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Sperm in Competition

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I. INTRODUCTION

The sperm of external fertilizers are usually simple in design and largely similar (Franzen 1956, 1970). By contrast, internal fertilizers produce an often bizarre gametic fauna that includes giants extending many times the length of the male, immobile dwarfs, active sperm lacking genomes, and polyflagellated projectiles. An attractive explanation for this diversity is the relatively greater variance among internal female genitalic environments as compared with the homogeneity of open water. Additionally, sperm deposited internally may have to be equipped for various stays in the female tract and structured to penetrate eggs whose surfaces and chemistries are adapted to a variety of oviposition habitats (in part, Baccetti 1972, Cohen 1977).

Such elemental diversities of time, terrain, and proximate mission, however, may be insufficient to explain the range of sperm morphology and behavior. For example, Cohen (1977) found a surprising inverse relationship between the complexity of flagellar fiber arrangements and the distance the gamete must swim. Head and midpiece structures are frequently most elaborate where the journey is the least difficult, and no particularly clear correlation exists between the relative complexities of sperm and the egg membranes they penetrate (Cohen notes that the very complex sperm of gastropods penetrate eggs that are "effectively naked").

What other factors are responsible for evolution of diversity in sperm? Competition for fertilization is a likely context. Consider again the problem of gamete morphology in external and internal fertilizers. Certain antagonisms are likely to be more acute among internal fertilizers. Competition between sperm concentrated in a storage organ or other niche of the female system could be aggressively resolved by physical or chemical means unlikely to be effective in the more diffuse cloud of an external ejaculate, and the short time between gamete release and external syngamy restricts the scope of competition between ejaculates. Whether fertilization is internal or external there are circumstances where females will be confronted with multiple ejaculates. When females retain their eggs they are more able to choose the paternity of their offspring through sperm manipulation. If so, internal fertilization places a premium on sperm that circumvent such choice by force or "deceit." The more abundant opportunities for internally fertilizing adults or their sperm to influence sperm competition may be partially responsible for the adaptive radiation of their gametes.

While opportunities for competition may be greater in internal fertilizers, the motives are universal. There are at least five ways competition could have influenced gametic evolution and these occur in or between three levels of organization: competition among ejaculates; within ejaculate conflict; conflict between the male parent and his gametes; competition between sperm and choosing females;

and competition between nuclear programming and organelles located in sperm. The following is an attempt to discern the mark of such conflicts on the forms of gametes, the structures of their populations, and the architecture of the organs that deal with them.

II. INTRA EJACULATE COMPETITION AND MALE/GAMETE CONFLICT

A. Competition Among Sibling Sperm and the Loss of Gamete Individuality

Sperm have a dual nature. As cells of a male's body, they serve as tools of his reproductive interests. At the same time, they are microorganisms typically with one of what can be quite a number of possible genomes. In the latter role, they encounter competition for ova from tens to tens of millions of siblings.

Selection at the gametic level may not be harmonious with selection on the diploid adult. A male's interest is to obtain the greatest possible number of fertilizations. Competition among his sperm might initially be a matter of indifference, but means of resolving competition could evolve that would lower the quality of the ejaculate as a whole. A gene expressed in a gamete that poisoned, injured, or stole resources from sibling sperm can increase in frequency (carnivorous protozoa and antibiotics hint at possible aggressive forms).¹ Because the sperm of an ejaculate have a 0.5 probability of sharing the identical "violent" allele, damage to the ejaculate could increase until the cost balanced the benefits of less competition due to fewer gametes (similar to sibling conflicts described by Trivers 1974). Where violent sperm are immune to their own weapons or "recognize" and preferentially destroy nonviolent sperm, ejaculate efficiency could sink to half that of sperm sibships not containing a "violent" allele. When more successful alleles are sex-linked, the number of zygotes per ejaculate need not be reduced for diploid interests to be challenged. Offspring sex ratios will be unadaptively distorted when one sex chromosome gives an advantage to its bearer over the vessel of its homolog (Hamilton 1967, Maynard Smith 1978).

Conflicts between diploid and haploid generations in animals and higher plants might have a predictable outcome. An individual that provides resources to another

¹Rothstein (1979) argues that inhibitory traits should be rare, since their value is directly correlated with their frequency. That is, when inhibitory alleles arise, their ability to influence the average performance of large numbers of competing genes is apt to be low compared with the cost involved in inhibiting. This argument lacks force when applied to gametes. Among sperm, a mutation that survives one generation will automatically occur in 50% of the next population, *i.e.*, half the sperm in an ejaculate of a male heterozygous for inhibition will be inhibitors.

possesses a means of manipulating the recipient (Alexander 1974). A sperm's body consists of cytoplasm obtained directly from the male. There would be abundant opportunities for an adult to adjust the cellular machinery of its sperm to muzzle gametic gene expression.

Male suppression is a possible explanation for the apparent inability of the sperm genome to influence its phenotype (Sivinski 1980; Crow 1979, who argues that "Whatever the evolutionary reasons for the nonfunctioning of genes in sperm cells may be . . ." expression of sperm genes would result in more opportunities for adaptations to arise that damage siblings; Dawkins 1982). The evidence for the absence of haploid effects, *i.e.* transcription of genes within sperm, is considerable (*e.g.*, citations in Beatty 1975a, b). McCloskey (1966) and Lindsley and Grell (1969) in continuation of Muller and Settles' 1927 work have shown that *Drosophila melanogaster* sperm nearly devoid of chromosomes can differentiate and function. When matched with eggs that have a corresponding excess of chromosomes, normal individuals can be produced. Mouse sperm with whole chromosome duplications and deletions are functional and capable of fertilizations (Ford 1972). Variances of morphological characters of sperm in inbred (homozygous) and outbred (heterozygous) lines of mice are not significantly different, demonstrating that genotypic diversity need not result in phenotypic variety (Beatty 1971, 1975; Pant 1971).

There are suggestions, however, that sperm genes may not be completely mute. Whatever results in the greater than average success of *t*-allele-bearing sperm in heterozygous rodents appears to take place sometime between meiosis and fertilization (Braden 1958, 1960, 1972; Yanagisawa *et al.* 1961). Differences in *t* and + sperm head antigens have been found (Yanagisawa *et al.* 1974). DNA-dependent RNA polymerase has been discovered in mouse late spermatids (Moore 1972; see also section IV). Perhaps during evolutionary conflicts resulting from different and conflicting directions of selection, gametic genes break through the diploid's blockade and enjoy temporary expression (see the discussion of "arms races" in Dawkins and Krebs 1979).

Microgametophytes (pollen) are, in many ways, functional equivalents of sperm. It is puzzling, then, that haploid effects are common in pollen (Mulcahy 1975, 1979; Mulcahy and Kaplan 1979; see section II). Differences in the population structure of the two forms of "gametes" might account for the disparity in haploid expression. Sperm are typically in close proximity to large numbers of siblings, whereas pollen can be more diffusely spread. "Ejaculate" mixture in wind pollinating species seems likely. Even the dense masses of pollen on bees often come from several plants, increasing the likelihood that after deposition on a style, nearby competitors are unrelated. The opportunity for pollen to affect siblings unfavorably may be considerably less than for sperm (Sivinski 1980; a notable exception occurs in plants where large numbers of sibling gametophytes are packaged together in pollen dispersal units: see Wilson 1979). The mechanics of

insemination make plants more vulnerable than animals to self-fertilization. Expression and recognition of the haploid genome can prevent inbreeding (see Heslop-Harrison 1975, also Bremermann 1980).

Selective asymmetries between levels of organization will influence the frequency and form of adaptations. In sperm, because of the opportunities for "parental" manipulation, we might find more "altruism" and less aggression than predicted by the coefficient of relatedness between gametes.

B. Sperm in Groups: Cooperation, Manipulation, and Evidence for Diploid-haploid Conflict

A modest-size metazoan's abilities exceed the summed capacities of half a billion conspecific protozoa. With this in mind, Cohen (1975) asked why redundant sperm, supposedly produced as a shotgunlike means of hitting upon an ovum, have not been selected to form multicellular coalitions better at fertilization (in the case of man, ". . . a planarianlike organism exquisitely suited for finding the egg."). While not attempting to answer Cohen's query (see Sivinski 1980, and citations; Parker, this volume), it should be pointed out that sperm occasionally do function in groups, and that castes of specialized gametes form conglomerates of some, if less than metazoan, complexity (see Fig. 1).

Under certain circumstances, ejaculate efficiency can be enhanced by grouping sperm into multicellular units. For participating gametes, however, group existence bears a price, the closer proximity of competitors (see Alexander 1974, discussion of benefits and drawbacks to sociality). Males and sperm might disagree as to the extent of cooperation (again, see Trivers' discussion of parent/offspring conflict, 1974). Where some sperm, by performing a specialized role within the group, actually lower their own chances of fertilizing an egg, the potential for conflict between haploid and diploid generations is particularly great. Adaptations that appear to be resolutions of such conflicts suggest a history of haploid expression and diploid suppression.

There are several multi-sperm formations that seem to be aggregates of equals. All potentially increase their probability of penetrating an egg by their association. Some of this grouping is clearly produced by the metazoan. Sperm, particularly insect sperm, are commonly packaged in bundles that break apart in the vas deferens or female tract. These packets are sometimes mobile and have been mistaken for single sperm (Nur 1962). Bundled gametes are often amassed under proteinaceous caps that may serve as sources of nutrition or concentrations of enzymes that break down genital tract secretions for assimilation (citations in Mackie and Walker 1973). A cluster consists of descendants from a single spermatocyte that have remained in proximity through development. Their numbers depend on how many mitotic divisions occur prior to meiosis (*e.g.*, in the grasshopper

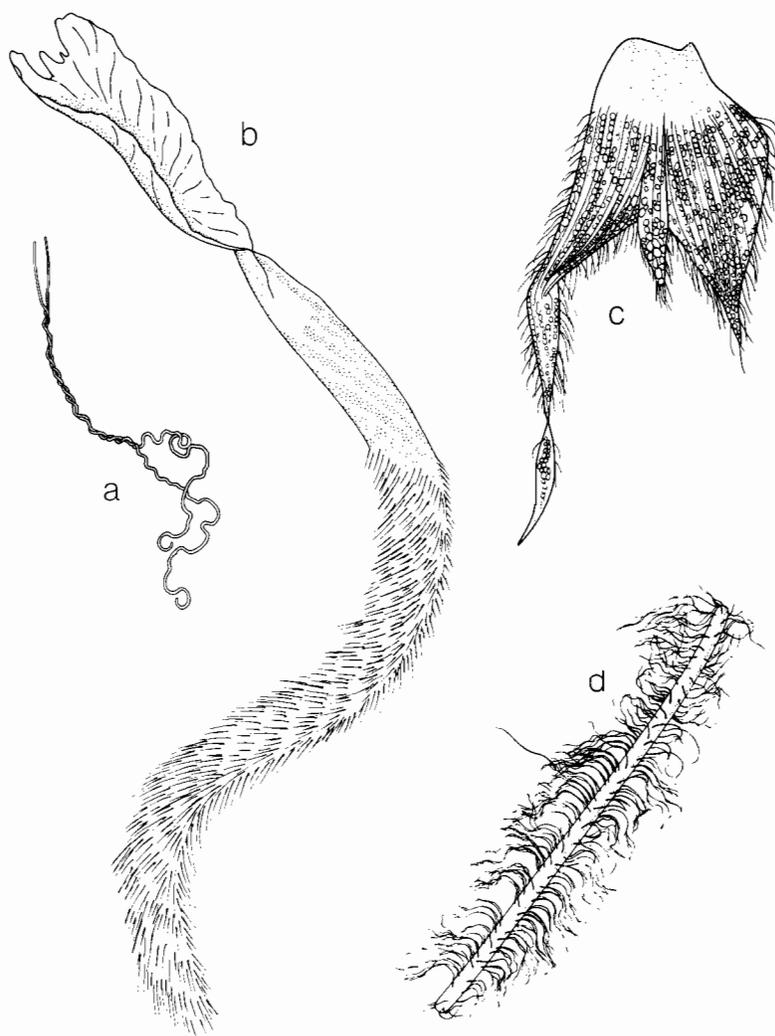


Fig. 1. Sperm in groups (not to scale). A. Paired sperm of the silverfish, *Thermobia domestica* (redrawn from Bawa 1964). B. The apyrene sperm of the mollusk, *Clathrus clathrus*, and its fertile eupyrene passengers (redrawn from Fretter 1953). C. Another atypical molluscan sperm (*Cinctescala eusculpta*) with typical sperm attached (redrawn from Nishiwaki 1974). D. Spermatostyle and associated spermatozoa of a gyrinid beetle, *Dineutus* sp. (redrawn from Breland and Simmons 1970). Drawing by Susan Wineriter.

Melanoplus sp., seven premeiotic divisions result in 512 sperm. See White 1955, Virkki 1969, Kurokawa and Hihara 1976, for the peculiar relationship between bundle number and phylogenetic position; also Sivinski 1980a).

Other relationships occur where free, mature gametes join together in the ducts of the male reproductive system. Sperm of some whirligig beetles (Gyrinidae) become attached in groups of 100 or more to rodlike objects, spermatostyles, as they pass through the vas deferens (see Fig. 1d). Partially disintegrated rods have been recovered from spermathecae. Spermatostyles are moved by the efforts of their crew, but loose sperm are also motile (Breland and Simmons 1970). The function of these aggregates is obscure. The sperm may benefit from material in the spermatostyle, or perhaps they deliver the rod as a parental investment to the site of female absorption (see also section III). The rods might even be useful in competition with rival ejaculates, perhaps as a means of allowing large groups of siblings to force themselves toward and then occupy privileged positions in the spermatheca.

Paired spermatozoa are a rare, but widely distributed, phenomenon. Pairing may occur in the testes, e.g., the silverfish *Thermobia domestica* (Thysanura), or during passage down the vas deferens, as in the water beetle *Dytiscus marginalis* (Bawa 1975). In *T. domestica*, sperm are only motile when anterior thirds of a pair are entwined (Bawa 1964; see Fig. 1a; similar union occurs in another silverfish *Lepisma saccharina*: Werner 1964). *Dytiscus marginalis* sperm are motile as individuals but have adaptations for paired life, including spurs that mesh at points of attachment (Mackie and Walker 1974; Bawa 1975). Other gametes typically joined at the head with tails and midpieces free are found in the millipede *Polydesmus* sp. (Reger and Cooper 1968), the mollusk *Turritella* (Idelman 1970), woolly opossum (Phillips 1970), and opossum (Holstein 1965; for the numerologist, marsupials have two-channeled vaginas, bifurcated penises, and some have sperm that swim in pairs). In the beetle *Colymbetes*, groups of three or more are formed (Mackie and Walker 1974).

Pairing probably represents some sort of cooperation, but to what purpose is unclear. Two flagella might generate more motive power (Afzelius 1970). The sperm of the millipede *Polydesmus*, however, are odd, crescent-shaped objects without flagella, and apparently unmotile (Reger and Cooper 1968). Other suggested functions include protection of each others' acrosomes (the tip of the sperm, important in fertilization) or enhanced ability to penetrate an ovum (Mackie and Walker 1974).

Assuming probably unrealistically high levels of haploid expression, partnerships might become increasingly uneasy as fusion of egg and sperm pronuclei approaches. Given sperm are not genetically identical products of the second spermatocyte, the cost of having an attached competitor may, at some point, outweigh the advantage of its cooperation. Both sperm are equally related to the male, who should program gametes to remain together until all benefits of the coupling are realized.

A potential conflict could arise over the point where siblings are to be jettisoned. The presence of a common rival, another male's ejaculate, might modify gametic selfishness and select for extended unions. It is better to aid a "sibling" gamete within range of fertilization than to compete as an individual, on an approximately equal basis, with unrelated gametes.

Among haploid-expressing sperm, then, the length of pairing might be directly related to the degree of sperm competition between or among males. While hardly compelling as evidence, the two known pairing durations of insect sperm are worth comparing. *Dytiscus marginalis* sperm are paired in the male tract, but are mostly single in the spermatheca (Mackie and Walker 1974, Bawa 1975). *Thermobia domestica*, however, are found together in female storage organs (Bawa 1975). While multiple matings are typical of female silverfish, the potential for sperm competition is not necessarily high. Females must replenish sperm supplies shed at each adult ecdysis (Sweetman 1938, Hinton 1981). Male *D. marginalis*, during days-long couplings, fill their mates' vaginas with bright white cement that hardens on exposure to air. Females are "corked shut" from fall to winter, suggesting very low levels of sperm competition (Balduf 1935).

Unlike cooperating equals there are a number of specialized sperm morphs that, by nature of their role, have little probability of obtaining fertilizations and constitute a sort of "worker caste." The enormous transport cells of some mollusks are cases of extreme dimorphism. They have literally become "mobile penises," carrying thousands of brother gametes upon their tails. These mammoth vessels swim up the female tract as far as the ovaries, liberating smaller sperm as they go (Fig. 1b and c; Fretter 1953). Large, multiflagellated sperm of certain snails entangle masses of normal gametes, either concentrating or helping to propel siblings during copulation. Once in the female, their midpieces degenerate, perhaps to provide nutrition for siblings (Woodard 1940, Hanson *et al.* 1952; extensive reviews in Nishiwaki 1964, and Fain-Maurel 1966). Other sperm morphs in mollusks are fusiform objects of little motility, which may serve solely as food sources for ejaculate mates (Pelseneer 1935, Hanson *et al.* 1952). Among Lepidoptera, a class of atypical sperm probably "displace or inactivate eupyrene sperm from previous matings or delay further mating by the female" (R. Silbergeld *et al.*, pers. comm.).

Specialized sperm serving peculiar, nonfertilizing functions are also genetically unusual. They either lack genomes altogether (**apyrene** sperm) or contain only part of the normal chromosomal complement (**oligopyrene** sperm; gametes with complete haploid genomes are **eupyrene**).

Is it possible that incomplete nuclei result from parental pruning of rebellious gametic genomes? Modification of a sperm for a supportive role results in a lower probability that it will participate in a zygote. A "gene" that allowed a "worker" spermatocyte to complete normal fertile development at the cost of ejaculate as a whole might increase in frequency if the greater success of helped "siblings" did not offset the cost of sterility; that is, among the gametes of diploids the

probability of sharing a gene is typically 0.5. Such a gene would be an outlaw, resistant to “parental” manipulation that forces cells into forms with less than average chances of obtaining fertilizations. A male could squash gametic rebellion by removing damaging genes from his sterile caste; that is, take the genome from the cell.

An absence of chromosomes could indicate a history of haploid gene expression acting in the context of parent-offspring conflict. A test of the argument lies in nuclear constituency of specialized sperm in haplo-diploid species. Since sperm of a haploid male are genetically identical, there should be no selection for gametic rebellion or genetic disenfranchisement (see also Starr, this volume). I know of only one relevant case.² Male rotifers are thought to be haploid and practice a sort of traumatic insemination. The first objects to enter the female are rigid rods produced by atypical, immobile spermatozoa. These sperm degenerate after extruding the rod and never encounter ova (Koehler and Birky 1966; the projectiles may be useful in breaching female tissue: Koehler 1965). Atypical sperm have “intact nuclei.”

C. Haploidy and Competition in Ova

Eggs are another class of gametes that could provide comparative evidence for male/sperm conflict. Ova rarely compete for fertilization and so might, by previous argument, escape suppression by the diploid genome. Do haploid effects, perhaps related to choice of sperm, occur in eggs? An answer of “not likely” is indicated by the lack of time in which a haploid ovum genome could express itself. In animals as diverse as pigeons, dogs, and roundworms, expulsion of even the first polar body takes place after penetration by the sperm. Only rarely does the second division

²One type of specialization, extra chromosomes, automatically renders sperm infertile. Polyploids could provide additional amounts of nucleic acid constituents and associated proteins to zygotes formed by eupyrene ejaculate mates (see Fain-Maurel 1966; and citations). Because males passing such sperm run the risk of losing offspring by producing polyploid zygotes, this form of investment might arise only when ova discriminate against sperm with chromosomal abnormalities (see Ito and Leuchtenberger 1955, for evidence of such discrimination in a clam; chromosomal abnormalities may be very widespread: Cohen 1975). Once such morphs are established, they might evolve further specializations as “helpers.” Since gene expression is not necessarily curbed, it is difficult to imagine polyploidy as a means of enforcing parental dictation of a helper role.

A number of invertebrates produce diploid, tetraploid, or higher ploid sperm (sperm with excess chromosomes are referred to as hyperpyrene; see Fain-Maurel 1966). They are usually larger versions of eupyrene sperm, leading to suspicions that they result from meiotic error. Some, however, are made in species-specific numbers and are occasionally very abundant. In the annelid *Allolobosphora caliginosa* they “. . . smother the typical line with their number” (Chatton and Tuzet 1943). Others bear morphological peculiarities suggestive of specialized roles. Certain carabid beetles, for instance, have hyperpyrene sperm with multiple flagella (Bouix 1963). There is nothing to prevent parental investment via hyperpyrene sperm in haplo-diploid species. Several wasps and ants have giant polyploid gametes (citation in Fain-Maurel 1966; see section III).

and haploidy precede fertilization (Cohen 1971, 1977). This last-minute finale to oogenesis suggests that (1) ovular choice or other possible haploid expressions are unimportant and that reduction is selected to occur only with the imminent arrival of the sperm pronucleus, or (2) haploidy is disadvantageous and selection favors retention of the diploid genome.

Among the costs of reduction is the loss of nuclear programming. The “lampbrush” configurations of chromosomes during oocyte growth and organization suggests active RNA transcription, a poor time for discarding genetic material. Chromosome repair may only be possible in the presence of a homolog making haploids vulnerable to lesion (Bernstein *et al.* 1981). Perhaps less plausible but in keeping with the spirit of this discussion are certain risks inherent in haploidy prior to the completion of cell provisioning. A gene appropriating excess resources could leave other eggs with an alternative allele undervictualized, decreasing the fecundity of the parent. The diploid can preclude female-egg conflict by limiting the range of an “outlaw” gene’s expression, *i.e.* by keeping all mutations in the company of cooperative, probably dominant alleles. Reduction to haploidy almost always takes place outside of the ovary, the oocyte’s source of supply.

A possibility of post-oocyte growth competition for resources exists as well, and might aid in explaining the rarity of sexual dimorphism in zygotes, *i.e.* offspring at the end of parental investment in the absence of parental care. When males determine sex, the danger of the wrong “sexed” sperm penetrating an inappropriate investment may force homogametic females into equal distribution of resources among her ova (Sivinski 1980; assuming eggs/females can’t effectively choose sperm on the basis of the sex chromosome they contain; see section III). On the other hand, heterogametic females might be vulnerable to intragenomic competition, where genes on sex chromosomes might strive to acquire a richer cytoplasm than is in the parents’ interest. In the two unambiguous instances of egg sexual dimorphism I’m aware of, gender is determined maternally but not by simple heterogametic sex chromosomes. Female eggs of the marine worm *Dinophilus apatris* are much larger than male eggs. Sex determination occurs prior to meiosis, perhaps due to the balance of multiple factors in the maternal genome (Bacci 1965). In the peach scale *Pseudolacaspis pentagone*, male eggs are white and female eggs coral pink, indicating some difference in the nature of parental investment. Sex is determined cytologically (Brown and Bennett 1957). A case resembling a predicted conflict occurs in the common grackle, where heterogametic females tend to produce larger male eggs but the relationship between size and sex is not invariable (Howe 1976, 1977).

Oddly enough, considering its breathless finish, ovarian meiosis often begins early in female development and then pauses shortly after the onset of the diplotene stage of prophase I, the orientation of homologous chromosomes into tetrads (Austin and Short 1972). In humans, for example, meiosis starts in the female embryo but is completed following ovulation, a hiatus of up to 50 years. Stop and

go meiosis can be seen either as a brake to impending haploidy (at loci not affected by crossovers) or as an early chromosomal assortment driven by competition to occupy that portion of the oocyte destined to become the ovum and avoid the genetic death of inclusion in the first polar body. This latter view requires pre-determination of chromosomal fate early in meiosis. The first chromosome to occupy the favorable location in the cell would have won the first round in its struggle for perpetuation to the certain cost of its homologue. Jockeying for position could force such a critical stage of meiosis father and farther back into development (it is tempting to consider chromosome crossovers being manipulated by a polar body-bound allele to attach itself to a more fortunate chromatid and consign its competitor to the void).

III. INTEREJACULATE COMPETITION

Phenotypic characteristics of sperm dictated by the male's diploid genotype are referred to as diploid effects. In the absence of haploid expression, sperm competitions become contests between extensions of adult genomes. As might be expected, different males produce gametes of different abilities. When female chickens, mice, rabbits, and cattle are artificially inseminated with similar numbers of sperm from two or three males, sperm from particular animals are consistently more effective in obtaining fertilizations (Beatty 1975a, b; and citations: "It is an exception for equal numbers of sperm to produce equal numbers of offspring").³

For diploid effects to evolve by interejaculate competition, adults must potentially place unrelated sperm together. Variance in the characteristics of the sperm themselves might provide the motive for multiple inseminations. Ejaculate mixture could be "deliberate." Discriminating females might actively arrange competition between gametes. Proximity leading to conflict could also be merely the effect of selection acting in other contexts.

Note that unusual sperm are occasionally found in taxa with unusual opportunities for ejaculate mixture, e.g. the termite *Mastotermes darwinensis* whose colonies contain multiple reproductives (see Sivinski 1981 and citations), and birds of the snipe family Scolopacidae whose females produce multiple clutches over relatively short periods of time, each preceded by mating with a different male (J. van Rhijn, pers. comm.; see McFarlane 1963).

³In the wasp *Dahlbominus fuscipennis*, gametes from males bearing a mutant have an advantage over wild type competitors (Wilkes 1966). Diploid effect is an inappropriate term, since males are haploid, but this is another example of male genotype correlated with the competitive ability of sperm.

A. Female Encouragement of Sperm Competition

Gametophyte (pollen) fitness can be related to the fitness of the sporophyte it cooperates in producing. Genes that are transcribed in both haploid and diploid genomes have an “overlapping” pattern of expression (Mulcahy 1979). To the extent that selection acts similarly in the two contexts, fitness of an overlapping haploid is a predictor of fitness in the diploid and, presumably, vice versa. In corn, for instance, the speed of pollen tube growth is positively correlated with seedling weight, ear weight, and kernel weight of the resultant plant (Ottaviano *et al.* 1980).

Females could benefit in such instances by passively accepting fertilizations by victors of gametic competition. Statistically, better fathers could be obtained for offspring by pitting together large numbers of competitors. Paternal filtering through intense competition may be partially responsible for success of angiosperms which receive massive, simultaneous doses of pollen from insect symbionts (Mulcahy 1979).⁴ Selection of gametes could be intensified if females produce a challenging genital environment in which only the most “vigorous” could reach an egg (again, see Mulcahy 1979, for a discussion of the importance of stylar tissue as an “impediment” to fertilization; see also section III for discussion of female choice of compatible sperm genomes).

An equivalent form of selection could occur in animals if sperm fitness predicts offspring quality. Females might solicit ejaculates from numerous males without any precopulatory regard for their quality (this supposes heritable differences in sperm competitiveness perhaps due to recurrent mutation: see Borgia 1979).

Gamete fitness need not guarantee its genetic program’s success in a diploid genome. Alleles might have favorable expression in gametophyte or sperm but bear disastrous pleiotropic effects into the diploid. Evening primrose demes are thought to contain genes that result in inferior winter survival but that are maintained by their prowess when part of pollen grain genomes (Henderson Nilson 1923, in Haldane 1932). Mouse sperm carrying *t*-alleles are more likely to win fertilizations, but resultant animals bear effects ranging from short tails to homozygotic sterility (Lewontin 1970; see Alexander and Borgia 1978).

Genes expressed in the haploid generation may not be expressed in the diploid (nonoverlapping, in terminology of Mulcahy 1979). It would seem that the greater the difference between the environments of the haploid and diploid generations,

⁴Cohen (1967, 1971, 1975, 1977) has long championed a related argument, that dangers inherent in crossovers leave only a few sperm with intact chromosomes in each ejaculate, and that the female can recognize and/or filter these individuals through haploid effects. He supports his position with a significant correlation between the number of sperm per egg and the number of chiasmata per genome (see, however, Wallace 1974; Parker, this volume). If haploid effects are common, the correlation could also be consistent with males providing undamaged haploid genome samples to choosing females. The greater the potential genetic variance (*i.e.*, the recombination rate) within an ejaculate, the larger the ejaculate would need to be to contain the best possible sperm for a particular egg or female (Sivinski 1980a).

the more likely it would be for distinct sets of genes to evolve for the production of organism and gamete. Sperm in the internal genitalia of a female probably have less in common with the organism that deposited them than male microgametophytes and sporophytes of higher plants whose open air and multicellular worlds overlap. If so, the portion of the diploid genome reflected in the sperm phenotype may predict very little about the nature of the genes that produced the diploid phenotypes.

Where all correlations between sperm and offspring quality are equally possible, females could select mates at both individual and gametic levels. Even occasional exposure of ova to the sperm of two or more males would generate selection for females to produce sons not only with the ability to obtain mates, but also able to pass a competitive ejaculate. Information on an adult male's quality could probably be more easily obtained than insights into the uncorrelated qualities of his ejaculate. Females might discriminate at the two levels by choosing several of the best available adult phenotypes and allowing their sperm to compete.

Some patterns of mating are consistent with expectations of competition encouragement. Mated short-tailed crickets, *Anurogryllus arroreus*, respond to calling males and, presumably, mate more than once before any eggs are laid (T. Walker 1980). Other copulatory strategies suggest gametic level selection is unimportant. *Drosophila melanogaster* remate only after ca. 78% of the first ejaculate is exhausted (Gromko and Pyle 1978). Subsequent fertilizations are accomplished by sperm that have had the opportunity to compete, but the late introduction of the second ejaculate is hardly indicative of an arranged sperm confrontation.

Where females accept the results of competition between sperm or encourage it by gathering antagonists and providing arenas, the paternity of offspring should be independent of the order of mating. In insects and other taxa, the last, sometimes the first, males to copulate obtain the majority of subsequent fertilizations. Predictable paternity on the basis of order demonstrates adult influence over fertilization (Parker 1970, males protecting paternity generate order effects; Walker's 1980 argument for female control of ordering not relevant here, since females would abandon ordering to maximize competition). Order effects do not prove that competition between sperm is absent. Adult strategems could obscure the smaller struggle within. Low variance, *i.e.*, high predictability, in last or first male fertilization rates, however, would refute the contention that competition between sperm is important in determining paternity (note that high variance could result from differences in competitive ability of adults, not necessarily differences between sperm). Measurements of variance in natural populations of insects have apparently not been made (see Walker 1980). Among rodents, variance in order effects seem to be considerable (*e.g.*, Levine 1967; Dewsbury, this volume).

B. Incidental Proximity of Ejaculates

Females may mate with more than one male for reasons other than arranging competition or replenishing completely exhausted sperm stores. An effect of such behavior is placing together unrelated ejaculates. A result of proximity would be selection for sperm to obtain fertilizations at the cost of rivals. Walker (1980) has reviewed the adaptive significance of multiple mating. Advantages include increasing genetic diversity, mating with males of increasing genetic superiority, increased predation protection for females (see Sivinski 1980b, for evidence of greater survival in mating female stick insects), and transfer of nutrients. This last benefit is of particular interest in considering some curious aspects of sperm morphology. Multiple copulations in the context of female mate choice, as opposed to filtering mates through sperm competition, are considered in section IV.

C. Paternal Investment Via Sperm: Implications for Sperm Competition

The number of sperm accepted by a female usually exceeds the number of ova she will produce. One possible reason for the redundancy is the use of additional sperm as a parental investment (see Gwynne, this volume). A female, for example, might store and release multiple sperm as a nutritional boost to the zygote (Afzelius 1970). Polyspermy, more than one sperm penetrating the ovum, occurs in selachians (Ruckert 1899), urodeles (Jordan 1893), reptiles (Oppel 1892), bryozoans (Bonnevie 1907), birds (Blount 1909), and insects (Richards and Miller 1937; citations in Mackie and Walker 1974; see, however, Lefevre and Jonsson 1962).

Insect sperm often contain large mitochondria whose configuration is radically changed to a crystalline form during spermiogenesis. Peculiarities of the crystal are consistent with a paternal investment. They do not possess the biochemical activity of mitochondria, are structurally stable during the life of the sperm, and are metabolically inactive in terms of sperm activity. Many contain large amounts of protein and are completely absorbed by the zygote (Perotti 1973, Bacetti *et al.* 1977).

Some male animals, primarily arthropods, produce huge gametes that might contribute resources to zygotes regardless of the selective reasons for their gigantism (see following subsection on sperm polymorphism). In the featherwinged beetle, *Ptinella aptera*, they are twice as long as the adult (Taylor 1981, 1982). Other ptiliids have sperm that are only slightly less enormous relative to body size. *Bambara invisibilis* females can store only ca. 28 sperm (Dybas and Dybas 1981). At 14 mm some sperm of the house centipede, *Scutigera forceps*, are longer than the testes and nearly as long as the animal itself (Ansley 1954). Painters frog,

Discoglossus pictus, has 2.3 mm sperm; bundles of sperm are visible with the naked eye (Favard 1955). Ostracod spermatozoa can be relative titans, 10 mm long, many times the male length (Bauer 1940). *Drosophila melanogaster* sperm average 1.7 mm; in other *Drosophila* they reach ca. 15 mm (Beatty and Burgoyne 1971, Perotti 1975). Mitochondrial derivatives compose 50% or more of their volume (Perotti 1973). The club-shaped sperm of ticks range from 1 to 7 mm (Rothschild 1961, Austin 1965). Heavy-bodied sperm of the clerid beetle *Divaes bipustulatus* stretch 10 mm. Most of the tail is composed of derivatives (Mazzini 1976). Sperm of the backswimmer *Notonecta glauca* are 15 mm long, with a volume of $38,000 \mu^3$. Mitochondrial crystals occupy 90% of these sluggish giants (Afzelius *et al.* 1976).

Peculiar nonfertilizing gametes may be forms of paternal investment. Oligopyrene sperm in some molluscs may penetrate trophic eggs, ova that are later consumed by sibling larvae (Dupouy 1964); they might do so to enhance the eggs' value as food. Instances of pseudogamy (parthenogenesis "stimulated" by sperm) are also suggestive of paternal investment through gametes. The sperm makes no genetic contribution but must penetrate the egg for development to proceed. Perhaps eggs pirate material from male gametes (see Lloyd 1979, Sivinski 1980a). The relative size of the egg and sperm differs across pseudogamous taxa. As dimorphism increases, the less likely it is that sperm can contribute significantly to the zygote (assuming no polyspermy). The entire ejaculate, however, could still be nutritionally useful to the female.

There are advantages to males who invest directly in the zygote with enriched sperm rather than indirectly, through substances absorbed by the female. Indirect investments increase future fecundity, but may provide for ova a male does not fertilize due to subsequent inseminations by other males. A shortened time between resource transfer and deposition in a zygote minimizes the probability of a female dying before producing the investing male's offspring.

Storage difficulties inherent in small animals maintaining large, perhaps resource-laden, sperm might select for frequent copulations and the mixing of rival ejaculates. *Drosophila melanogaster* sperm are relatively big and copulatory patterns indicate females remate to replenish diminished sperm stores (*e.g.*, Gromko and Pyle 1978).

Sperm and ejaculatory fluids might be used by a male as a nuptial gift to a mate. Rather than benefiting zygotes, resources would serve as investments in the fecundity and good health of his offspring's mother (see Thornhill 1976, 1980; Gwynne, this volume, for discussions of paternal investment). Bedbugs probably use the massive ejaculates they receive as food (Hinton 1974). In the purple martin ectoparasite *Hesperocimex sonorensis*, females inseminated by well-fed males produced three times as many eggs as those paired with starving males (Ryckman 1958). Further evidence of ejaculate value might be inferred from the homosexual relationships in Cimicidae. Males of the bat bedbug *Afrochimex* are transvestites, with pseudofemale paragenital structures that apparently invite homosexual attentions.

Hinton (1964) felt these sodomies were a means of food sharing, an inappropriate argument since it proposes the feeding of sexual rivals. Aid in stealing an ejaculate for consumption might account for the mimicry (see Lloyd 1979, who argues that inviting male attentions reduces the fertilizing capabilities of rivals). Some insect sperm storage organs suspiciously resemble stomachs. The spermathecae of morabine grasshoppers are capable of holding 800 times the ejaculate of similar-sized relatives. Much of the proteinaceous material held by the spermatheca is destroyed by a range of enzymes (Blackith 1973).

Where females benefit directly from male investment, and zygotes only indirectly, males become particularly vulnerable to exploitation. A female collecting seminal material for her own nutrition might harbor the remains of several unrelated ejaculates competing for fertilizations (see, however, Gwynne, this volume, whose correlation between paternal investment and assurance of paternity would indicate lower than expected levels of competition).

D. Strategies of Competition: Getting There

Cohen (1977) has remarked on a puzzling negative correlation between flagellar complexity in sperm and the distance of their average journey. The epitome of his paradox are the globular spermatozoa of cycads. Covered with a fur of flagella, they travel about half the length of their body. (Arthropod sperm are sometimes much longer than the journeys they undertake.)

When interejaculate competition is possible, emphasis on distance is misleading. No matter how short the race, the object is to win. Among competitors starting together, *i.e.* at random, distance is immaterial compared with relative velocity. Even co-occurrence of short distance and high speed need not be unexpected. Parker (1970) has argued that competition to be nearer ova has been important in the evolution of intromission devices. Greater intrasexual competition, resulting in deeper penetration toward the site of egg production might simultaneously produce more effective gametic propulsion.

A gamete can get there first not only through speed, but by leaving first. Sperm in the storage organs of insects often show a sort of perpetual agitation or excitement prior to a fertilization (*e.g.*, Lefevre and Jonsson 1962, Taylor 1982). It is possible that the disturbance is the collective result of competitors jockeying for position.

Competition in time might account for the extraordinary reproduction of the fish ectoparasite *Gyrodactylus* (Trematoda). Unequally developed products of a polyembryonic partitioning of the ovum lodge inside siblings. A parent contains an embryo which has another embryo within it, which holds yet another embryo bearing a tiny fourth, and final, embryo (Dawes 1968). In hermaphroditic matings reminiscent of couplings between Russian dolls, sperm introduced into the adult

reach all the nested embryos (Cohen 1977). It is possible that sperm attempting to get a jump on future rivals could have played a role in the evolution of this hyperviviparity. The initial stage might have resembled the occasional cases of mother-daughter insemination in the livebearing guppy *Poecilia reticulata*. Sperm reaching the hollow offspring-containing ovary inseminate both generations (Spurway 1953, Cohen 1977). If mates are rare, small internalized siblings that permit insemination increase their chances for sexual reproduction.

Sperm might succeed not only by leaving first or proceeding more rapidly, but also by leaving more often. One such case occurs in the bedbugs. Insemination in bedbugs and their relatives is traumatic. Sperm are injected through the body wall and homosexual injections occur in the Cimicidae, Plokiophilidae, and Anthocoridae (Carayon 1974). Among male *Xylocoris maculipennis* (Anthocoridae), sperm of the "mounter" migrate to the "mountee's" seminal vesicles, expanded portions of the vas deferens that serve as holding pens for sperm. Here they mingle with the victim's sperm and are found in his subsequent ejaculates (Carayon 1974). Parasitization of a rival's genitals multiplies a male's ability to deliver sperm (Lloyd 1979). Males would be expected to resist "rape" and sperm might have adaptations to infiltrate defenses. Phagocytosis of sperm occurs in both sexes of some related bedbugs (Carayon 1966). In *X. maculipennis*, the sperm are not attacked but do wait a curiously long 24 h before moving toward the reproductive tract. Rapist *X. maculipennis* have apparently countered any defenses raised to date. Sperm of traumatic inseminations, in general, tend to have enlarged motor organelles, presumably to overcome the mechanical resistance inherent in travel through a body (Baccetti and Afzelius 1976). In other species of homosexual parasites, should they occur, perhaps the converging defenses of an exploited male intensifies selection for power.

The potential for genital parasitization by mobile cells exists in certain vertebrates as well. Primordial germ cells migrate to regions of gonadal development through the bloodstream in some mammalian embryos. In cases where placental circulations become fused prior to the cells' arrival at gonadal primordia, cells from one embryo can reach developing siblings. This results in gonads which contain the genotypes of both individuals (Austin and Short 1972: exchange of germ cells has been considered an accidental occurrence).

E. Strategies of Competition: Eupyrene Sperm Polymorphism

Sperm within an ejaculate, all with complete genetic complements and apparently capable of fertilization, sometimes display striking polymorphisms. Sperm classes in the stinkbug *Arvelius albopunctatus* have nuclear volumes of 200, 400, and 1600 μ^3 (Schrader and Leuchtenberger 1950). Differences are due to nuclear proteins and RNA. (Several genera of tropical pentatomids have apyrene sperm

formed in the "harlequin" lobe of the testes, Schrader 1960.) Certain *Drosophila* species have two, three, and, in a single case, perhaps four sperm size classes ranging from 46μ to 430μ (Beatty and Sidhu 1969, Beatty and Burgoyne 1971).

Can these morphs result from sperm competition? Big gametes might swim faster, block exits, or force smaller gametes out of storage organs. Featherwinged beetles have relatively gigantic sperm. A large number of females collected by Dybas and Dybas (1981) had "a single large spermatozoon protruding outside the body from the vagina," suggesting that gametes themselves might sometimes block reinsemination. The expense of large, tough sperm, useful in experienced females carrying rival ejaculates, coupled with the advantages of providing great numbers of sperm to virgins, might result in dimorphisms (Sivinski 1980a). Producing numerous small gametes might also increase representation in a mixed ejaculate and raise the probability of fertilization. If so, large and small gametes could lie on opposite ends of a competitive spectrum. Males which combine the alternatives would be reminiscent of sporting weapons that anticipate any game with a rifle mounted over a shotgun (a strategy perhaps parallel to the postulated mother-determined distribution of digger and patroller haploid male bees, Alcock 1979; and fighting and pacific haploid male parasitic Hymenoptera in figs, Hamilton 1979).

The distribution of the different gamete sizes within the female is sometimes suggestive of divergent fates. In *Drosophila* species, all morphs are passed to the female, but are not randomly distributed among storage organs. Only the largest occupy the ventral receptacle (Beatty and Burgoyne 1971), a storage organ distinct from the spermatheca and whose contents are typically the first to be used for fertilization (Fowler 1973). The occupancy of the best site by the largest morph could be indicative of an ability to move more rapidly than small competitors whose efforts would presumably be comparable to tiny siblings. It could also be a tactic on the level of the male parent who directs the size classes to different locations in the female tract, with large ones being sent to the front where competition is greatest. Sperm-trimorphic *Drosophila pseudoobscura* are an exception to the rule; the ventral receptacle and spermathecae are drained at about the same rate (Patterson 1947). Equal utilization, as it occurs in at least this one species, is counter to the above explanations.

Animals with eupyrene sperm polymorphisms have female storage organs. Storage can increase the probability of ejaculate mixing and, hence, competition. Natural populations of sperm-trimorphic *Drosophila pseudoobscura* are known to have high rates of multiple inseminations (Cobb 1977, Levine *et al.* 1980). Females of the sperm-dimorphic *D. subobscura*, however, rarely mate more than once (Maynard Smith 1956). If size classes in this latter species are not an anachronism from a polyandrous past, polymorphism might serve other than a competitive purpose.

Schrader (1960) has suggested that the largest sperms in pentatomids provide resources for the zygote with their disproportionate amounts of nuclear RNA and

proteins. Why, then, are there masses of impoverished sperm? The benefit to a male of differential investment in offspring is not entirely clear. In some *Drosophila* species, the largest sperm may participate in forming the first zygotes. Males might provide extravagantly for their firstborn simply because the probability that a female will survive to produce subsequent offspring is low. Small gametes could merely be cheap insurance that a rarely encountered female Methuselah will continue to bear a male's offspring. Relatively precipitous drops would be expected in the natural survivorship schedules of polymorphic species. Interestingly, the short morphs of the sperm-trimorphic *Drosophila obscura* are rare in storage organs, although they are known to be common in the uterus after copulation (Beatty and Sidhu 1969). Small sperm may serve as material reserves for larger sperm, or as a paternal investment.

Yet another alternative is that large sperm last longer in storage organs, bulky food reserves being translated into longevity. This is doubly unlikely in *Drosophila* species, as large sperm are the first used or are used at a similar rate as smaller siblings, and the large protein stores of the mitochondrial crystals are not metabolized by the sperm (see subsection on paternal investment).

IV. COMPETITION BETWEEN CHOOSING FEMALES AND SPERM

A. Postcopulatory Female Choice

Females are thought to enhance their reproductive success by the choice of mates (Borgia 1979, Thornhill 1980). When choice is limited to discrimination between adults, the further from the end of parental investment a female chooses between mates, the more she could benefit from her selection (for the implications of gametic level filtering see preceding section). To decide before fertilization avoids gamete wastage (Mecham 1961). A decision prior to copulation precludes the hazards, time loss, and energetic expense of extraneous mating (see Parker 1974, Sivinski 1980b). To discriminate between mates at a distance aids in forestalling rape or the persistent, perhaps dangerous, attentions of unwanted males.

It might be expected, then, that postcopulatory choosing between males by favoring particular sperm would be uncommon. There are circumstances, however, where females might be forced, or prefer, to choose between mates by identifying and manipulating their sperm. Ejaculates compelled into mated females by genetically inferior rapists might be discarded (see Thornhill 1980b). A female wishing to enhance the genetic diversity of offspring might try to suppress the sperm of previous mates (see Walker 1980). When a female signals to attract mates, as in

the bulk of pheromone-emitting insects, she surrenders the ability to discriminate as a distance. Here, and in other systems where males are difficult to avoid or simultaneously compare, it might prove less expensive to engage in multiple copulations and then choose a mate by sorting sperm. Courtships that attract predators or cost females time would make it convenient to internally discriminate between cellular models of male genotypes (see Daly 1978, for some phenotypic costs of sexual behavior).

The machinery of choice could be either morphological or chemical. Chemical complexity of the female and ovum offers a number of potential means of choosing (discussion of female/sperm interaction in Fowler 1973, Cohen 1977; see Yanagimachi 1977). The elaborate genitalia and multiple sperm storage organs of some insects might perform ejaculate sorting. The female tract and associated muscles are a major factor in the movement of many sperm (Hinton 1964; Blackith 1973 argues for spermathecal filtering; citations in Walker 1980).

Males and their sperm should attempt to subvert female discrimination. Penile complexity could be due to selection for "little openers, snipers, levers, and syringes" that circumvent female choice (Lloyd 1979; see Waage 1979, this volume). Sperm might resist manipulation by being too large to imprison in various nooks of the female tract or carry structures that lodge in membranes and resist transportation. Barbs on grasshopper sperm might give the female greater traction for moving the cell (Afzelius 1970), but barbs could also be a means of maintaining position. A number of arthropod sperm are aflagellate and immobile, a surrender that could evolve under absolute female control (see Baccetti and Afzelius 1976; also Dallai 1979).

Choosing females might seek additional information about male quality in the nature of their ejaculates. Searching for signs of fitness in cells could result in miniature versions of the advertisements, deceptions, and scrutinies that characterize the intersexually selected macroscopic world (see Trivers 1972). In this vein, ejaculate size could provide females with a means of judging male vigor, gametic exuberance being a display of an ability to accrue resources (Wilson 1979, discussing excess pollen per ovule). Not all sperm redundancy ("excess" sperm per egg) is consistent with this hypothesis. In insects, while females often expel or digest a portion of the ejaculate, more sperm are stored and maintained than are strictly necessary for fertilization (see Sivinski 1980a). There seems to be little gain in materially supporting an extraneous portion of a no longer informative display. Enlarged sperm, like enlarged ejaculates, might demonstrate male success. There is evidence against this proposal in the negative correlation between sperm size and number among related insects (White 1954, 1973; Virkki 1969; Kurokawa and Hihara 1976; see Sivinski 1980a). If males invest in fewer, larger sperm, they are not revealing any greater resource accrual.

Titanic sperm, as sometimes encountered in arthropods, are sufficiently bizarre to suggest intersexually selected ornamentation, peacocks' tails on the cellular

level. However, the cost to females of accommodating such monstrosities would be expected to put an early finish to runaway selection for elaborateness (see Fisher 1930 for runaway sexual selection; also Thornhill 1979). It is conceivable that females could read the constituents of sperm as a chemical abstract of its manufacturer's quality. Males might eventually load their sperm with a library of informative compounds forcing enlargement of the gametes (see Thornhill 1980; and citations for discussion of display information content).

B. Choosing Gender Through Sperm Preference

Females might wish to choose the gender of their offspring because of local mate competition (Hamilton 1967, Borgia 1980), local resource competition (Clark 1978), the correlation between parental physical condition and offspring reproductive success (Trivers and Willard 1973; see, however, Williams 1979), the attractiveness of the father and presumably his sons (Burley 1981), and local scarcity of one sex (Verner 1965, Werren and Charnov 1978). In the common circumstance of male determination of offspring gender, this can be accomplished prior to fertilization only by biased production of gametes by "cooperating" males or female discrimination between sperm. Manipulation of gender by mothers requires a haploid effect in sperm or a phenotypic label left over from an earlier stage of spermatogenesis to recognize gamete "sex" (a possible exception could occur in the body louse *Pediculus humanus*, where some males sire sons, others daughters; Hindle 1919).

Where sex chromosomes differ in size, there would likely be at least a tiny phenotypic difference in weight or nuclear dimension between X and Y gametes (the nuclear ultrastructure of X and O sperm differs in the homopteran *Dalbulus maidus*; Kitajima and Da Cruz-Landim 1972). A number of artificial separation techniques, however, have suffered a history of unrepeatability (Beatty 1975; see however Pinkel *et al.* 1982). Some suggestive evidence of gender expression in sperm does exist. Delayed fertilization in some frogs, flies, mealybugs, butterflies, and copepods results in male-biased sex ratios (Werren and Charnov [1978] argue that delayed fertilization is indicative of a local male scarcity that females capitalize on by producing sons). Among Werren and Charnov's examples are male heterogametic organisms, which in the absence of differential mortality of zygotes are apparently choosing gender at the gametic level. A maternally inherited cytoplasmic factor in humans seems to recognize and destroy Y sperm, thereby assuring its own reproduction (Leinhart and Vermelin 1946, in Grun 1976; discussed by Eberhard 1980). Sex ratios of *Drosophila melanogaster* offspring sometimes vary with the age of the father. Sons predominate in the eggs fertilized by young males, daughters in those sired by older males. Mange (1970) has argued that the difference is due to preferential use of sperm by females. There are several *Drosophila* examples of

nonrandom utilization associated with various disomic or attached forms of X and Y chromosomes (reviewed by Fowler 1973). It is not clear whether these nonrandom recoveries are due to competition or preference, but they are suggestive of gender expression in the sperm phenotype. In haploid-expressing pollen, the greater success, under certain conditions, of X-bearing gametophytes is thought to be due to choice exerted by the style rather than competition between grains (Lewis 1942; as discussed by Hamilton 1967).

Homogametic females choosing the gender of their offspring are in conflict with the discarded "sexed" sperm, but not necessarily the male who provided the ejaculate. Males lose fertilizations to competitors, however, where sperm redundancy is low and additional copulations are required to provide a sufficient quantity of correctly sexed gametes (e.g., *Drosophila melanogaster*, where stored sperm-to-egg ratios approach 1:1, Lefevre and Jonsson 1962). When sex ratios are biased to minimize competition between siblings, multiple paternity generates yet another conflict (see Hamilton 1967 for the effects of inbreeding on within-brood competition and sex ratio). From the father's, but not the mother's, point of view the sibship contains unrelated individuals and males would prefer to produce the minority sex. Borgia (1980) has suggested that male sperm might mimic female sperm under conditions of local mate competition and so produce extra sons by subterfuge. One characteristic available for recognition would be the presence of sex chromosome antigens. It is worth noting that, in mammals, all sperm carry Y antigens (McLaren 1965, Katsch and Katsch 1965, Cohen 1971). For ubiquitous Y antigens to be an evolved mimicry, biased sex ratios in mammals must usually favor males. Local resource competition resulting in male biases occurs in at least one mammal, the prosimian *Galago crassicaudatus* (Clark 1978), but requires female control of resources, a stable saturated environment, and inflexible territory boundaries, a peculiar set of phenomena.

Males in haplo-diploid species are related only to the diploid of the following generation and might strive to produce extra daughters (J. Brockman, unpubl. ms). A peculiar case of sperm polymorphism in a haplo-diploid species was historically interpreted as sex ratio control by sperm. In the parasitic hymenopteran *Dahlbominus fuscipennis*, there are five sperm morphs; two morphs characterized respectively by sinistral (left-handed) and dextral (right-handed) coilings reach the spermatheca (Lee and Wilkes 1965, Wilkes 1965). Sinistral sperm were thought to be unable to penetrate the micropyle, thereby capping unfertilized eggs and producing males (Wilkes and Lee 1965). It is not clear why a female would abandon control of sex ratio to a potential antagonist. One possible benefit, male investment via infertile gametes in a mother's sons, fails to find support in the incomplete penetrance by sperm. It is even less obvious why males would produce a sperm that resulted in the development of an individual containing no genes of direct paternal descent. A male could benefit only under conditions of local mate competition where he would initiate the production of mates for his daughters (the sexes

might not disagree as to sex ratio here). Male progeny, however, are known to increase with adult female density, demonstrating female control of offspring gender in response to changes in local mate competition (Victorov and Kochetova 1973). The evidence of outbreeding casts doubt on male production by left-handed sperm.

V. COMPETITION AMONG SYMBIOTIC GENOMES

A number of replicating entities coexist alongside the chromosomes. Mitochondria, plastids, plasmons, bacterioids, fungi, virus, and various other bits of programming pass down the generations via gametes. Conflicts of reproductive interest between replicators might lead to selfish manipulation of their gametic vehicles (see Eberhard 1980, for a review of organelle competition).

Gamete volume could be a limiting factor for replicators inherited through the cytoplasm. Mitochondrial DNA (= mtDNA), for example, is enormously more abundant in ova than sperm: $10^6:1$ genomes in clawed frogs (Dawid and Blackler 1972). This results in a serious competitive disadvantage for any mtDNA that happens to be located in a male, assuming that the proportion of paternal mtDNA in the zygote foretells its relative abundance in the ova and sperm of the following generation. The disadvantage might be tempered by larger sperm carrying increased cargos of mtDNA. The bulk of the gargantuan sperm of certain insects consists of mitochondrial crystals; mtDNA may be abundant in these derivatives (Perotti 1973). Such giant cells are similar to what might be the expected production of a mitochondrial genome able to influence sperm size (Sivinski 1980a). Organelles with primarily maternal inheritance might destroy "male" sperm. The resulting sex ratio bias benefits organelles but runs counter to the interests of both parents (Eberhard 1980).

A manipulative organelle would come into conflict with a nuclear genome programmed to allocate a certain amount of resources to a particular number of sperm. From the mitochondrial point of view, male (*i.e.* nuclear) fecundity could drop precipitously before selection disfavored further gamete inflation (recall the $10^6:1$ abundance ratio). Victory would be expected to go to the nucleus, sheer size and diversity offering possibilities of control that would exhaust the genetic repertoire of an organelle. Beck *et al.* (1971) identified 63 nuclear genes affecting mitochondrial functions in yeast, while yeast mitochondria are believed to contain only 60-70 cistrons (Kroon and Saccone 1976).

A sperm-borne organelle's fate after fertilization is not always clear (Gillham 1978). In many cases, replicators appear to degenerate (citations in Eberhard 1980). Either maternal organelles somehow take advantage of numbers to remove

competitors or the nucleus attempts to preclude inoculation by parasites, *i.e.* organelles less controllable than those already present. Where sperm inflation of organelle DNA in sperm has been attempted, organelle death could represent an ovum's means of protecting its future son's virility. Grun (1976) suggests that ova kill male line replicators to prevent sex between the maternal and paternal organelle populations, precluding dangerous recombinants (a domesticating adaptation that might be described as spaying the Red Queen; see Van Valen 1973, for Red Queen theory; see, however, Eberhard 1980).

VI. DISCUSSION AND CONCLUSIONS

There are at least five arenas of conflict occurring in and between three selection levels that could influence the evolution of sperm. It is a measure of ignorance that I have argued that some aspects of sperm biology could evolve in nearly all of these contexts. Gigantic sperm, for example, are considered as a means of paternal investment, agents of aggressive displacement, displays of male quality, and the monstrous constructions of meddling organelles. The evidence that would permit choosing among or discarding all these alternatives is, to my knowledge, inconclusive or unavailable.

While admitting ignorance of the particulars of gametic evolution, it seems almost inevitable that gametic diversity is, in part, the result of conflict. The opportunities available to sperm to experience and resolve competition are enormous. They are, after all, the last pre-synaptic clue to male quality, the farthest cellular extension of the male body into the sometimes contrary world of female reproductive interests, and, beside the egg, the closest complex objects to the fusion of pronuclei, the final resolution of most male contention.

VII. SUMMARY

The variety of sperm morphology and behavior is not easily explained by adaptation to genital or egg topology. Competitions and conflicts in situations such as the following may influence the evolution of spermatozoa.

(1) Sperm of a male, bearing a coefficient of relatedness of 0.5 to many or most ejaculate mates, could compete in ways that lower the effectiveness of the ejaculate as a whole. The present absence of phenotypic expression (haploid effect) by genes in sperm may be an adaptation to suppress such "outlaws." Peculiar "worker" sperm who aid ejaculate mates but are not suited for fertilizing often

lack genomes altogether. Chromosomes may have been removed as the final resolution of male/sperm conflicts.

(2) Males produce sperm of different fertilizing abilities. If these differences are heritable and if ejaculates occasionally mix then females wishing competitive sons might encourage competition between sperm through multiple matings. Such an argument could be refuted through low variance in order effects (which male in a series of mates obtains what proportion of fertilizations).

(3) Sperm from different males may be put in competition as an effect of unrelated selection for multiple matings. One advantage to repeated insemination may be harvesting of resources present in sperm themselves. Giant protein-rich gametes, in particular, may be specialized bearers of paternal investment.

Once ejaculate mixture becomes sufficiently commonplace, sperm may evolve to defeat rivals spatially, *e.g.* through structures that allow more rapid movement or by novel directions of approach, *e.g.* through the body cavity in cases of traumatic insemination. Occasionally gametes overcome competitors temporally as in cases of hyperviviparity, the fertilization of embryos. The evolution of sperm polymorphisms may be due to differences in the competitive terrain of the female reproductive tract.

(4) Females might sometimes exercise postcopulatory mate choice by manipulation of sperm. Gametes that resist such choice would be at an advantage. In theory a common context for female sperm sorting would be attempts to control offspring gender. Such activities would be hampered by the lack of gene expression in sperm.

(5) A number of non-nuclear nucleic acids occur in gametes. There are potential conflicts between these and nuclear genes, *e.g.* organelles may be best represented in the next metazoan by being present in large numbers in inflated sperm. Competitions are most likely to be won by nuclear genes given their greater number and range.

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REFERENCES

- Afzelius, B. A. 1970. Thoughts on comparative spermatology. In *Comparative Spermatology*, B. Baccetti (ed.), pp. 565-571. Academic Press, New York.

- Afzelius, B. A. (ed.) 1975. *The Functional Anatomy of the Spermatozoon*. Pergamon Press, Oxford.
- Afzelius, B. A., B. Baccetti, and R. Dallai. 1976. The giant spermatozoon of *Notonecta*. *J. Submicrosc. Cytol.* 8:149-161.
- Alcock, J. 1979. The evolution of intraspecific diversity in male reproductive strategies in some bees and wasps. In *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum (eds.), pp. 381-402. Academic Press, New York.
- Alexander, R. D. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 5:325-383.
- Alexander, R. D., and G. Borgia. 1978. Group selection, altruism, and the levels of organization of life. *Annu. Rev. Ecol. Syst.* 9:449-583.
- Ansley, H. R. 1954. A cytological and cytophotometric study of alternative pathways of meiosis in the house centipede (*Scutigera forceps*, Rafinesque). *Chromosoma* 6:656-695.
- Austin, C. R. 1965. *Fertilization*. Prentice-Hall, Englewood Cliffs, NJ.
- Austin, C. R., and R. V. Short. 1972. *Germ Cells and Fertilization*. Cambridge University Press, Cambridge.
- Baccetti, B. 1972. Insect sperm cells. *Adv. Insect Physiol.* 9:315-395.
- Baccetti, B. 1979. Ultrastructure of sperm and its bearing on arthropod phylogeny. In *Arthropod Phylogeny*, A. P. Gupta (ed.), pp. 609-644. Van Nostrand Reinhold, New York.
- Baccetti, B., and B. A. Afzelius. 1976. *The Biology of the Sperm Cell*. S. Karger, Basel.
- Baccetti, B., and R. Dallai. 1978. The spermatozoon of Arthropoda. III. The multiflagellate spermatozoon in the termite *Mastrotermes darwiniensis*. *J. Cell Biol.* 76:569-576.
- Baccetti, B., R. Dallai, and B. Fratello. 1973. The spermatozoon of Arthropoda. XXII. The 12 + 0, 14 + 0 or aflagellate sperm of Protura. *J. Cell Sci.* 13:321-335.
- Baccetti, B., R. Dallai, V. Palline, F. Rosati, and B. A. Afzelius. 1977. Protein of insect sperm and mitochondrial crystals. *J. Cell Biol.* 73:594-600.
- Bacci, G. 1965. *Sex Determination*. Pergamon Press, Oxford.
- Balduf, W. V. 1935. *The Bionomics of Entomophagous Coleoptera*. E. W. Classey, Hamton, England.
- Bauer, H. 1940. Über die chromosomen der bisexualen und der parthenogenetischen rasse des ostracoden *Heterocyris incongruens* Ramd. *Chromosoma* 1:620-637.
- Bawa, S. R. 1964. Electron microscope study of spermiogenesis in a firebrat insect *Thermobia domestica* Pack. *J. Cell Biol.* 23:431-444.
- Bawa, S. R. 1975. Joined spermatozoa. In *The Functional Anatomy of the Spermatozoon*, G. A. Afzelius (ed.), pp. 259-266. Pergamon Press, Oxford.
- Beatty, R. A. 1971. The genetics of size and shape of spermatozoon organelles. In *Proc. Int. Symp. Genetics of the Spermatozoon*. Organizer, New York.
- Beatty, R. A. 1975a. Genetics of animal spermatozoa. In *Gamete Competition in Plants and Animals*, D. L. Mulcahy (ed.), pp. 61-68. No. Holland Publ. Co., Amsterdam.
- Beatty, R. A. 1975b. Sperm diversity within the species. In *The Functional Anatomy of the Spermatozoon*, B. A. Afzelius (ed.), pp. 319-327. Pergamon Press, Oxford.
- Beatty, R. A., and P. S. Burgoyne. 1971. Size classes of the head and flagellum of *Drosophila* spermatozoa. *Cytogenetics* 10:177-189.
- Beatty, R. A., and N. S. Sidhu. 1969. Polymegaly of spermatozoan length and its genetic control in *Drosophila* species. *Proc. R. Soc. Edinb. Sect. B (Biol. Sci.)* 71:14.
- Beck, J. C., J. H. Parker, W. X. Balcauag, and J. R. Matoon. 1971. Mendelian genes affecting development and function of yeast mitochondria. In *Autonomy and Biogenesis of Mitochondria and Chloroplasts*, N. K. Boardman, A. W. Linnane, and R. M. Smillie (eds.), pp. 194-204. No. Holland Publ. Co., Amsterdam.
- Bernstein, H., G. S. Byers, and R. E. Michod. 1981. Evolution of sexual reproduction: Importance of DNA repair, complementation, and variation. *Am. Nat.* 117:537-549.
- Blackith, R. E. 1973. Clues to the Mesozoic evolution of the Eumastacidae. *Acrida* 2:5-28.
- Blount, M. 1909. The early development of the pigeon's egg, with especial reference to polyspermy on the origin of the periblast nuclei. *J. Morphol.* 20:1-64.
- Bonnevie, E. 1907. Untersuchungen über keimzellen. II. Physiologische polyspermie bei bryozoen. *Z. Naturwiss. Jena* 41:567-598.

- Borgia, G. A. 1979. Sexual selection and the evolution of mating systems. In *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum (eds.), pp. 19-80. Academic Press, New York.
- Borgia, G. A. 1980. Evolution of haploidy: Models for inbred and outbred systems. *Theor. Popul. Biol.* 17:103-128.
- Bouix, G. 1963. Sur la spermatogenese des *Carabus*: Modalite et frequence de la spermiogenese atypique.
- Braden, A. W. H. 1958. Influence of time of mating on the segregation ratio of alleles at the T-locus in the house mouse. *Nature* 181:786-787.
- Braden, A. W. H. 1960. Genetic influences on the morphology and functions of the gametes. *J. Cell. Comp. Physiol.* 56:17-29.
- Braden, A. W. H. 1972. T-locus in mice; segregation distortion and sterility in the male. In *The Genetics of the Spermatozoon*, R. A. Beatty and S. Gluecksohn-Waelsch (eds.), pp. 289-305. Organizers, New York.
- Breland, O. P., and E. Simmons. 1970. Preliminary studies of the spermatozoa and the male reproductive system of some whirligig beetles (Coleoptera:Gyrinidae). *Entomol. News* 81:101-110.
- Bremermann, H. J. 1980. Sex and polymorphism as strategies in host-pathogen interactions. *J. Theor. Biol.* 87:671-702.
- Brown, S. W., and F. D. Bennett. 1957. On sex determination in the diaspine scale *Pseudolacaspis pentagona* (Targ.) (Coccoidea). *Genetics* 42:510-523.
- Burley, N. 1981. Sex ratio manipulation and selection for attractiveness. *Science* 211:721-722.
- Carayon, J. 1966. Traumatic insemination and the paragenital system. In *Monograph of Cimicidae*, R. L. Uniager (ed.), pp. 81-166. Hornshafter, Baltimore, MD.
- Carayon, J. 1974. Insemination traumatique heterosexuelle et homosexuelle chez *Xylocoris maculipennis* (Hem. Anthocoridae). *C. R. Acad. Sci. Paris D* 278:2803-2806.
- Chatton, E., and O. Tuzet. 1943. Sur la formation des gonies polyvalentes et des spermies geantes chez deux lombriciens. *C. R. Acad. Sci. Paris D* 77:710-712.
- Clark, A. B. 1978. Sex ratio and local resource competition in a prosimian primate. *Science* 201:163-165.
- Cobb, G. 1977. Multiple insemination and male sexual selection in natural populations of *Drosophila pseudoobscura*. *Am. Nat.* 111:641-656.
- Cohen, J. 1967. Correlation between sperm 'redundancy' and chiasma frequency. *Nature* 215:862-863.
- Cohen, J. 1971. Comparative physiology of gamete populations. *Adv. Comp. Physiol. Biochem.* 4:268-380.
- Cohen, J. 1973. Crossovers, sperm redundancy and their close association. *Heredity* 31:408-413.
- Cohen, J. 1975a. Gamete redundancy-wastage or selection? In *Gamete Competition in Plants and Animals*, D. L. Mulcahy (ed.), pp. 99-144. No. Holland Publ. Co., Amsterdam.
- Cohen, J. 1975b. Gametic diversity within an ejaculate. In *The Functional Anatomy of the Spermatozoon*, B. A. Afzelius (ed.), pp. 329-339. Pergamon Press, Oxford.
- Cohen, J. 1977. *Reproduction*. Butterworths, London.
- Crow, J. F. 1979. Genes that violate Mendel's rules. *Sci. Am.* 240:134-143.
- Daily, M. 1978. The cost of mating. *Am. Nat.* 112:771-774.
- Dallai, R. 1979. An overview of atypical spermatozoa in insects. In *The Spermatozoon*, D. W. Fawcett and J. M. Bedford (eds.), pp. 253-265. Urban and Schwarzenberg, Baltimore, MD.
- Dawes, B. 1968. *The Trematoda*. Cambridge University Press, Cambridge.
- Dawid, I. B., and A. W. Blackler. 1972. Maternal and cytoplasmic inheritance of mitochondrial DNA in *Xenopus*. *Dev. Biol.* 29:152-161.
- Dawkins, R. 1982. *The Extended Phenotypes*. W. H. Freeman, Oxford.
- Dawkins, R., and J. R. Krebs. 1979. Arms races between and within species. In *The Evolution of Adaptation by Natural Selection*, J. Maynard Smith and R. Holliday (eds.), pp. 487-511. The Royal Society, London.
- Dupouy, J. 1964. La teratogenese germinale male des gastropods et ses rapports avec l'oogenese atypique et la formation des oeufs nourriciers. *Asch. Zool. Exp. Gen.* 103:217-368.

- Dybas, L. K., and H. S. Dybas. 1981. Coadaptation and taxonomic differentiation of sperm and spermathecae in featherwinged beetles. *Evolution* 35:168-174.
- Eberhard, W. G. 1980. The evolutionary consequences of intracellular organelle competition. *Q. Rev. Biol.* 55:231-249.
- Fain-Maurel, M. 1966. Acquisitions recents sur les spermatogeneses atypiques. *Annee Biol.* 513-564.
- Favard, P. 1955. Spermatogenese de *Discoglossus pictus* Otth. etude cytologique de maturation du spermatozoid. *Ann. Sci. Nat. Zool.* 17:370.
- Fisher, R. A. 1940. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Ford, C. E. 1972. Gross genome unbalance in mouse spermatozoa, does it influence capacity to fertilize? In *The Genetics of the Spermatozoon*, R. A. Beatty and S. Gluecksohn-Waelsch (eds.), pp. 359-369. Organizers, New York.
- Fowler, G. L. 1973. Some aspects of the reproductive biology of *Drosophila*; Sperm transfer, sperm storage and sperm utilization. *Adv. Genet.* 17:293-260.
- Frazen, A. 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. *Zool. Bidr. Upps.* 31:355-482.
- Frazen, A. 1970. Phylogenetic aspects of the morphology of spermatozoa and spermiogenesis. In *Comparative Spermatology*, B. Baccetti (ed.), pp. 29-46. Academic Press, New York.
- Fretter, V. 1953. The transference of sperm from male to female prosobranch, with reference, also, to the pyramidellids. *Proc. Linn. Soc. Lond.* 164:217-224.
- Gillham, N. W. 1978. *Organelle Heredity*. Raven Press, New York.
- Gromko, M. H., and D. W. Pyle. 1978. Sperm competition, male fitness and repeated mating by female *Drosophila melanogaster*. *Evolution* 32:588-593.
- Grun, P. 1976. *Cytoplasmic Genetics and Evolution*. Columbia University Press, New York.
- Haldane, J. B. S. 1932. *The Causes of Evolution*. Longmans, Green, and Co., London.
- Hamilton, W. D. 1967. Extraordinary sex ratios. *Science* 156:477-488.
- Hamilton, W. D. 1979. Wingless and fighting males in fig wasps and other insects. In *Sexual Selection and Reproductive Competition in Insects*, M. S. Blum and N. A. Blum (eds.), pp. 167-220. Academic Press, New York.
- Hanson, J., J. T. Randall, and S. T. Bayley. 1952. The microstructures of the spermatozoa of the snail *Viviparus*. *Exp. Cell Res.* 3:65-78.
- Heslop-Harrison, J. 1975. Male gametophyte selection and the pollen-stigma interaction. In *Gamete Competition in Plants and Animals*, D. L. Mulcahy (ed.), pp. 177-190. No. Holland Publ. Co., Amsterdam.
- Hindle, E. 1919. Sex inheritance in *Pediculus humanus* var. *corporeis*. *J. Genet.* 8:167-277.
- Hinton, H. E. 1964. Sperm transfer in insects and the evolution of haemocoelic insemination. In *Insect Reproduction Symposium No. 2*, K. C. Highnam (ed.), pp. 95-107. R. Entomol. Soc., London.
- Hinton, H. E. 1974. Symposium on reproduction of arthropods of medical and veterinary importance. III. Accessory function of seminal fluid. *J. Med. Entomol.* 11:19-25.
- Hinton, H. E. 1981. *Biology of Insect Eggs. Vol. 1*. Pergamon Press, Oxford.
- Holstein, A. F. 1965. Elektronmikroskopische untersuchungen am spermatozoon des opossum (*Didelphys virginiana* Kerr). *Z. Zellforsch. Mikrosk. Anat.* 65:905-914.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex and brood reduction in the common grackle. *Ecology* 57:1195-1207.
- Howe, H. F. 1977. Sex ratio adjustment in the common grackle. *Science* 198:744-746.
- Idelman, S. 1960. Evolution de la spermatogenese chez un mollusque prosobranch *Turritella communis*. *Proc. Eur. Reg. Conf. Electron Microsc.* 2:942-946.
- Ito, S., and C. Leuchtenberger. 1955. The possible role of the activation process of the clar *Spisula solidissima*. *Chromosoma* 7:328-329.
- Jordan, E. O. 1893. The habits and development of the newt (*Diemyctylus viridescens*). *J. Morphol.* 8:269-366.
- Katsch, S., and G. F. Katsch. 1965. Perspectives in immunological control of reproduction. *Pac. Med. Surg.* 73:28-43.
- Kitajima, E. W., and C. DaCruz Landim. 1972. An electron microscopic study of the process of differentiation during spermiogenesis in the corn leaf hopper *Dalbulus maidis* Del. and W. *Rev. Biol.* 8:5-19.

- Koehler, J. K. 1965. An electron microscope study of the dimorphic spermatozoa of *Asplanchna* (Rotifera). I. The adult testes. *Z. Zellforsch. Mikrosk. Anat.* 67:57-76.
- Koehler, J. K., and C. W. Birky. 1966. An electron microscope study of the dimorphic spermatozoa of *Asplanchna* (Rotifera). II. The development of "atypical spermatozoa." *Z. Zellforsch. Mikrosk. Anat.* 70:303-321.
- Kroon, A. M., and C. Saccone. 1976. Concluding remarks. In *The Genetic Function of Mitochondrial DNA*, C. Saccone and A. M. Kroon (eds.), pp. 343-347. No. Holland Publ. Co., Amsterdam.
- Kurokawa, H., and F. Hihara. 1976. Number of first spermatocytes in relation to phylogeny of *Drosophila* (Diptera:Drosophilidae). *Int. J. Insect Morphol. Embryol.* 5:51-63.
- Lee, P. E., and A. Wilkes. 1965. Polymorphic spermatozoa in the hymenopterous wasp *Dahlbominus*. *Science* 147:1445-1446.
- Lefevre, G., and V. B. Jonsson. 1962. Sperm transfer, storage, displacement and utilization in *Drosophila melanogaster*. *Genetics* 47:1719-1736.
- Levine, L. 1967. Sexual selection in mice. IV. Experimental demonstration of selective fertilization. *Am. Nat.* 101:289-294.
- Levine, L., M. Asmussen, O. Olvera, J. R. Powell, M. E. de la Rose, V. M. Salceda, M. I. Baso, J. Guzman, and W. W. Anderson. 1980. Population genetics of Mexican *Drosophila*. V. A high rate of multiple insemination in a natural population of *Drosophila pseudoobscura*. *Am. Nat.* 116:493-503.
- Lewis, D. 1942. The evolution of sex in flowering plants. *Biol. Rev.* 17:46-67.
- Lewontin, R. C. 1970. The units of selection. *Annu. Rev. Ecol. Syst.* 1:1-18.
- Lindsley, D. L., and E. H. Grell. 1969. Spermiogenesis without chromosomes in *Drosophila melanogaster*. *Genetics Suppl.* 61:46-67.
- Lloyd, J. E. 1979. Mating behavior and natural selection. *Fla. Entomol.* 62:17-34.
- Mackie, J. B., and M. H. Walker. 1974. A study of the conjugate sperm of the dytiscid water beetles *Dytiscus marginalis* and *Colymbetes fuscus*. *Cell Tissue Res.* 143:505-519.
- Mange, A. P. 1970. Possible non-random utilization of X and Y bearing sperm in *Drosophila melanogaster*. *Genetics* 65:95-106.
- Mazzini, M. 1976. Giant spermatozoa in *Divaes bipustulatus* F. (Coleoptera:Cleridae). *Int. J. Insect Morphol. Embryol.* 5:107-115.
- Maynard Smith, J. 1956. Fertility, mating behavior and sexual selection in *Drosophila subobscura*. *Genetics* 54:261-279.
- Maynard Smith, J. 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge.
- McFarlane, R. W. 1963. Taxonomic significance of avian sperm. *XIII Int. Ornithol. Congr. Ithaca* 91-102.
- McLaren, A. 1965. Growth of male young in mothers immunized against Y antigen. *Transplantation* 3:28-38.
- McCloskey, J. D. 1966. The problem of gene activity in the sperm of *Drosophila melanogaster*. *Am. Nat.* 100:211.
- Mecham, J. S. 1961. Isolating mechanisms in anuran amphibians. In *Vertebrate Speciation*, W. F. Blair (ed.), pp. 24-61. Univ. Texas Press, Austin, TX.
- Moore, G. P. M. 1972. A cytological demonstration of the DNA-transcription enzyme RNA polymerase during mammalian spermatogenesis. In *The Genetics of the Spermatozoon*, R. A. Beatty and S. Gluecksohn-Waelsch (eds.), pp. 90-96. Edinburgh.
- Mulcahy, D. L. (ed.). 1975. *Gamete Competition in Plants and Animals*. No. Holland Publ. Co., Amsterdam.
- Mulcahy, D. L. 1979. The rise of the angiosperms: A genecological factor. *Science* 206:20-23.
- Mulcahy, D. L., and S. M. Kaplan. 1979. Mendelian ratios despite nonrandom fertilization? *Am. Nat.* 113:419-425.
- Muller, H. J., and F. Settles. 1927. The non-functioning of genes in spermatozoa. *Z. Indukt. Abstammungs-Vererbungslehre* 43:285-312.
- Nishiwaki, S. 1964. Phylogenetic study on the type of the dimorphic spermatozoa in *Prosobranchia*. *Sci. Rep. Tokyo Kyoiku Daigaku Sect. B* 11:237-275.
- Nur, U. 1962. Sperms, sperm bundles and fertilization in a mealy bug *Pseudococcus obscura* Essig (Homoptera, Coccoidea). *J. Morphol.* 111:173-183.
- Oppel, A. 1892. Die befruchtung des reptilieneies. *Arch. Mikrosk. Anat.* 39:215-290.

- Ottaviano, E., M. Sari-Gorla, and D. L. Mulcahy. 1980. Pollen tube growth rates in *Zea mays*: Implications for genetic improvement of crops. *Science* 210:437-438.
- Pant, K. P. 1971. Patterns of inheritance in the midpiece length of mouse spermatozoa. In *The Genetics of the Spermatozoon*, R. A. Beatty and S. Gluecksohn-Waelsch (eds.), pp. 116-119. Organizers, New York.
- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.* 45:525-567.
- Parker, G. A. 1974. Courtship persistence and female guarding as male time investment strategies. 48:157-184.
- Patterson, J. T. 1947. The insemination reaction and its bearing on the problem of speciation in the *Mulleri* subgroups. *Texas Univ. Publ.* 4720:37-41.
- Pelseneer, P. 1935. *Essai d'Ethologie Zoologique*. Brussels.
- Perotti, M. E. 1973. The mitochondrial derivative of the spermatozoon of *Drosophila* before and after fertilization. *J. Ultrastruct. Res.* 44:181-198.
- Perotti, M. E. 1975. Ultrastructural aspects of fertilization in *Drosophila*. In *The Functional Anatomy of the Spermatozoon*, B. A. Afzelius (ed.), pp. 57-68. Pergamon Press, Oxford.
- Phillips, D. M. 1970. Ultrastructure of spermatozoa of the woolly opossum *Caluromys philander*. *J. Ultrastruct. Res.* 33:381-397.
- Pinkel, D., B. L. Gledhill, S. Lake, D. Stephanson, and M. A. Van Dilla. 1982. Sex preselection in mammals? Separation of sperm bearing X and "O" chromosomes in the vole *Microtus oregoni*. *Science* 218:904-906.
- Reger, J. F., and D. P. Cooper. 1968. Studies on the fine structure of spermatids and spermatozoa from the millipede *Polydesmus* sp. *J. Ultrastruct. Res.* 23:60-70.
- Richards, A. G., and A. Miller. 1937. Insect development analysed by experimental methods, a review, I: Embryonic stages. *J. N.Y. Entomol. Soc.* 45:1-60.
- Rothschild, Lord. 1961. Structure and movements of tick spermatozoa (Arachnida, Acarii). *Q. J. Microsc. Sci.* 102:239-247.
- Rothstein, S. I. 1979. Gene frequencies and selection for inhibitory traits with special emphasis on the adaptiveness of territoriality. *Am. Nat.* 113:317-331.
- Ruckert, J.: Festschr. 1899. Zum 70. Geburtstag von Carl von Kupffer, Jena.
- Ryckman, R. E. 1958. Description and biology of *Hesperocimex sonorensis*, new species, an ectoparasite of the purple martin (Hemiptera:Cimicidae). *Ann. Entomol. Soc. Am.* 51:33-47.
- Schrader, R. 1960. Evolutionary aspects of aberrant meiosis in some Pentatomidae (Heteroptera). *Evolution* 14:498-508.
- Schrader, R., and C. Leuchtenberger. 1950. A cytochemical analysis of the functional interrelationships of various cell structures in *Arevelius albopunctatus* (De Geer). *Exp. Cell Res.* 1:421-452.
- Sivinski, J. 1980a. Sexual selection and insect sperm. *Fla. Entomol.* 63:99-111.
- Sivinski, J. 1980b. The effects of mating on predation in the stick insect *Diaphomera veliei*. *Ann. Entomol. Soc. Am.* 75:553-556.
- Spurway, H. 1953. Spontaneous parthenogenesis in a fish. *Nature* 171:437.
- Sweetman, H. L. 1938. Physical ecology of the firebrat *Thermobia domestica* (Packard). *Ecol. Monogr.* 8:285-311.
- Taylor, V. A. 1981. The adaptive and evolutionary significance of wing polymorphism and parthenogenesis in *Prinella* Motschusky (Coleoptera:Ptidiidae). *Ecol. Entomol.* 6:89-98.
- Taylor, V. A. 1982. The giant sperm of a minute beetle. *Tissue & Cell* 14:113-123.
- Thornhill, R. 1980a. Competitive, charming males and choosy females: Was Darwin correct? *Fla. Entomol.* 63:5-30.
- Thornhill, R. 1980b. Rape in *Panorpa* scorpionflies and a general rape theory. *Anim. Behav.* 23:52-59.
- Trivers, R. L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man, 1871-1971*, B. Campbell (ed.), pp. 136-179. Aldine-Atherton, Chicago.
- Trivers, R. L., and D. E. Willard. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179:90-92.
- Van Valen, L. 1973. A new evolutionary law. *Evol. Theory* 1:1-30.

- Verner, S. 1965. Selection for sex ratio. *Am. Nat.* 99:419-421.
- Victorov, G. A., and N. I. Kochetova. 1973. On the regulation of sex ratio in *Dahlbominus fuscipennis* Zett. *Entomol. Rev.* 52:434-438.
- Virkki, N. 1969. Sperm bundles and phylogenesis. *Z. Zellforsch. Mikrosk. Anat.* 101:13-27.
- Waage, J. K. 1979. Dual function of the damselfly penis: Sperm removal and transfer. *Science* 201:916-918.
- Walker, T. J. 1980. Reproductive behavior and mating success of male short-tailed crickets: Differences between and within demes. *Evol. Biol.* 13:219-260.
- Walker, W. F. 1980. Sperm utilization strategies in nonsocial insects. *Am. Nat.* 115:780-799.
- Wallace, H. 1974. Chiasmata have no effect on fertility. *Heredity* 33:423-429.
- Werner, G. 1964. Untersuchungen über die spermiogenese beim silberfischen, *Lipisma saccharina* L. *Z. Zellforsch. Mikrosk. Anat.* 63:880-912.
- Werren, J. H., and E. L. Charnov. 1978. Facultative sex ratios and population dynamics. *Nature* 227:349-350.
- White, M. J. D. 1954. Patterns of spermatogenesis in grasshoppers. *Aust. J. Zool.* 3:222-226.
- White, M. J. D. 1973. *Animal Cytology and Evolution*, 3rd ed. Cambridge University Press, London.
- Wilkes, A. 1965. Sperm transfer and utilization by the arrhenotokous wasp *Dahlbominus fuscipennis* (Zett.) (Hymenoptera:Eulophidae). *Can. Entomol.* 97:647-657.
- Wilkes, A. 1966. Sperm utilization following multiple inseminations in the wasp *Dahlbominus fuscipennis*. *Can. J. Genet. Cytol.* 8:451-461.
- Wilkes, A., and P. E. Lee. 1965. The ultrastructure of dimorphic spermatozoa in the hymenopteran *Dahlbominus fuscipennis* (Zett.) (Eulophidae). *Can. J. Genet. Cytol.* 7:609-619.
- Williams, G. C. 1979. The question of adaptive sex ratio in outcrossed vertebrates. In *The Evolution of Adaptation by Natural Selection*, J. Maynard Smith and R. Holliday (eds.), pp. 567-580. R. Soc., London.
- Wilson, M. F. 1979. Sexual selection in plants. *Am. Nat.* 113:777-790.
- Woodard, T. M. 1940. The function of the apyrene spermatozoa of *Goniogasis laqueata* (Say). *J. Exp. Zool.* 85:103-123.
- Yanagimachi, R. 1977. Specificity of sperm-egg interaction. In *Immunobiology of Gametes*, M. Edidin and M. H. Johnson (eds.), pp. 255-285. Cambridge University Press, Cambridge.
- Yanagisawa, K., L. Dunn, and D. Bennett. 1961. On the mechanism of abnormal transmission ratios at the *t*-locus in the house mouse. *Genetics* 46:1635-1644.
- Yanagisawa, K., D. R. Pollard, D. Bennett, L. C. Dunn, and E. A. Boyse. 1974. Transmission ratio distortion at the *t*-locus: Serological identification of two sperm populations in *t*-heterozygotes. *Immunogenetics* 1:91-96.