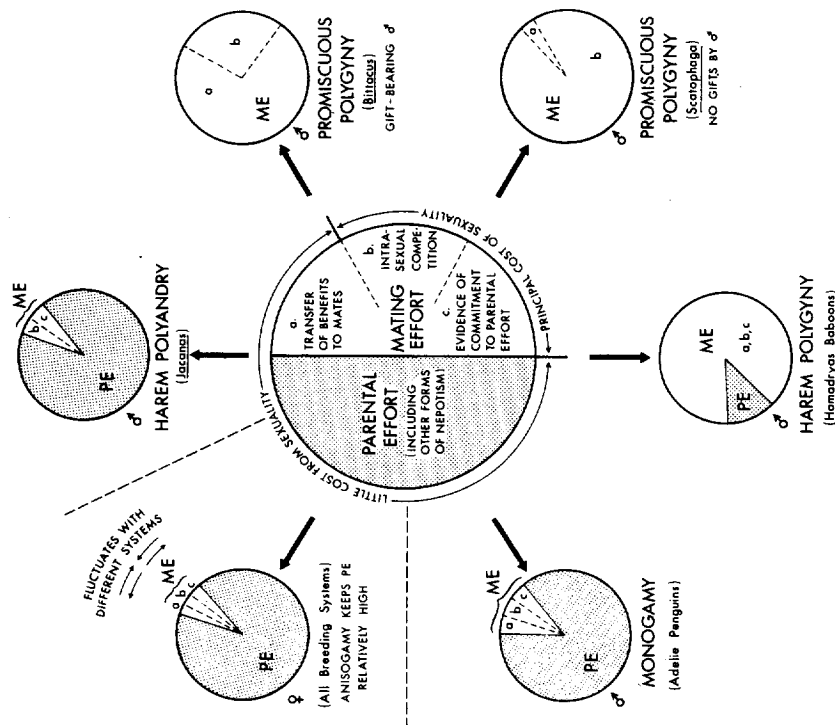


Fig. 1. Subdivisions of reproductive effort and their effects on the cost of sexuality (large circle). Expected distributions of parental and mating effort in male and female in different breeding systems (small circles). The different diagrams are not intended to be quantitative except in relation to one another; variation within the breeding systems should not change their relationships. Thus, among males, we expect mating effort to be lowest in harem polyandry. In monogamous systems mating effort is probably higher in males than in females because of anisogamy. Distribution of reproductive effort varies less among females than among males, with greatest proportions of female mating effort in polyandrous and harem-polygynous systems in which the male is parental, and least in monogamous systems. In harem-polygynous systems female mating effort will be high when both males and females vary greatly in ability to dispense parental benefits.

from the mating.

The most unambiguous example of the first kind of mating effort is probably competitive interactions among males in nonresource-based leks (Alexander, 1975), such as found in the European Ruff (Hogan-Warburg, 1966) or the American Sage Grouse (Wiley, 1973). Transfer of benefits may have effects similar to parental effort in lowering the cost of sexuality (Williams, 1975; and see below) by causing a high proportion of the resources garnered by males to be converted into investment in offspring. "Gifts" of prey (Mecoptera: Thornhill, 1976), glandular secretions (Orthoptera: Alexander and Otte, 1967), or a burrow with a food cache (the short-tailed cricket: West and Alexander, 1963) may increase the amount of resources actually available for each brood of offspring and simultaneously reduce the extent of possible polygyny among males. In the case of single offspring per mating, some benefits transferred to females as part of securing matings seem to meet Trivers' (1972) definition of parental investment, but would be excluded because they are part of the male's effort to obtain matings. Some behavior by males may have multiple effects with respect to mating effort. Thus, in the course of holding territories, males may simultaneously (1) demonstrate their phenotypic vigor by direct competition with other males, (2) start nests for the female, and (3) indicate a likelihood of later investment in offspring (for example, by exclusion of predators on eggs or young from their vicinity).

MATING EFFORT AND THE COST OF SEXUALITY

Trivers' introduction of the concept of mating effort as a subdivision of reproductive effort may be coupled with the attempts of various recent authors to understand the costs and benefits of sexuality. Thus, in asexual populations reproductive effort is all expended as parental effort; by definition there is no mating effort. The existence of mating effort, then, is a consequence of sexuality, and, in turn, the so-called "costs of sexuality" (Crow and Kimura, 1965; Maynard Smith, 1971a, b; Williams and Mitton, 1973; Williams, 1975) are attributable largely to the existence of mating effort. Efforts to identify and quantify these costs have nevertheless been both controversial and confusing (e.g., Barash, 1976; Treisman and Dawkins, 1976).

Under density-independent conditions asexual clones can sometimes multiply twice as fast as similar sexual populations because all offspring are females capable of reproduction on their own. This effect, resulting from what has been termed the "cost of producing males" in the sexual population, has

been cited as the principal disadvantage of sexuality (Crow and Kimura, 1965; Maynard Smith, 1971a; others). Williams and Mitton (1973) also identified a "cost of meiosis," which they defined as "the 50% loss in genetic material in meioticogenesis." Williams (1975) referred to the "50% hazard per generation" suffered by each allele as a result of meiosis, which he contrasted with the 100% expectation of every allele in an asexual species of being represented in every offspring.

These various costs are not always 50%, nor are they inevitable concomitants of sexuality. None of them precisely describes the principal costs of sexuality. Their values, however, do change together. Thus, Maynard Smith (1971a) pointed out that a consistently self-fertilizing hermaphrodite largely escapes the cost of making males because only a small proportion of the reproductive soma need be devoted to producing sperm to fertilize the available ova. Similarly, Williams (1975) stated that the cost of making males is negligible in monogamous species in which the male and female invest equally in the offspring. In both of these cases, the brood size can be increased to produce almost the same potential rate of increase as in a parthenogenetic species. This essential doubling of brood size also appears to counteract the 50% hazard otherwise suffered by each allele, and because male and female functions are similar, there is little or no cost of making males (Ghiselin, 1974). The extreme contrast would be with a gonochoristic species in which the males contributed no parental effort and in which the cost of sexuality would be 50%.

As Maynard Smith and Williams (1976) imply, the assignment of a principal cost of sexuality to loss of genetic material during oögenesis is spurious since genetic material as such is relatively inexpensive; haploidy in gametes does not materially alter the amount of parental effort necessary to produce a given number of gametes. The cost of sexuality thus does not refer to the genetic materials as such, but to the genetic materials in which the parent invests. It is the cost of omitting genetic material from zygotes destined to receive expensive parental investment and of having this genetic material replaced by genetic material from a partner who does not invest in the zygote, or who invests less. As in gamete dimorphism, it is a result of competition among members of the sex investing less in each offspring for mating privileges with the sex investing more in each offspring. It represents a diversion of parental effort--from contributions that might enhance reproductive competition with other species or asexual forms, to mating effort, which only affects the question of which males within the species will be most successful in mating. It is a diversion, however, that may help the individual carrying it out. Thus, males which devote all of their

reproductive effort to improving their mating success (by means other than by giving the female material benefits) may be viewed as parasites of the parental effort of their mates. They pay no cost of diverted parental effort except through their daughters. Yet, as a consequence, ultimately, of the dimorphism of gametes and their specialization to unite only with unlikes, a female in such a species cannot improve her reproduction by producing only males if she thereby creates a local surplus of males, reducing the number of matings available to her sons. Nor can she win by producing males which divert mating effort to parental effort if other females' sons which do not do this achieve sufficiently more matings to secure a greater genetic representation among descendants.

The cost of mating effort is thus borne by the population, but the cost of forbearing it would be borne by the individual through reduced success in sexual competition. A parallel exists in the suggestion of Hamilton (1971) that tendencies to live in groups may continue to intensify, even if they lower the average fitness of a population, because individuals who do not live in groups are rendered so vulnerable to predators by those who do.

THE MALE-FEMALE INTERACTION AS RECIPROCITY

The male-female interaction can be regarded as a form of reciprocity or as mutualism. Systems of reciprocity, however, are generally viewed as evolving toward symmetry or balance in the exchange (Trivers, 1971; Alexander, 1974), while the male-female interaction seems to have evolved in a highly asymmetrical fashion. A basic question in understanding the male-female phenomenon is that of understanding the nature of this asymmetry and how and why it has come about.

The implication of symmetry in reciprocal interactions is in the value to the recipients of the resources or items exchanged. There is no implication that the same items must be exchanged. Rather, systems of reciprocity must arise and succeed most often when the participants are specialized to deliver, inexpensively, mutually useful but different items. Presumably, symmetry in reciprocal interactions evolves because (1) each participant gains by adjusting interactions to its own advantage, (2) participants have some choice in accepting or rejecting interactions, or in interactions with particular partners, and (3) participants have some ability to alternate or exchange roles in interactions. All of these conditions are probably met in the systems of social reciprocity that we usually envision as evolving toward symmetry. When participants are in fact bound to a certain role (e.g.,

that of offering a specialized product that may sometimes be overabundant) or to a certain system (e.g., are unable to choose partners, change social groups, or escape the necessity of engaging in exchanges), then the first of the above three characteristics of systems of reciprocity, it seems, will inevitably lead to inequities and asymmetry.

In the case of males and females, each is bound to the role of its own sex in most gonochoristic forms, and we suggest below that such asymmetry in functions may have preceded gonochorism and hence preceded asymmetry between individuals. Once sex is inevitable, individuals are also bound to some kind of recombining interaction. These two facts together mean that situations could feasibly arise in which even if some members of one sex (say, females) are able successfully to favor members of the other sex (males) who reciprocate more completely than others, and to do so to their own (the females') advantage (i.e., thereby outreproduce other females), still, males that fail to reciprocate might so increase their reproduction as to outrace nonreciprocating males and eventually displace entirely the reciprocating tendency in males. This situation would lead to increased polygyny and decreased male parental effort.

If females favor males who reciprocate or show parental effort, then how could nonreciprocating males secure enough matings to win as a class, reducing the extent of reciprocity from males available to females? Aside from changes in the extrinsic environment, the only obvious way this can occur is through deception and desertion by males, the likelihood of which cannot be detected or entirely avoided by females. Such deception and desertion need not be of great magnitude in individual cases for evolution to proceed toward lower male parental effort against the interest of all females and the more parental males. Indeed, across evolutionary time the participants in any continuing system of reciprocity are expected to improve their ability to detect and respond to cheating, thus minimizing the amount occurring in any given interaction and establishing a base of expectations which will generally account for the great bulk of the actual exchange. The notion that deception involves only a relatively small proportion of the exchange of any long-evolved system is more commensurate with Trivers' (1971) analysis of reciprocal altruism than with his (1972) analysis of the male-female interaction in which he seems to imply a much greater amount of deception, especially on the part of the male (see also Borgia, this volume).

Monogamy, then, and symmetry in the male-female contract--which seems always to be secondary in higher organisms (arthropods and vertebrates)--must evolve only when parental effort by males is so rewarded that less parental males cannot

as a class outrace their more parental fellows. These rewards, as with all nepotism, have two components: (1) degree of genetic relatedness to putative offspring ("confidence" of paternity) and (2) extent of increases in the reproductive success of assisted offspring.

We assume that evolutionary specializations involving asymmetry--for example, specializations of females to be parental and of males to be promiscuous and nonparental--retard or reduce the likelihood of evolution toward symmetry of reproductive effort in many cases. Thus, initial male-female differences in the sizes of their gametes and later their relative amounts of parental effort and mating efforts, deriving originally from lowered likelihood of success of dispersing gametes and lowered confidence of paternity, reduce the relative likelihood of females, compared to males, gaining from additional matings. If one starts with primitive sexes in which one sex becomes more parental than the other, it is to be expected that the more parental sex will, as a result of specialization, subsequently be able to give parental care less expensively than the less parental sex. This effect, moreover, is likely to be cumulative. It increases the likelihood that females, compared to males, will evolve to invest even more heavily in offspring. As a result, females do not have as much reproductive effort left after one mating as do males, and females usually do not have the same possibility of realizing an enormously high reproductive success. Along with this long-term cumulative effect throughout the history of every genetic line, variations in confidence of maternity and paternity have continually influenced, in a proximate fashion, the differences between the sexes in their apportionment of reproductive effort.

Trivers (1972) argued that a parent's decision to invest further in an offspring depends upon the amount already contributed, considering desertion a theoretical temptation for the partner that has made the lesser investment, particularly if the difference is great. He further argues that the temptation to desert results because if no offspring are raised, the loss to the deserter is less than that of his partner. Therefore, selection would favor the partner remaining with the offspring.

Dawkins and Carlisle (1976) noted that the costs and benefits to a parent of deserting or not deserting a particular offspring actually depend, not on the amount already invested, but on the amount required to complete the investment--to make the offspring reproductive. This amount does not differ for the two parents, so it cannot account for the original male-female asymmetry in parental effort. Amounts

that is, the cost of raising an offspring is the same for both parents. In very different

of past investment and required future investment correlate inversely only when the required total investment and the return on the investment are consistent. When these values fluctuate extensively, as they certainly do in the rearing of different offspring in different situations, then the amount invested cannot be used as a reliable indicator of the expense that will be required to make the offspring reproductive. Moreover, it is not clear that the parent which has expended more parental effort on a brood has necessarily expended more of its total reproductive effort--which is what determines how much is left to be used in the production or rearing of another brood.

In a theoretical case, if one parent in a monogamous pair had tended one offspring and the other had tended another and one parent were suddenly killed, the remaining parent should arrange its parental effort so as to produce the most grandchildren without relationship to its personal investment in the two different offspring. A real example involves marsupials, most of which start a second offspring while an older sibling is in the pouch (Low, 1978). If the older offspring turns out to be timed wrongly in regard to food availability in the uncertain Australian environment, or if its mother is hotly pursued by a predator, it is discarded and the second offspring, held in a diapause stage before this happens, resumes its development. The offspring with the greater investment is thus discarded in favor of the offspring with the lesser investment, because the latter is more likely to become a reproductively profitable investment (see also Dawkins and Carlisle, 1976).

This argument may influence our view both of the early stages of evolutionary divergence of the sexes and of the reason why the female more often becomes the more parental sex. Reasoning backwards from modern species, in an anisogametic ancestor of an organism showing no parental care to the zygote, one might suppose that the sex producing the larger gamete is likely to become the more parental sex if parental care is subsequently extended to the zygote. Trivers (1972) argues that this likelihood would stem from the differential investment of the two sexes in the gametes, leading to the general tendency of females to be more parental than males. But the arguments just presented suggest that a difference in the phenotypic investment of the two sexes in a particular zygote should not in itself affect their tendencies to be subsequently parental toward the zygote. Moreover high male parental effort is not restricted, as Trivers' argument would suggest, to species in which the investments of the sexes in the gametes or in the newly formed zygote are most nearly equal. Instead it seems to be concentrated in forms which vary as much as possible in this regard: high-fecundity

fish with small eggs, low-fecundity birds with large eggs, and mammals with long gestation periods. What common elements, if any, exist among gibbons, songbirds, and male-brooding fish to cause their similar trends toward high male parental effort?

The adaptive significance of decisions by parents about whether or not to invest further in particular offspring appears likely to derive from cost-benefit outcomes involving three factors:

1. The likelihood that the dependent or juvenile involved is indeed the parent's own offspring--hence, its genetic relatedness to the parent.
2. The ability of the offspring to use additional parental care to improve the parent's reproduction through the offspring's own reproduction. Included will be the amount of parental investment required to bring the offspring to maturity and the offspring's likelihood of reproductive success, based on its current phenotypic attributes and physical condition, and such other factors as the season, population density, and likelihood of severe competition. Also included is the extent of the male's specialization as a parent; the most useful kind of parental investment may be very expensive or even impossible for him to provide. Thus, no male mammal has evolved to lactate despite the high probability that offspring have been lost in many species because of this inability. Nor have male birds in monogamous species evolved to contribute extensively to the food reserves of the fertilized egg, even though they may have evolved behavioral contributions which compensate for the greater early investment of the female. This fact suggests that male and female apportionments of mating and parental effort are in modern species largely divorced from the reasons for maintenance of their different regimes of investment in individual gametes.
3. The costs and benefits to the parent of alternative actions such as (a) efforts at further mating; (b) the probability of surviving to reproduce during another, perhaps better, season; (c) the presence of other dependent or needy juvenile relatives; and (d) need, relatedness, and expected success of offspring in potential subsequent broods. In general, additional matings yield more for a male than for a female, and they may be relatively inexpensive as compared to a first mating if the initial mating involved establishing a dominant position in a hierarchy or group of males or securing a good position in a lek. The number of a male's offspring may multiply as he multiplies his number of matings; while, for females, additional

matings may increase only the quality of their offspring. Such slight benefits to the female may not compensate the time, energy, and risks expended in additional matings (Bateman, 1948; Trivers, 1972).

This set of hypotheses predicts that higher parental effort by males than by females is most likely to generate in two situations: (1) in forms in which the male has more control than the female over fertilization--hence a greater "confidence" of parenthood (e.g., many fishes and some amphibians with external fertilization) and (2) in forms--like birds, reptiles, amphibians, and insects--in which (a) oviposition and fertilization are closely linked (hence confidence of paternity can remain high), (b) the eggs are relatively large (hence the female's remaining reproductive effort will likely be relatively low), and (c) the male's courtship behavior preadapts him to a continuation of parental care (hence it makes male parental care relatively inexpensive). In any of these cases it will be difficult to tell if the male actually exerts more parental effort than the female owing to the very different kinds of parental effort by the two sexes and to problems in distinguishing mating and parental effort.

To answer the question asked earlier, it is one or another combination of the following that is common to gibbons, songbirds, and male-brooding fish: (1) offspring able to benefit from additional parental care, (2) lowered likelihood of profit to males from seeking additional matings, (3) relative ease of paternal investment, and (4) high confidence of paternity. (A) (Borgia, 1972)

ORIGINS OF GAMETE DIMORPHISM: AN ALTERNATIVE SUGGESTION

The origin of gamete dimorphism represents the original massive diversion of parental effort into mating effort. In modern sexual metazoans two kinds of selective action on gametes can be distinguished--those affecting their ability to become part of a zygote and those affecting their abilities to succeed once they have become part of a zygote (Parker et al., 1972). In other words, it is possible to imagine that some kinds of gametes are slightly more successful than others at locating and uniting with other gametes to form zygotes, but that this ability is incompatible with maximizing the likelihood that the resulting zygote will succeed. Similarly, those gametes with the greater likelihood of surviving and reproducing if they happen to become part of a zygote may necessarily fail to possess attributes making them most competitive in becoming part of a zygote in the first place. To say it another way, opposing selective forces operating before

and after zygote formation may cause the evolution of two kinds of gametes, specifically, those that we call sperm and eggs; the same two kinds of selective forces may lead to the evolution of two kinds of individual organisms specialized to produce sperm and eggs, namely, males and females. Parker et al. (1972) have shown how these divergences and specializations might have evolved from a simple beginning involving only variations in gamete size. They suggest that an initial variance in the investment per offspring by different parents would alone be sufficient to lead to a disruptive selection on the sizes and other attributes of gametes and cause the evolution of males and females.

Parker et al. begin with an organism which, like many marine invertebrates today, expels its gametes in large numbers into the surrounding medium, perhaps at special times. Any gamete may unite with any other gamete; sperm and eggs have not yet evolved. They note that parents producing smaller gametes can make more of them, thereby, under some conditions at least, increasing the number of their gametes that will find and unite with other gametes. Parents producing larger gametes, on the other hand, must produce fewer of them. At least, initially this may mean either (1) that they are less likely to locate and unite with other gametes but more likely to produce a surviving zygote if they are successful in uniting, or (2) that they are less able to locate and unite with other larger gametes and are thus less able to produce the largest zygotes, which are most likely to survive.

Parker et al. note that if the survival likelihood of a zygote formed by small gametes uniting with one another is sufficiently low, and the competitive likelihood of two large gametes actually uniting is sufficiently low, the most frequently successful zygote will be formed of one small and one large gamete. A disruptive selection will result because of the two alternative routes to reproductive success. The smallest gametes will be more likely than others to locate and unite with the largest gametes, and the largest gametes will be likely to survive no matter with whom they unite. Parker et al. showed that if likelihood of survival increases with the square or cube of the volume of the zygote, the smallest gametes are more successful than intermediate-sized gametes, though not as successful as the largest gametes. A frequency-dependent disruptive selection is thus generated favoring the largest and the smallest gametes. From such a beginning, it is easy to envision increases in gamete dimorphism, with the elaboration of locomotive and guidance devices in sperm, until large eggs are virtually assured combination with a sperm and are eventually afforded the opportunity of

some selection among those available. Sexual competition among gametes, then, might be expected to lead to small gametes aggressively locating and uniting with large gametes. Both kinds of behavior suggest the onset of locomotion and forced combination or penetration of other gametes, which is now the characteristic behavior of sperm as contrasted with that of eggs.

Conversely, large gametes may be expected to become selective once their union with some kind of gamete is virtually assured. Perhaps they would evolve to resist union with the first gametes to arrive in their vicinity or become available until some kind of competition among aggressive gametes somehow indicates competitors likely to produce offspring superior in the same competitive situation. Hence, in all probability this led to the process of sperm "penetration" (and of the necessity of "penetrating" the female gamete) and the production of many sperm by even monogamous males evolved. That the general tendencies of small motile gametes and large non-motile gametes (sperm and eggs, respectively) have been selected in parallel to the behaviors of their respective bearers (males and females) is apparent; in polygynous species in which the male's parental effort is minimal, males tend to be aggressive in courtship, females coy. It may be speculated that both eggs and relatively sedentary females, such as spiders on webs, which show coyness, and even all females that encourage the attention of nearby males by forcing noisy or obvious courtship chases, may to some extent be generating their own private leks within which males can better be compared or must compete directly to win the female (Alexander, 1975; Cox and LeBoeuf, 1977). Such females are able to control male behavior because the female and her eggs represent resources needed by the male and sperm, respectively (Bateson, 1948; Trivers, 1972).

Parker et al. also argue effectively that eggs (large gametes) will be incapable of resisting the losses associated with uniting with sperm (small gametes), since the latter will evolve more rapidly because of their greater numbers (hence greater variety of mutants, more intense selection, and faster rate of adaptation) (see also Hamilton, 1967; Lewontin, 1970). Eggs, then, will be forced to retain enough reserves to yield viable zygotes when united with the smallest successful sperm. It is also likely that eggs are less capable of discrimination between sperm with reserves and those without reserves than females are capable of choosing males on such bases, both because of the more rapid rate of evolution of sperm (Hamilton, 1967; Lewontin, 1970; Parker et al., 1972) and because eggs may be less able than females to evolve means of recognizing uncoupling of stored reserves in sperm from their indicators.

Apparently, eggs also have little ability to discard an accepted sperm in favor of others that have not yet penetrated. Perhaps this effect is best hypothesized as an evolved ability by sperm to monopolize the egg once the sperm has entered the cytoplasm of the egg. To say it still another way, sperm generally lack the capability of capturing the reproductive potential of an egg already entered by another sperm. Females, as opposed to eggs, do however possess abilities to choose among males, or among sperm, even after mating. Although precedence of the sperm of the last male to mate with a female (Parker, 1970) may be viewed as a beneficial result of certain mating strategies by males, it is also one of many reasons why a female is not wholly bound to produce the offspring of a male just because she has already mated with him. Other such mechanisms include all of the various forms of abandonment of zygotic offspring associated with "overproduction" of eggs (for references, see Lack, 1968; Alexander, 1974).

Abilities of females to reject particular males as the genetic contributors to the zygotes in which they will invest extensively as parents thus appear to be considerably more effective than eggs' abilities to reject sperm. This ability seems concentrated in species with internal fertilization, although high male parental effort is not.

The conclusion of Parker et al. (1972) on the points treated here is this:

Thus the disruptive effect noted (in the previous sections) over one generation could lead directly over several generations to the establishment of stable primary sexual dimorphism (anisogamy, the male-female phenomenon, and a 1:1 sex ratio) with the assumption only that gamete size is controlled by simple dominance (p. 543).

Parker et al. thus begin with something resembling a multicellular marine organism which expels gametes into the surrounding medium where the gametes unite to form zygotes outside the bodies of their parents, postulating a gradual appearance of anisogamy from disruptive selection on gamete sizes. An alternative scenario may be constructed by beginning instead with a unicellular or acellular ancestor which--as in some modern bacteria, diatoms, and ciliates--passed or exchanged genetic materials during a conjugatory process. In modern ciliates haploid micronuclei, devoid of cytoplasm or other resources, are exchanged during conjugation in what might be viewed as a highly evolved system in which the timing of the exchange and the nature of the materials exchanged probably represent a specialized minimizing of the likelihood and extent of cheating or lopsidedness in the exchange. In a sense, such an organism is equivalent to an anisogametic hermaphrodite with internal fertilization. In this view, the

exchanged micronuclei function as sperm and the organism itself is equivalent to the female element or the ovum. Such "protogametes" would have developed with the appearance of sexual recombination. Because the packages of genetic information transferred during sexual recombination would likely be small relative to the receiving cell, the inequality of investment between parents may actually have preceded the formation of true gametes.

We assume that the basis for the transfer of investment-free packages of genetic materials during conjugation arises from the relative inability of the transferring organism to maintain the association between transferred genes and resources; this inability is to be compared with its ability to maintain the association between resources and the genes it retains within itself. We regard this situation as roughly paralleling the problem of paternity certainty in higher organisms and as crucial to understanding the early divergence of male and female functions.

If hermaphrodites mate only once, parental and mating effort are likely to be extended similarly by each individual. However, in cases where monogamy cannot be guaranteed and copulations are relatively inexpensive, hermaphrodites may gain from placing sperm in a large number of other individuals with the possibility of gaining from their parental effort. The production of large amounts of sperm, and effort expended in matings beyond what is necessary for an individual to secure sperm to fertilize its own eggs, might be considered "male" behavior by hermaphrodites. In outbreeding populations male and female effort by hermaphrodites should contribute equally to genetic representation in the succeeding generation.

Following the reasoning of Fisher (1958), this should lead to equal amounts of effort expended on each type of sexual behavior and to either specialization of individuals in one or the other type of behavior or to an equal expenditure of each type of effort by a given individual. Independently of how sexual behavior is distributed among individuals, high levels of male activities without parental effort will lead to increases in the costs of sexuality as discussed above.

We ask whether multicellular organisms which release their gametes to unite in the surrounding medium, of the sort necessary for the operation of the model of Parker et al., might not have been derived from an hermaphroditic unicellular (or acellular) ancestor like that envisioned above. Two directions for the evolution of "external" gametes could then be imagined. In one line, increasing tendencies to be non-motile or sessile may have reduced the likelihood that direct transfer of haploid nuclei could be effected; in another line, such direct transfer may have been restricted because of

tendencies toward multicellular states. In a multicellular organism, as contrasted with a unicellular one, it would be physically more difficult for each individual cell to conjugate, and tendencies of the haploid nuclei to move successfully through the surrounding medium would be favored. The same might occur if sessile organisms were near one another but not in direct contact; a predecessor might be very long conjugation tubes, such as are observable in some bacteria.

In the case of sessile organisms, we might envision the evolution of alga-like forms, and, ultimately, the entire plant kingdom. Considering modern algae, which include both anisogametic and isogametic forms, it seems possible that isogamety, in which all gametes are fairly large and locomotory, could evolve from the kind of unicellular "anisogamety" just described (rather than vice versa) if the gametes, or haploid forms, were subject to high mortality and uncertainty in regard to the length of time and amount of effort required to locate another gamete with which to unite. Under such conditions the minimum effective size of the gamete could be fairly large and determine the isogamety. The presence of chlorophyll in the isogametes of modern algae, which in itself imposes a certain lower limit in size, appears to support this idea. From such organisms, or more directly from the unicellular "anisogametic" form described above, it is possible to envision the evolution of modern anisogametic multicellular plants--in the former case, perhaps through the kind of disruptive selection on gamete size described by Parker et al. (1972).

Similarly, in an "animal" line, with forms perhaps paralleling *Volvox* in some ways, one may envision specialization of cells in certain portions of the group ("body") to produce gametes capable of moving through the surrounding medium to enter cells in other colonies. Such primitively multicellular organisms would still, like ciliates, represent hermaphroditic, anisogametic, internally fertilizing forms, with the gametes moving between them representing sperm. From such forms the evolution of "external" fertilization would involve the release of haploid units, ova or macrogametes, into the surrounding medium rather than acceptance of "sperm" or microgametes by female elements. Presumably such release could evolve because such "eggs" had become costly to carry, were more effective dispersers, were safer from predators than the parent, or because more eggs could be produced that way. In this scheme internal fertilization in modern Metazoa, and isogamety wherever it occurs, would be secondarily evolved, and gonochorism would be derived from hermaphroditism.

The most important point for understanding the modern asymmetries between male and female is that females evidently never relinquished to the degree that males did their control

over the fates of individual gametes. The confusion of parental investment with parental effort is more understandable in light of this consideration, since it explains why the greater investment in individual gametes has enabled females more often than males to gain by a greater overall parental effort.

MATING EFFORT AND SEXUAL ASYMMETRY IN PAIR FORMING AND COURTSHIP SIGNALING

There is a close correlation between the proportion of a female's prezygotic reproductive effort expended as mating effort and the degree to which males are able and willing to provide resources for offspring, whether as part of their own mating effort or as parental effort. The greatest differences among males as desirable mates will occur when varying amounts of resources or benefits are coupled with their provisions of sperm to the female. Accordingly, we may expect that when females signal males to them (as in many Lepidoptera), the expenditure and risk will be slight (as in the production of a pheromone) unless the male brings to the mating an ability and willingness to contribute parental effort. Extensive searching for mates (as in silkworms and other moths), costly signaling devices (as in acoustical Orthoptera and cicadas), or expensive combinations of searching and signaling (as in fireflies) are likely to be restricted to males. When males provide no material benefits and cannot defend resources useful to females, then the difference between leks visited by females (as in the European Ruff [Hogan-Warburg, 1966] and the Sage Grouse [Wiley, 1973]) and stationary females visited by groups of competing males (as in silk moths [Riley, 1895] and garter snakes [Devine, 1977]) may simply be in whether the stationary individuals or the moving ones undergo the greater expense (calories plus risk); in each case we expect the males to be forced into this role. Females seem unlikely to expend effort in seeking out lone males which are not controlling or offering resources additional to sperm. Males with nothing but sperm to offer, it follows, are unlikely to signal as isolated individuals, although it does not follow that males signaling in groups necessarily are offering nothing but sperm to females. Rather, males with nothing but sperm to offer should be expected to locate resources important to females and should (1) either seek or call females in the same vicinity, (2) defend from other males areas rich in resources, or for that matter the resources themselves, (3) control the resources so that the female is forced to modify her behavior in favor of the males with resource control, or (4) attempt to intercept females on their way to the resources.

ORIGIN AND BASIS OF THE MALE-FEMALE PHENOMENON

If one observes males signaling in relative isolation (as in field crickets (*Gryllus*: Alexander, 1961)), it should be regarded as crucial to discover what kinds of resources important to females the males are controlling or offering.

The general tendency for long-range sexual pheromones to be concentrated in females, while long-range visual and acoustical signals are concentrated in males, we believe has two bases. First, pheromones are less likely to be perceived by a wide array of predators and parasites since they tend to evolve to a much greater degree as narrow couplings of receptor and signaling devices or even as systems involving one receptor for each signal (Kaissling, 1971; O'Connell, 1972; Roelofs, 1975). Conversely, a very wide variety of either acoustical or visual signals, respectively, can be received (though not necessarily differentiated from one another) by the same sensory apparatus because of the relatively great potential for patterning such signals without altering their carrier frequencies. This quality makes visual and acoustical signals potentially visible to a much wider array of predators, hence more dangerous to produce.

Acoustical and visual signals are also more directional and individual-specific at close range. This not only makes them more effective but increases the risk of using them. In particular, such signals would be likely to outcompete pheromones when males are clumped or densely distributed as signalers. On this basis, acoustical and visual signals should be the rule in leks. Even if males in some such species initially signaled pheromonally, we would expect them to evolve to use acoustical and visual signals at close range, eventually replacing even long-range chemical signals with visual or acoustical ones. Visual and acoustical signals also seem more likely in rapidly changing situations, such as male-male aggression, since they are both more instantaneous and more versatile.

It is testimony to the significance of the refinement of Darwinism by Williams (1966a) [causing us to ask ourselves continually what are the units of selection] that so much work on sexual behavior--including, for example, that on acoustical behavior of Orthoptera, patterning of firefly signals, lepidopteran and other sexual pheromones, and butterfly visual signals--until recently had been carried out without questions like those asked above in mind (e.g., see Alexander, 1975). What had previously been regarded as species isolating mechanisms are to a large degree evolved instead in the context of sexual selection and competition within the species.

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