

## SEXUAL SELECTION AND INSECT SPERM\*

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“And if I am, who am I? The heritage I supposedly transport? But how can I be both vessel and contents?”—a sentient sperm (Barth 1968).

Males produce the smaller gamete. The inconsequence of sperm in comparison to the enormity of eggs has dominated the evolution of male characteristics (Trivers 1972). Females, with their clutches of expensive ova, are limiting resources for which males compete in a variety of ways (Blum and Blum 1979). These different manifestations of masculinity have perhaps, in turn, influenced the radiation of insect sperm morphology and behavior.

The following related questions arise from a consideration of sperm both as microorganisms and tools of male reproductive interests: i) Why are there more sperm than eggs? ii) Do sperm behave as individuals? iii) Do competition between ejaculates and conflicts of interest between females and the sperm they contain result in gametic adaptations? Notes on topics indirectly bearing on these problems are placed in an appendix.

Why are sperm-to-egg ratios greater than 1? Some mites and insects transfer fewer than 2 sperm per ovum, but these are exceptions to the rule of tens or hundreds of sperm for every egg (Cohen 1971, 1975, 1977). Since only 1 of the multitude can genetically participate in the zygote, why go to the expense of producing such a mass?

Males may swamp the female reproductive system with sperm to block the introduction of rival ejaculates (Parker 1970). A contrasting argument holds that gametic exuberance is largely symbolic, a display of a male's ability to obtain resources. Females may make decisions about which male's gametes to use based on the dimensions of their mates' ejaculates (Mary Willson 1979, discussing excess pollen per ovule).

These hypotheses have 2 difficulties explaining the full range of insect sperm-to-egg ratios:

i) Even in insects whose females mate only once, males transfer excess sperm. In the monogamous mosquito *Aedes aegypti*, for instance, the male passes 2000 sperm to a female who will lay about 85 eggs (Jones 1968, Christopher 1960). There are, in such cases, no rivals to block or post-copulatory choices between males to be made.

ii) Neither specifies an advantage to females who accept excessive numbers of sperm. While the female sometimes expels or digests a portion of the male's ejaculate, the part she stores, and possibly maintains, is often still in excess of the number of ova. Of the 2000 *Aedes* sperm, about 1000 will make their way to the spermatheca (Jones 1968).

Why, then, do males produce more sperm than a female keeps and why does she keep more than she needs? In some cases, males may pass large numbers of sperm as a nuptial gift, a contribution to the good health and fecundity of his offspring's mother (see Thornhill 1976, 1980). It is possible that many are digested in the female genital tract as a source of nourish-

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ment (Bacetti and Afzelius 1976). A female might store and release multiple sperm as a nutritional boost to the zygote (Afzelius 1970). Polyspermy, more than 1 sperm penetrating the ovum, is common in insects (Richards and Miller 1937, Davey 1965).

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 resource cache. 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, Baccetti et al. 1977).

Male arthropods sometimes produce huge gametes which are probably able to contribute significant resources regardless of the selective reasons for their great size.<sup>1</sup> In the ptinid *Ptinella aptera*, they are as long as the adult (Taylor, in Hamilton 1979). *Drosophila melanogaster* sperm average 1.7 mm long, while in other *Drosophila*, they reach ca. 15 mm (Beatty and Burgoyne 1971). Mitochondrial derivatives compose 50% or more of their volume (Perotti 1973). The club-shaped sperm of ticks can range from 1 to 7 mm (Rothschild 1961, Rothschild 1965 as cited in Cohen 1977). Heavy-bodied sperm of the clerid beetle *Divaletes bipustulatus* stretch 10 mm. Most of the tail is occupied by derivatives (Mazzini 1976). Sperm of the backswimmer *Notonecta glauca* are 15 mm long. Mitochondrial crystals comprise 90% of these sluggish giants (Afzelius et al. 1976).

Instances of pseudogamy (parthenogenesis "stimulated" by sperm) are suggestive of paternal investment. The sperm makes no genetic contribution but must penetrate the egg for development to proceed. Perhaps eggs pirate material from victimized male gametes (Lloyd 1979). Parthenogenic females of *Ptinus clavipes mobilis*, a feather-winged beetle, must copulate with males of a bisexual relative (Woodroffe 1958, Moore et al. 1956). Pseudogamy also occurs in bark beetles of the genus *Ips* (Lanier and Oliver 1966, Smith 1971; similar phenomena are known in nematodes and flatworms, as cited by White 1973; Oligochaete worms, Christensen and O'Connor 1958; salamanders, McGregor and Uzzel 1964; and fish, Schultz 1971. Pseudogamy is suspected in some scorpions and psychid moths, White 1973).

It can be argued that pseudogamy is only a stage through which a newly derived parthenogenetic line might pass. Sperm may not contribute to the embryo but merely provide a developmental trigger required by a genome adapted to syngamy. Such a proposal is not convincing when applied to large highly radiated taxa. Armoured scale (Diaspidoidea) have an unusual sexual system that resembles pseudogamy. Males are mostly haploid but arise from fertilized eggs; the embryo eliminates the paternal genome (Brown and Bennett 1957, White 1973). Absorption of the sperm followed by its genetic disenfranchisement may be a case of resource larceny by the male-producing ova.

Various Cimicoidea practice traumatic insemination: injection of sperm through the female body wall into the hemocoel (Carayon 1966). Males of the bat parasite, *Afrocimex*, are transvestites, bearing pseudo-female paragenital structures which apparently invite homosexual attentions.

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<sup>1</sup>This and subsequent superscript numbers refer to notes in the appendix, p. 105.

Hinton (1964), noting phagocytosis of sperm, felt these sodomies were a means of food sharing, an unappealing hypothesis since it proposes the feeding of sexual rivals. Aid in stealing an ejaculate for consumption or reducing the fertilizing capabilities of other males might account for the mimicry (see, however, Lloyd 1979).

There are potential advantages to males who invest directly in the zygote with enriched sperm instead of indirectly, through substances digested 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.

Male investment via sperm might lead to a large sperm mass, but not necessarily large numbers of sperm. Multitudes of gametes may be required to find and efficiently fertilize an ovum; however, there are examples of high efficiency (some Diptera and Hymenoptera release about 1 sperm per egg, Lefevre and Jonsson 1962; Wilkes 1965) and as Cohen (1975) asks, why has selection not favored coalition of redundant cells into elaborate haploid metazoans better at fertilizations? (In the case of man ". . . a planarian-like organism exquisitely suited for finding the egg.")<sup>2</sup> High mortality in the female tract would again, presumably, select for fewer, better-endowed sperm, not great numbers of impoverished, less able gametes (see Lack 1954, Williams 1966 for discussion of the evolution of increased parental care in relation to juvenile mortality).

There are genetic attributes of an ejaculate that are dependent on the magnitude of the gamete population and these could be the selective context of sperm redundancy. Eggs and female reproductive tracts are the products of recombination and differ among themselves. The best sperm to survive in a female, penetrate a particular ovum, and complement that egg's genotype may be a statistical rarity. Unusual recombinations are more likely to be present in a large ejaculate, but they have a proportionately poorer chance of being included in the zygote as the number of competitors increases. Some filtering or choice is necessary. In a sense, an ejaculate would serve as a lek from which the egg would choose its mate. This type of choice is distinct from female discrimination between males on the basis of ejaculate size. Intraejaculate choice could generate the production of large ejaculates by males and their acceptance by females even in monogamous species.

Zimmering et al. (1970) consider the possibility that females prefer certain sperm genotypes and Hartl and Childress (1971) discuss some additional possible examples. The greater success, under certain conditions, of X-bearing pollen is thought to be due to choice exerted by the style rather than competition between grains (Lewis 1942 as discussed by Hamilton 1967). Delayed fertilization sometimes results in male-biased sex ratio (Werren and Charnov 1978). Preferential acceptance of Y (or O) sperm is 1 possible means of producing greater numbers of males (among Werren and Charnov's examples, Lepidoptera and copepods have heterogametic females.) Choice does not explain why females of haplo-diploid honeybees store 10 per ovum when sperm clumping would tend to expose eggs to genetically identical gametes (Ruttner 1956, Taber 1955).<sup>3</sup>

A related argument assumes the rigors of meiosis result in unavoidable

genetic errors, with perhaps 1 in 4 crossovers resulting in infertile sperm. If so, there are so many sperm because only a fraction are capable of fertilizing an ovum. Cohen (1973, 1975) has calculated a highly significant correlation between the log of sperm per egg and chiasma frequency per meiosis (see, however, Wallace 1974 and Cohen's 1975 response).<sup>4</sup>

*Are sperm individuals?:* Any choice between gametes relies on the discriminator, whether picking the best or eliminating the unviable, to have some insight into an individual sperm's genotype. Sperm have a dual nature. They are cells of the male parent's body and have phenotypic characteristics dictated by the male's diploid genotype, so-called diploid effects. At the same time, they are little animals, usually with a unique haploid genotype and potentially able to express their individuality through haploid effects. A difficulty that faces arguments depending on intraejaculate choice is that diploid effects do occur and haploid effects are rare ("... not typical of animals," Beatty 1975).

McCloskey (1966) and Lindsley and Grell (1969) in a continuation of work begun by Muller and Settles (1927) have found that sperm nearly devoid of chromosomes can differentiate and function. Comparisons of the variances of morphological characters between inbred (homozygous) and outbred (heterozygous) lines show no significant differences (Beatty 1971, Pant 1971). However, there is at least 1 unambiguous case of haploid effect, the greater success of sperm containing allele *t* in heterozygous mice (Braden 1958, 1972).

Why is the sperm phenotype generated, in part, by genes it does not possess? The answer may be that haploid genotypes run the risk of exposing recessive deleterious genes. A male heterozygous for a detrimental gene at a locus concerned with sperm function could lose half his ejaculate if the gametes generated their own phenotype. Competition between parent and gamete, perhaps leading to suppression of haploid genomes by their diploid progenitors, can occur in the context of sex-linked "meiotic" drive (Hamilton 1967, Maynard Smith 1978). If 1 sex-chromosome gives its bearer an advantage in obtaining fertilizations over the vessel of its analog, the offspring sex ratio will be unadaptively distorted (see Cohen 1971 for further, primarily proximate, arguments for the lack of haploid effects). A suspicion arises that these arguments are insufficient, since haploid effects occur regularly in other contexts: the gametophyte generation of plants, including pollens, and haploid animal males (see Mulcahy 1975; the latter are irrelevant in terms of sex-linked drive).

Why haploid effects should be more frequent in pollen than sperm is puzzling, since they are, in many ways, functional equivalents. Could there be a class of genes whose expression in gametes would be detrimental to male animals but not plants? There are differences in the population structure of the 2 types of "gametes." A sperm is a member of a dense herd of siblings while pollen, particularly if wind rather than animal-borne, can be diffusely spread and are unlikely to be in proximity with close kin. A gene whose product affects neighboring gametes could have very different fitnesses in the 2 environments. A pollen grain that inhibits its neighbor on a style removes a competitor of itself and, probably, the diploid parent. Sperm acting in the same manner would cost a heterozygous male a substantial portion of his ejaculate. Males that provide the sperms' somatic

inheritance may possess a means of containing haploid effects to protect their ejaculate (Alexander 1974).

*Gametes and Competition:* To what extent have sperm been molded by competition between adults? Lloyd (1979) has pointed out that females might manipulate sperm for genetic and nutritional reasons. If so, sperm may have adaptations to resist certain locational transfers tract. It has been suggested that the barbs on grasshopper sperm allow the female greater traction for moving the cell (Afzelius 1970), but barbs could also be a means of maintaining position.

In order to defend against the introduction of a rival's sperm, male insects will couple for months, make mates smell like a male, or leave their detached genitalia lodged in the vagina. Offensive tactics include displacing or even removing the first male's ejaculate (Parker 1970, Lloyd 1979, Waage, 1979). The bizarre menagerie of insect sperm types may owe its variety to parallel selection for defense and offense inside the female. Perhaps things such as mating frequency and female manipulation of sperm will explain why, in 2 apterous hexapod taxa, the Thysanura and Protura, 1 has sperm that swim in tandem, while the other has gametes that are immobile discs (Bawa 1964; Fig. 1 *in* Baccetti et al. 1973). Other sperm lacking self propulsion occur in some nematoceran Diptera, aleyrodids, and higher termites (Baccetti 1972, 1979). In the latter, monogamous males (kings) live alongside queens for extensive periods of time, making competition between ejaculates unlikely. The primitive termite *Mastotermes darwiniensis* is doubly unusual; it produces multiflagellate sperm (~100 tails) and several secondary reproductives are present in the place of a primary pair (Baccetti and Dallai 1978; Fig. 1 *in* Hill 1942). A possibly more complicated sexual system might be reflected in the elaborate male gamete.

Adult male polymorphisms illuminate by contrast the costs and benefits of "masculine" behavior. Antlerless deer and silent crickets are successful alternatives to the expense and danger of combat and broadcasting (Gadgil 1972, Cade 1980). Polymorphisms occur in sperm as well, suggesting the possibility that the female reproductive tract is a complex competitive environment.<sup>5</sup> There appear to be 2 major categories of polymorphisms. In the first, sperm with a normal haploid genotype are accompanied by morphs with no, too few, or too many chromosomes. These infertile cells are frequently gargantuan and could provide resources for the fertile sperm, the female, or the zygote (Fretter and Graham 1964). They may be needle-like objects released in advance of fertile cells to breach cuticular barriers (Koehler 1965) or enlarged to provide transport across distances and at speeds beyond the ability of the fertile sperm. In prosobranch marine molluscs, some of which are sessile, the trend has reached its extreme. Giant plate-like cells carry thousands of fertile sperm on a thickened tail (Purchon 1977). Such cellular transports are the functional equivalents of a mobile penis, an advantage to an immobile male. Less dramatic dimorphisms occur in Lepidoptera. The anucleated flagellar apparatuses probably function as boosters to fertile sperm (Friedlander and Gitay 1972). The distances travelled are not extreme by marine mollusc standards, but can be relatively long for an insect, due to the complexity of the female reproductive tract (see Davey 1965; insect sperm rarely swim farther than 10X their length, Cohen 1977).

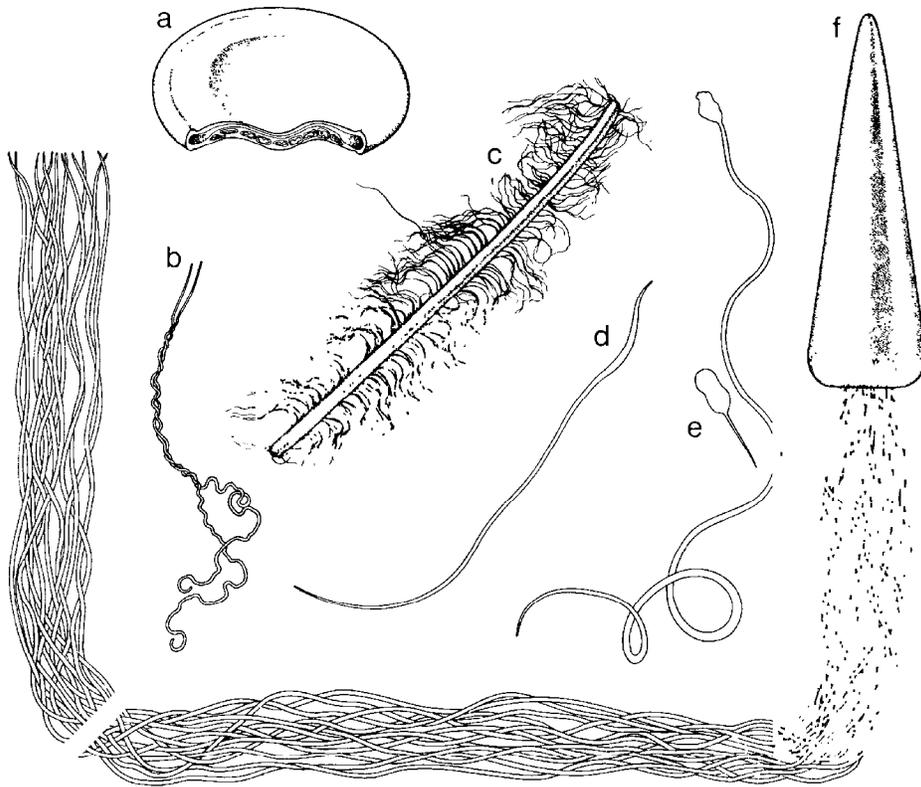


Fig. 1. An arthropod sperm sampler (not drawn to scale): a) The immobile disc-shaped sperm of the proturan, *Eosentomon transitorium*. After ejaculation it assumes a cuplike configuration ( $6\ \mu\text{m}$  in dia.; redrawn from Baccetti et al. 1973). b) Entwined sperm of the firebrat, *Thermobia domestica*. Sperm swimming in tandem are a rare but widely distributed phenomena in the animal kingdom. (See Footnote 2. Sperm are  $600\text{--}650\ \mu\text{m}$  long, redrawn from Bawa 1964.) c) The spermatostyle and associated spermatozoa of a gyrenid beetle, *Dineutus* sp. The rods are flexible in the epididym but rigid in the posterior part of the male reproductive tract and in the female. (See footnote 2. Rods are  $800\text{--}1000\ \mu\text{m}$  and sperm are  $\sim 150\ \mu\text{m}$ ; redrawn from Breland and Simmons 1970.) d) A typical threadlike insect sperm, from the firefly, *Pyroactomena barberi* ( $120\ \mu\text{m}$  long). e) Dimorphic sperm from the symphylan, *Symphylella vulgaris*. The tail of the larger sperm is  $60\ \mu\text{m}$  long; the smaller sperm tail is only  $4\ \mu\text{m}$ . The little gamete is much more abundant (redrawn from Rosati et al. 1970). f) A multi-flagellate spermatozoa from the Australian termite, *Mastotermes darwiniensis*. This is the first such sperm discovered in animals but polyflagellism is common in plants. (The cone is  $9\ \mu\text{m}$  long and the tail is  $100\ \mu\text{m}$ ; redrawn from Baccetti et al. 1978).

In a second class of polymorphism, several sizes exist, all with the apparently proper haploid genome, and all potentially able to fertilize eggs. Among pentatomids, there are commonly 3 such morphs with, in 1 case, respective nuclear volumes of  $200$ ,  $400$ , and  $1600\ \mu^3$  (Schrader and Leuchtenberger 1950). The biggest bears a disproportionate amount of RNA and proteins. White (1973) suggested that these are resources for the zygote.

But why, then, invest in a multitude of small impoverished sperm if large ones are both genetically functional and carry the male's investment? In several species of *Drosophila* (other than *melanogaster*), there are 2, 3 and, in 1 case, perhaps 4 sperm size classes. Interestingly, all are transferred in the ejaculate but are not randomly distributed in the female tract. In *subobscura* and *pseudoobscura*, only the longest are found in the ventral receptacle (a storage organ distinct from the spermathecae, Beatty and Burgoyne 1971). The distribution of the size classes may reflect specializations for competition at different times of the female's reproductive life.

Perhaps huge gametes aid in displacement, forcing smaller ones from storage, blocking their exit, or winning races down ducts. The expense of producing large tough gametes, useful in experienced females containing multiple ejaculates coupled with the advantages of providing great numbers of sperm to virgins, could select for males that produce a dimorphic ejaculate (a situation somewhat similar to the distribution of fighting and pacific haploid male parasitica in figs, Hamilton 1979).

It would be revealing to compare the abilities of males with different degrees of sperm polymorphism to displace previous ejaculates. Unfortunately, there do not seem to be comparable data available. *Drosophila melanogaster* sperm are monomorphic. Females remate after ca. 78% of the first ejaculate is exhausted. The following male displaces some of the old sperm and fertilizes an average of 16% of a female's ova (Gromko and Pyle 1978). In the sperm-trimorphic *D. pseudoobscura*, second males obtain 18% of fertilizations (Cobb 1977), but I have no information to what extent the original ejaculate is exhausted before remating (i.e. actual displacement of sperm). Females of the sperm-dimorphic *D. subobscura* rarely mate more than once (Maynard Smith 1956). If sperm competition ever occurs, its extent is unknown.

As is obvious, none of the questions originally posed has received any satisfactory answer. I believe, however, that the paradigms developed in studies of metazoan behavioral ecology can be profitably turned on the same creatures' gametes.

#### APPENDIX

<sup>1</sup>Mitochondrial DNA (=mtDNA) may be abundant in the crystalline derivatives (Perotti 1973). The quantity of mtDNA in the sperm could influence the proportion of paternal mtDNA in the sperm and ova of the following generation (inheritance of mtDNA may appear to be solely maternal due to typically enormous amounts of mtDNA in ova compared to sperm—1,000,000:1 in clawed frogs, Dawid and Blackler 1972). An mtDNA that is more abundant in sperm cells than its competitors would increase in frequency. If mitochondrial programming exerted an influence on sperm size, the ultimate result might be sperm modified to carry large amounts of mtDNA. Such organelles would come into immediate conflict with a nuclear genome programmed to allocate a certain amount of resources in a particular number of sperm (Alexander and Borgias 1978, discussion of outlaw genes).

<sup>2</sup>Insect sperm are commonly packaged in bundles that break up in the vas deferens or female tract (White 1954, Nur 1962, Robinson 1966, Virkki 1969). When motile, the bundles have been mistaken for sperm themselves (Nur 1962).

Paired gametes are a rarer phenomenon. In the firebrat, *Thermobia domestica*, 2 sperm wrap their anterior ends about each other and are motile

only when so entwined (Fig. 1b; Bawa 1964). Sperm are joined at the head in other taxa, leaving midpieces and tails free (dytiscid beetles, Mackie and Walker 1974; the millipede *Polydesmus* sp., Reger and Cooper 1968; woolly opossum, Phillips 1970; opossum, Holstein 1965; the mollusc *Turritella*, Idelman 1960). Suggested advantages of pairing include protection of each other's acrosomes during genital journeys or enhancement of ability to penetrate the egg (Mackie and Walker 1974 and citations; tandem sperm may enter an ovum together). A pair of flagella might generate more motive power in the fluid environment of the female tract (Afzelius 1970).

Ejaculates of some gyrinids contain rodlike objects (spermatostyles), on each of which 100 or more sperm are attached by their heads. Partially disintegrated rods have been recovered from the spermathecae. Spermatostyles can be moved by the efforts of their "crew" but free sperm are motile as well (Fig. 1c; Breland and Simmons 1970).

The function of these aggregates is obscure. They might serve to concentrate the gametes of a particular male (an advantage in competition for fertilizations?). Sperm could aid in delivering material in the spermatostyle to the female, or perhaps benefit by proximity with spermatostyle material.

<sup>3</sup>While the mitotically produced sperm of a haploid male can have only 1 complete genetic program, the morphology and fertility of such sperm can differ. In the eulophid *Dahlbominus fuscipennis*, there are 5 sperm morphs; 2 morphs characterized respectively by sinistral (left-handed) and dextral (right-handed) coilings reach the spermatheca (Lee and Wilkes 1965). There is some evidence that the sperm morph, rather than discontinuing sperm release, determines the sex of the offspring (Lee and Wilkes 1965, Wilkes 1965). Apparently, sinistral sperm cannot penetrate beyond the micropyle and so cap the unfertilized egg (Wilkes and Lee 1965). Females seemingly have abandoned the typical means of control over the offspring's sex ratio. One possible benefit of such a surrender, male investment via gametes, fails to find support in the incomplete penetrance by sperm. Gametes adapted for the production of individuals with no genes of direct paternal descent would most likely evolve in the context of inbreeding. The 1:9 sex ratio of isolated *D. fuscipennis* is evidence for such a mating system (see Hamilton 1967). However, male progeny increase with adult female density in Russian populations demonstrating female control of offspring gender (Victorov and Kochetova 1973). This ability might be due to preferential release of sperm but the implied outbreeding by sons of high density females casts doubt on the sex determining function of the morphs.

<sup>4</sup>In several insect orders, Virrki (1969) notes an inverse correlation between numbers of sperm produced and phylogenetic position (see also Kurokawa and Hihara 1976). After equating phylogenetic advancement with ecological specialization, he proposes that specialist organisms adapted to a narrow range of conditions would evolve means of genetic canalization. One means of lowering the genetic variance in an ejaculate is to decrease the number of gametes present. While low sperm numbers may lessen the probability of bad, i.e. unusual, recombinational events occurring, they simultaneously increase the likelihood of such a genome being incorporated into the zygote should it occur.

A further complication is a tendency for sperm enlargement with numerical reduction. Lower numbers could reflect a redirection of male investment in gametes due to resource transfer, competition between sperm or female life span and her ability to maintain sperm (see text).

<sup>5</sup>Ova are seldom in sexually competitive situations that might select for polymorphisms but female investments between offspring may differ and sexual dimorphisms in zygotes are possible. Fisher (1958) argued that investment in the sexes should be equal; this is typically translated into equal

numbers of males and females primarily because of even distribution of resources among ova. Does egalitarian investment mean that situations favoring ova dimorphism seldom arise, or that there are evolutionary constraints on patterns of maternal investment? T. J. Walker (personal communication) has suggested that, when the male genome determines sex (male heterogamety), there is the danger of "wrong-sexed" sperm fertilizing an inappropriately vitualized ovum. This uncertainty could force even-handed investment in ova. Any disparate resources are best bestowed after the sex of the zygote is determined. If so, dimorphic ova should be restricted to taxa with female control of offspring gender. Of the following cases of egg and spore dimorphism known to me, none appear to refute the hypothesis.

Egg capsules of the marine worm, *Dinophilus apatris*, contain large female eggs and much smaller male eggs. Sex is determined by the female prior to meiosis. The sex ratio, while highly variable, does not appear to conform with the expectations of Fisher's model (sex ratios 1:0.6 to 1:2 depending on strain, Bacci 1965; inbreeding could account for the direction of the bias, see Hamilton 1967).

Eggs of the peach scale have a color dimorphism; female eggs are coral pink and male whitish. Sex in armoured scale is determined cytologically. The female color presumably reflects the presence of a substance absent from the male (or vice versa) but unequally partitioned parental investment is not supported by usually even sex ratios (Brown and Bennett 1957).

Female birds are heterogametic, some produce offspring that are sexually dimorphic at the end of parental care, and in these eggs may vary in size. There is not, however, an invariable relationship between sex and egg size (Howe 1976, 1977). Why doesn't a sexual dimorphism at the end of parental care extend back into the zygotic/gametic stage? It is possible that some female heterogametics might still be uncertain over the sex of the genome that would come into possession of a particular parental investment. Meiotic divisions in vertebrates typically begin after the growth of the primary oocyte.

In liverworts, dwarf male gametophytes living epiphytically on females may or may not arise from a smaller spore. This size difference may depend on whether or not sex chromosomes are present (Rink 1935, not seen, *in* Ghiselin 1974).

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