

Evolution of Haplodiploidy: Models for Inbred and Outbred Systems*

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Several new models are proposed for the evolution of haplodiploidy. Each of these models is evaluated for its ability to explain (1) special problems associated with transition to haplodiploidy from a population of diploid and progenitors, (2) current patterns of population structure in haplodiploid and related species, and (3) the evolution of genetic systems similar but not identical to haplodiploid systems. Of the new models, three are based on special conditions associated with inbreeding. Close inbreeding provides for the automatic effects of reduced problems in expressing recessives, lowered differences in gain from heterozygosity (to produce both heterotic effects and a greater variety of offspring) between haploid and diploid males, effective protection of haploids from direct competition with diploids, and a mechanism for the spread of haplodiploidy through gains derived from increased ability to control sex ratio. These models differ in the context where gain from sex ratio control is expressed. Pathways for the evolution of haplodiploidy in outbreeding populations are also discussed. Females who parthenogenetically produce haploid males have high genetic relatedness to their sons. If the sperm of these males is used to make both sons and daughters, i.e., through matings with diploid females, there may be a net gain for haplodiploids. Another outbreeding model, modified from S. W. Brown (1964, *Genetics* 49, 797-817), deals with selection for females producing haploid males in populations where there are driving sex chromosomes. Biases created by drive in sex ratio may allow haplodiploid females to be the only effective producers of males in the population. Several of the new models explain the whole range of haplodiploid and related adaptations and provide predictions that appear to be more consistent with the known structure of contemporary populations than those available in current models.

INTRODUCTION

Only two major departures from the common pattern of diploid sexual reproduction occur among animals in which sex is determined at conception. Thelecytoky involves

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the abandonment of recombination between individuals. Problems in its evolution from diploid systems have been discussed in detail (see papers and references in Williams, 1971, 1975; and Maynard Smith, 1978). Haplodiploidy (arrhenotoky or male haploidy) is the only other widespread alternative. It usually involves the pathenogenetic production of haploid males that transmit only maternally derived genetic information. This mode of reproduction has received much less attention (recently only from Brown, 1964; and Hartl and Brown, 1970) even though it may occur in as many as one-quarter of all arthropod species and in some rotifers.

Among arthropods, haplodiploidy is the exclusive mode of reproduction in the orders Hymenoptera and Thysanoptera, and also occurs in Homoptera, Coleoptera, and mites and ticks (order Acarina). Haplodiploidy has had multiple origins in orders such as Coleoptera, in which it occurs in bark beetles of the genus *Xyleborus* and in the sole member of the family Micromalthidae, *Micromalthus debilis*. Two distinct Homopteran groups, whiteflies (Aleurodidae) and some coccids, produce haplodiploid males. In mites and ticks Heinemann and Hughes (1969) suggest 3 separate origins for haplodiploidy based on its occurrence in taxonomically distinct groups. This leads to a minimum estimate of 11 separate origins for haplodiploidy.

There are a variety of haplodiploid-like systems. Coccids, for example, employ several mechanisms for achieving functional male haploidy which include: (1) the common parthenogenetic production of males; (2) use of male sperm to initiate development but no incorporation of paternal genetic information (gynogenesis); and (3) so-called parahaploid systems in which a diploid set of genetic information occurs and is, to some extent, expressed in males, but the paternally derived set is heterochromatic and is not utilized in sperm production. Other haplodiploid-like systems occur in flies of the families Cecidomyidae and Sciariidae. In some species of these groups, individuals may be functional haplodiploids, and probably in all cases selective forces similar to those of haplodiploid species contributed to the evolution of their peculiar sexual systems. White (1973) reviews in detail descriptions of cytological mechanisms and relevant references for each of these insect groups.

Aside from representing a large fraction of invertebrate species, and being one of the few common deviations from diploidy, haplodiploid groups characteristically comprise large taxonomic categories, i.e., orders and families. This is in sharp contrast with thelytokous groups which are not only more abundant but, with few exceptions, are confined to taxonomic categories of low rank. The implication is that transitions to haplodiploidy from diploidy are less frequent than similar transitions to thelytoky but, once established, haplodiploids are less likely to go extinct than groups in which individuals are exclusively asexual reproducers.

The peculiarities of haplodiploidy suggest that considering the selective factors which cause its evolution is critical in developing a comprehensive view

of how all sexual systems operate and in understanding the elusive adaptive basis of sexuality. Haplodiploidy has been assigned a central role in the evolution of sociality in insects (Hamilton 1963, 1964a, b; but for a contrasting view, see Alexander, 1974) and it has extended our understanding of how sex ratio selection (Hartl, 1972) and sex-determining systems operate (reviewed by Kerr, 1974). In this report, I will describe and evaluate several models that may be useful in explaining the transition from diploidy to haplodiploid reproduction. Several problems are likely to be associated with this transition, and different models will be evaluated with respect to their ability to deal with these problems. Approaches to the problems are dependent upon the degree of inbreeding in antecedent diploid populations. Therefore the models I present are grouped in terms of their effectiveness in leading to haplodiploidy where inbreeding and outbreeding are dominant.

MODELS FOR THE EVOLUTION OF HAPLODIPLOIDY

Evolution of haplodiploidy is generally considered to be dependent upon overcoming important problems associated with the production of haploid males. In dealing with the evolution of haplodiploidy, special attention must be given both to the selective forces which cause its overall effects to be favored and to the array of antecedent conditions in diploid populations which might block its gradual evolution. Whiting (1945) and Hartl and Brown (1970) consider in detail some major difficulties expected to confront new haploid males. These include development of gametes in haploids, development of effective sex determination, expression of deleterious recessive alleles, initiation of development of unfertilized eggs, and gene dosage compensation. The diversity of these complications supports the view that very special circumstances are necessary to achieve transition from a diploidy to a haplodiploid genetic system.

Evolution of male haploidy has been considered almost exclusively in the context of outbreeding systems and, in most cases, available explanations are incomplete or cannot account for all cases of functional male haploidy (see below). Inbreeding conditions reduce many of the costs associated with the transition to haplodiploidy and I will first consider models which occur in populations with this type of breeding structure.

SELECTION FOR MALE HAPLOIDY IN INBREEDING POPULATIONS

A. Lowered Costs to Haploid Males

Brown (1964) pointed out that inbreeding would reduce the cost of becoming an initial haploid male. These individuals are preadapted by the expression of

homozygotes in natural backcrosses and would not suffer from the presence of numerous deleterious recessive alleles that would likely appear if male haploidy appeared in an outbreed population. Although such considerations led Brown to require at least minimal inbreeding as a prerequisite for the evolution of male haploidy, he seriously considered the evolution of this trait only in the context of random mating.

Inbreeding provides several additional effects that enhance the likelihood of haplodiploid evolution. One of these becomes evident if we restrict competition between haploid and diploid males to groups in which they are forced to mate with close relatives. Outbreeding haploid males would be unable to take advantage of the effects of heterosis, because they have only one locus for every allele. There is no absolute improvement for the haploids with inbreeding, but their competitors, the diploid males, are in a similar situation. Since genetic variation is severely reduced, diploids are likely to be homozygous for most alleles and therefore unable to experience expected benefits from heterosis. In this way inbreeding increases the relative fitness of haploids.

Effects of inbreeding also influence the relative worth of sexuality in haplodiploid and diplodiploid systems. Under any conditions, haploid males mitotically produce only one kind of sperm, but through meiosis, outbreeding diploid males may produce almost an infinite variety of sperm. Williams and Mitton (1973) and Williams (1975) suggest that sexual variation in the offspring that an individual produces may have important effects on offspring survivorship and reproduction. If this is true, haploid males would be at a disadvantage under conditions of unrestricted mate choice. Under close inbreeding, however, differences between haploid and diploid males are reduced because gametes of diploids, even though produced by meiosis, may become nearly identical due to homozygosity in parents. In addition, any possible variance in the quality of offspring that females might derive from mate choice (or through multiple matings) is reduced because close relatives who show only limited genetic differences form the array of potential mates.

Evaluation of other important effects of inbreeding requires an understanding of the effect of this form of breeding structure on the selection for alleles controlling the sex ratio of offspring produced by parents. Fisher (1958), in discussing sex ratio evolution in outbreeding populations, noted that where parents are unable to predict the quality of their offspring, the gain a parent realizes in each sex is proportional to its investment in the offspring of that sex. For instance, in males who are forced to compete openly for mates, parental gain through males is expected to be proportional to the overall investment in them. Different conditions seem to hold for inbreeding. Depending on the level of inbreeding, individual male offspring are guaranteed sexual access to their relatives so that the relationship between the level of parental investment and mating success through males seen in outbreeding populations breaks down. Under close inbreeding, in which competition between parental lines becomes

the primary level of selection, the production of more male offspring than are necessary to fertilize the brood leads to redundant functions among males. Recognizing this, Hamilton (1967) concluded that under inbreeding, or when competitive effects of brothers are more severe than the effects of nonrelatives, parents should produce investment ratios that favor females. Investment otherwise wasted on males might be spent more effectively on females who can enhance parental reproduction. Hamilton provided extensive data showing that sex ratios are biased when close inbreeding is common. In many cases, the size of males is also severely reduced, further enhancing the diversion of parental investment into daughters.

Recognizing the effects of reduced interbrood competition in inbreeding leads us to reconsider the importance of differences in quality between diploid and haploid males. With inbreeding, haploid males that might be considered "weak" for reasons given above are effectively buffered from sexual competition with highly adapted diploids. The haploids only need to successfully fertilize sisters before dying to allow their parents to be on a par with those producing diploids. Such shielding from sexual competition favors hypotheses for haplodiploid evolution in inbred systems, since haploid males never need to reach the level of adaptation necessary in models based on outbreeding.

A strong indication that inbreeding may lead to haplodiploidy comes from the concurrence of these two population characteristics. Neither haplodiploidy nor close inbreeding seems to be common among animals, yet all of the examples used by Hamilton to illustrate his argument about sex ratio control involved haplodiploid species. Among the remaining haplodiploid groups, inbreeding may be common, but the information on breeding behavior among haplodiploids is very limited.

In coccids, there are data which suggest that inbreeding is common in some species. Males commonly have an extremely short adult life expectancy; 50% die in the first 6-7 hr after emergence (Tashiro and Beavers, 1968; Beardsley and Gonzalez, 1975). In addition, biased sex ratios favor females (James, 1937; Brown and DeLotto, 1959) and there are tendencies for males not to feed past the second instar (Nur, 1967). Hughes-Schrader (1948) characterizes males as "typically weak" and many authors describe them as difficult to find.

Hamilton's arguments involve the division of parental effort to achieve female-biased sex-related investment ratios. In coccids parents do not directly provide for offspring after eggs are laid. Males may help their sisters by reducing the nutrients they draw from a plant, or portion of a plant, resulting in enhanced resource availability and reproductive gain for their sisters.

In coccids dispersal of females occurs before sexual maturity, and sometimes opportunities for sib matings may be severely limited. A review by Beardsley and Gonzalez (1975) suggests that the maximum distance of active migration by females under natural conditions may be on the order of several meters. Under these conditions, individuals may commonly mate with close relatives. However,

female larvae may be carried by wind out of the range where sib matings are likely, and, in these cases, outbreeding represents the only opportunity for female insemination. Even so, gain from sex ratio control through intermittent inbreeding (see below) remains one of the few plausible selective forces favoring haplodiploid evolution under these conditions.

Little information seems to be available on the mating systems of aleurodids, but their minute size and patchy distribution suggest a situation similar to that of thrips where inbreeding is known to occur (Lewis, 1973). Patchy distributions are also known for *Micromalthus* which are usually restricted to rotten logs. I have found little information on breeding relationships in rotifers and previously suspected that inbreeding might be common because of poor powers of dispersal. However, on discovering their tendency to produce eggs resistant to long periods of desiccation and freezing, spatial colonization may not be as important as one might otherwise imagine, although important effects due to inbreeding may still occur.

Outbreeding is common in some male-haploid species. In Hymenopteran species such as the wasp *Bracon* (Hughes-Schrader, 1948) and the honey bee *Apis* (MacKensen, 1941) outbreeding has become the rule. In these cases, inbreeding interferes with the normal sex-determining mechanism (reviewed by Kerr, 1974) and commonly leads to the production of either weak or inviable diploid males. Females may also be affected (Kerr, 1976; Bruckner, 1978). Even so, obligate outbreeding by some species does not strongly detract from the argument that inbreeding has made important contributions to the origin of male haploidy among Hymenoptera. Successful inbreeding species might become outbreeders under conditions where there are high densities of males. Cowan (1978) has found that among clumped nests of hole-nesting wasps, the sons of one female may patrol nearby nests of unrelated females, apparently outbreeding. Where nests are far apart, males typically mate with their sisters. A similar relationship appears among tropical sawflies (Dias, 1976) in which offspring of one female emerge close together, and inbreeding is common at low density. As density increases, males from other broods compete for emerging females.

Hartl and Brown suggest that outbreeding models are suitable to explain the evolution of male haploidy in the Hymenoptera. As evidence they cite a report by Coppel and Benjamin (1965) who found that some sawflies and horntails swarm, a behavior which connotes a high degree of random mating. The implication is that the presence of outbreeding in this phylogenetically "primitive" group means that outbreeding was common among the first Hymenoptera. But behavior of modern sawflies may have changed greatly from the first haplodiploid Hymenoptera. Breeding behavior may be particularly susceptible to change, as discussed above, often varying with conditions of population density. Interestingly, Coppel and Benjamin (1965) and Benjamin (1955) describe biased sex ratios in Dipronids which indicate high levels of inbreeding. Moreover,

inbreeding is not restricted to Dipronid sawflies, but has been found in species of other families, e.g., *Diolcerus diasi* (Argidae: Dias, 1976) and *Dahlbominus fuscipennis* (Eulophidae: Baldwin *et al.*, 1964).

B. Sex Ratio Control and Selection for Haplodiploidy

In addition to allowing the transition to haplodiploidy to occur more easily, the correlation of male haploidy with inbreeding and the known ability of haplodiploid females to achieve sex ratio control (SRC) suggest a basis for favoring alleles causing the establishment of male haploidy. Diploids appear to have some difficulty in gaining the ability to control sex ratio, whereas for most haplodiploids the ability to control sex ratio is widespread. This may mean that only haplodiploids are able to bias parental investment and enjoy the almost twofold advantage from such biases that were described by Hamilton. In fact, the models developed by Hamilton, if adjusted for fitness reductions due to male haploidy, can be applied as the mathematical basis for advantage gained by haplodiploids in populations with varying levels of inbreeding.

Ghislain (1975, p. 199) also has noticed the correlation of inbreeding with male haploidy. He says, "The adaptive significance of male haploidy may have something to do with controlling the sexuality of offspring. At any rate, it functions that way now, in spite of other effects." He does not discuss the problem further. Here, I consider the gain from plasticity of sex ratio control for haplodiploids under three nonexclusive and possibly complementary conditions, which may have contributed to the establishment of haplodiploidy.

Some haplodiploids may have the advantage of immediate and appropriate biases in sex ratio, but selection could also work on diploids to develop a similar capability. Starting with an outbreeding diploidy population that is then forced to inbreed, we might envision an evolutionary race along different pathways for the development of a means to control sex ratio. There is reason to suspect that such control may be established more readily in haplodiploid organisms. Leigh (1977) and Alexander and Borgia (1978) have argued that due to a long history of selection against drive by sex chromosomes and the consequent lowering of fitness, selection has worked against nonrandom distribution of chromosomes into gametes, especially by sex chromosomes. Systematic biases in the meiotic distribution of all chromosomes limit the individual's potential gain from sexuality, and, in sex chromosomes, cause individuals to produce suboptimal sex ratios (see Verner, 1965; Borgia and Blick, 1979). A history of selection against segregational biases suggests a source of difficulty of new diploidy inbreeders in maximizing their gain by producing unequal sex ratios. It is on this basis that haplodiploidy appears as a more likely alternative for the control of sex ratio than a change in the genetic background of individuals which has been similarly selected to prevent biased segregation of chromosomes. Although it is difficult to find specific instances of support for canalization against

biased segregation of sex chromosomes, the great regularity of meiosis at least gives some credibility to this view.

Among diploid species, meiotic biases toward sex ratio deviations are relatively rare and are known only among Psocids (Schneider, 1955; Mockford, 1971), aphids (Hille Ris Lambers, 1966), some cladocerans (Fowler, 1909), and in Diptera. Among flies, cases of male-producing and female-producing genotypes are known from work by Metz (1926) on *Sciara*. Generally these lead to unisexual broods; however the overall sex ratio he reported from his laboratory studies is 1 : 1. But even such a pattern of biases toward females would be of little use in inbreeding populations. Situations are needed where only a small proportion of eggs develop into males. In *Drosophila pseudoobscura*, biases in sex ratios were found by Gershenson (1928). Policansky and Ellison (1970) showed that the majority of Y chromosomes degenerate, giving rise to strongly female-biased sex ratios, and occasionally males produced were sexually competent. Stalker (1961) considers the sex ratio trait of *Drosophila paramelanica*. This trait leads to destruction of Y-bearing male-producing sperm, resulting in female-biased sex ratios. Stalker points out that under natural conditions in which this type of drive is most prevalent, flies live at very low densities. It is possible that inbreeding may be common in these populations and that this irregular chromosomal behavior reflects a history of selection for sex ratio control. But the waste and imprecision of such mechanisms imply that they are results of inter-genomic conflicts of interest. In cases involving *Drosophila*, sterile males which are produced represent lost reproductive effort. This means little gain from SRC, and ability to vary sex ratio according to needs seems limited. In other invertebrate groups, such as aphids, precise sex ratio control among diploids does occur and is associated with complex life cycles that alternate between sexual and parthenogenetic production of males. This life cycle pattern is common to some haploids including *Micromalthus*, rotifers, one group of wasps, and some haploid-like Cecidomyid flies.

Evidence for sex ratio control in mammals is presented by Trivers and Willard (1973) who consider various species in which mothers appear to be able to correlate the sex of their offspring with their own physical condition (but see Meyers, 1978). Males are commonly produced most often by females in good physical condition. The reason given is that effective sexual competition in a polygynous species requires strong males who are more likely to be derived from good mothers. Females, on the other hand, can always get mated and mothers in poor condition who are able to devote less to each offspring profit most from making daughters. Ability to adjust sex ratio, however, need not come from meiotic control but may result from selective abortion of embryos (see Trivers, 1974; O'Gara, 1969). If abortions are the cause of the kind of sex ratio control seen in mammals, there is little opportunity for operation of a similar mechanism in other animals who invest heavily in eggs before sex is determined. Heterogametic females in Lepidoptera and birds may be able to vary primary sex ratio

according to their needs, but I know of no clear instances where this occurs (but see Howe, 1978; Fiala, 1979). Diploid termites appear to be able to control the sex ratios of reproducers. Both male and female juveniles serve as workers. Alexander and Sherman (1977) propose that sex ratio biases common in adults may result from different proportions of offspring of each sex developing into adults. It is interesting that for both mammals and termites, no biases in the meiotic mechanism favoring one or the other have been demonstrated and all differences can be accounted for by sex-related variation in mortality or patterns of development. In fact, it is the presence of the ability to control sex of offspring workers that is seen by some as the reason for the high frequency of eusociality among haploids (Alexander, 1974).

Selective killing of sperm by females where males are heterogametic might provide one mechanism for effective sex ratio control, especially if males and females agree on the sex ratio to be produced. However, where there is disagreement, as when females mate with several unrelated males, males might be expected to evolve resistance to killing of male-determining sperm. For instance, such male sperm might evolve to mimic characters carried by female-determining sperm in characters that are used by females to separate types.

C. Variable Levels of Inbreeding and SRC

Even conditions in which there is occasional inbreeding may give haploids an advantage even over diploid females who express adaptive biases in their sex ratio. Among arthropods, the haploid female's ability to vary the sex ratio of her brood by selectively fertilizing eggs permits her to rapidly adjust sex ratio according to levels of mate competition she anticipates for her sons with males from other broods. Such a mechanism may evolve as a female changing brood sex ratio if her copulation is interrupted, as occurs in the mite *Petrobia harti* (Boudreaux, 1963). SRC in diploids is likely dependent upon biases in the type of sperm which fertilizes eggs, or if females are heterogametic, on the behavior of their meiotic mechanism. Neither situation appears to give the diploid females a simple means of varying the sex ratio of their brood according to immediate contingencies. This limited ability to respond to changes in optimal sex ratio forces diploid females able to produce biased sex ratios to produce sex ratios of offspring that provide the best average gain over the conditions of mate competition that males of their broods are likely to meet. Haploids equal in other respects are expected to replace diploids where they occur together because of reproductive gains from their ability to better respond to situations where varying patterns of sex-related investment are valuable.

Haploid males need not always lose in sexual competition where outbreeding might occur. For example, haploid males commonly emerge before sisters, wait for them to eclose, and mate with them (solitary wasps, Cowan, 1978;

sawflies, Dias, 1976). Male mites may guard females before they eclose (Cone *et al.*, 1971). Hamilton (1979) describes weapons carried by inbreeding males that are used to discourage migrant males from mating with these males' female relatives. Paternity of offspring goes to the first males to mate with some female mites (Helle, 1967). Such a pattern would enhance the success of brothers because of their proximity. Sib mating within the mother, common in some mites (Elbadry and Tawfik, 1966), should reduce the success of potentially invading males. These adaptations foster inbreeding under even marginal conditions where outbreeding might otherwise be common. Their existence supports the idea that mothers and their sons can benefit greatly from inbreeding and SRC, perhaps even to the disadvantage of genes carried by the males' sisters.

D. *Mother-Son Matings and SRC*

Inbreeding may also lead to haplodiploidy in the context of mother-son matings. Haplodiploids with appropriate life histories have the opportunity for females to mate with their sons. Under conditions where mates are scarce, such matings may be valuable to females. Mother-son matings offer females the opportunity to make offspring whose success in reproduction is not dependent on their ability to find members of the opposite sex. Most previous discussion of advantage for unfertilized haplodiploid females from producing parthenogenetic offspring has involved only consideration of outbreeding by haploid sons (Brown, 1964; Hartl and Brown, 1970). However, such arguments tend to underestimate the value of haplodiploidy when mates are scarce. Outbreeding haploid males whose mother was unfertilized may have difficulty finding mates for themselves. And in cases where nearby females are found, brothers may be forced to compete for matings, lowering the average success among males within a brood. Thus, if mother-son matings are possible, the opportunity exists for significant reproductive gains by unfertilized haplodiploid females. Such matings also provide a system for the automatic adjustment of sex ratios to those which are appropriate for inbreeding conditions (see below). Evidence of mother-son matings is presented by several authors (Browne, 1922; Van Emden, 1931; Entwistle, 1964) for haplodiploid insects. Life histories of other haplodiploid insects in which generations overlap suggest that mother-son matings may have been important in some cases.

E. *Sex Determination and SRC*

Part of evaluating the sex ratio control model depends on developing an understanding of mechanisms which might allow for selection to operate and provide for the replacement of diploid by haploid males. Consideration of chromosomal behavior in sex-determining systems likely to lead to male haploidy makes hypotheses based on sex ratio control under inbreeding extremely attractive. Hartl and Brown (1970) consider a form of the XO/XX sex-deter-

mining system as a probable starting place for the evolution of haplodiploid systems. In such systems, diploid males produce two kinds of gametes, those containing autosomes and an X chromosome and those with only a set of autosomes (O). Females are homogametic and produce only X-bearing gametes; under usual conditions, the sex of the offspring is determined by the type of male sperm that fuses with an egg. If males are to arise from unfertilized haploid eggs, there are two possible results. The combination of a single X chromosome and one set of autosomes may cause maleness, and consistent with this sex-determining system, haploid individuals would develop as males. Or, females may have complete control of sex determination and may be able to override the sex-determining system common in diploids which might otherwise produce a female from a haploid individual. The XO type of sex-determining system is effective under extreme inbreeding; and under inbreeding, its relation to the success of the sex ratio deviation model becomes apparent. Because haploid males carry only X chromosomes, their sperm yields only female offspring. This sperm also gives females the capability of producing all females (by fertilizing all eggs), all males (by fertilizing none), or any intermediate combination (by controlling the proportion of eggs which are fertilized). By contrast, a similar female fertilized by a diploid male at most can produce half a brood of females; her only option is to increase the proportion of sons by failing to fertilize some of her eggs. If haploid mated females can be fertilized with a minimum commitment to male production, females have the opportunity to produce nearly twice as many fertilized female propagules as they would in a similar colony fathered by a diploid male. Intercolonial selection may then lead to the loss of diploid males.

In sex-determining systems in which males produce only one type of sperm, a potential problem exists if females allow all eggs of their broods to be fertilized; no males will be produced. The potential for gain through inbreeding under these conditions may be lost. However, production of small numbers of males might be achieved by several means. Selection may occur among genotypes which affect the proportion of eggs that go unfertilized and are eventually converted into males. For conditions of extreme inbreeding, only a very small proportion of eggs need to be unfertilized to provide the most advantageous sex ratios. Selection for sex ratio need not even depend on heritable differences in tendency to fertilize eggs and may come automatically in the context of mother-son matings. Initial eggs will develop into males who inseminate their mother and allow her to produce daughters. Such a system of automatic feedback insures that the female will produce offspring of both sexes with sex ratios favoring females. The success of such a strategy is dependent upon several factors including: the rate of male development, the reproductive lifetime of the female, and the rate at which she lays eggs in relation to her age.

An increase in the fraction of females a mother produces can be achieved by reducing the rate at which eggs are laid before she is fertilized. Presumably, eggs

laid early reduce the female's subsequent egg production. Since producing only a few males should guarantee her fertilization, the greatest output of females might be achieved by reducing the rate of oviposition until after she is fertilized. This appears to happen in some haplodiploid spider mites in which mother-son matings are considered likely (Helle and Overmeer, 1973). For example, unmated females in the genus *Tetranychidae* produce considerably fewer eggs than mated females, and unmated females live longer (Gutierrez, 1967; Nickel, 1960). Similar behavior is shown by the chalcid wasp *Melitobac acasia* (Browne, 1922). The ultimate refinement in gaining advantages from sex ratios in inbreeding while avoiding problems with developing control mechanisms occurs in the citrus pest *Icerya* (Hughes-Schrader and Monahan, 1966). Here, individuals apparently derived from haplodiploids have become self-fertilizing hermaphrodites.

Hamilton (1967) pointed out that the ability of insects and related classes to store sperm preadapts them to the evolution of precise sex ratio control through their ability to selectively fertilize eggs. Since females control the sperm inside of them, the ability to lay unfertilized eggs comes under their control and they need not rely on "misses" by the males' sperm. The ability not to fertilize a small proportion of eggs would be relatively simple to evolve, since there is no requirement for the development of new complex structures. Also precise control of sex ratio under different conditions could be developed relatively easily in response to cues describing proportions of young likely to be produced by other nearby females (Hamilton, 1967, considers these problems in detail).

SELECTION FOR MALE HAPLOIDY IN OUTBREEDING POPULATIONS

Costs to individuals from inbreeding in a population which has a history of outbreeding may be very high and inbreeding may only occur under extreme conditions. Sufficient laboratory data exist to support this view (Lerner, 1954). Birkey (1967) has correctly argued that haplodiploidy may increase the likelihood of inbreeding. Populations in which reproductively successful haploid males have been produced may, as a consequence, express most deleterious recessive alleles and thereby lower the expected cost of keeping individuals from inbreeding. There is now evidence of significant reductions in electrophoretically detected genetic variability in outbreeding haplodiploid populations (Metcalfe *et al.*, 1975; Snyder, 1974). Reductions in the cost of inbreeding in haplodiploid populations may then account for the association of haplodiploidy with inbreeding.

Previous attempts to deal with the diploid-diploid-haplodiploid transition have focused on selection in outbreeding populations (Brown, 1964; Whiting, 1945; Hartl and Brown, 1970). And even if we accept Birkey's explanation for the tendency for haplodiploids to inbreed, there is still a need to develop a model

that accounts for the evolution of male haploidy in an outbreeding population.

Early efforts toward explaining the evolution of male haploidy were developed by Schrader and Hughes-Schrader (1931) and Whiting (1945). Hartl and Brown reviewed each in detail and correctly concluded that none of these models are suitable explanations for the evolution of haplodiploidy. Brown (1964) and Hartl and Brown (1970) offer more realistic alternatives, that rely on the production of haploid males from otherwise useless unfertilized eggs. Yet even these cannot serve as general explanations. The requirement for a population with a steady supply of unfertilized eggs suitable to develop but commonly wasted, before the advent of haplodiploidy, is not satisfying because these females have other opportunities for resolving the problem of sperm shortage, e.g., inbreeding. Moreover, their models do not explain the evolution of haplodiploid-like systems in which females must be inseminated. Therefore at least in some cases we are required to search for descriptions of other systems that do not suffer from the same limitations.

A. Parthenogenetic Production of Males

Parthenogenetically produced males show a higher average degree of relatedness to their mothers than those produced in diploid-diploid systems. The differences in the patterns of relatedness of these two systems may provide a built-in advantage for haplodiploids when competing in an outbreeding system with diploid-diploids. Relationships can be illustrated if both genetic systems are compared for within- and between-type matings. For within-type matings diploid-diploid females show the same relatedness to all grandchildren. Haplodiploid females have the same relationships through their daughters, but those through their sons are variable with a high relationship to granddaughters ($\frac{1}{2}$), and no relatedness to grandsons. Such differences in relatedness to grandchildren yield the same genetic payoff as production of grandchildren through daughters and as production of all grandchildren in diploid-diploid systems if males and females have the same value.

Various results could come from between-type matings, but here we consider a system where the genotype of the female determines the kind of males that are produced independent of the type of sperm supplied by the male. The haplodiploid genotype is only expressed in females and causes its bearer to produce haploid sons parthenogenetically and daughters from fertilized eggs. Diploid-diploid females produce diploid sons and daughters even when mated with haploid males. In such a system one type of between-type mating allows haplodiploid males a relative gain from high relatedness to their daughters and genetic representation in their sons' sons which would not occur in within-type matings. Reciprocal crosses involving haplodiploid females and diploid-diploid males (Fig. 1) produce sons that have only maternally derived genetic informa-

tion. The average relationship of grandchildren to their diploid/paternal grandmother through genes identical by descent is $\frac{1}{4}$ for females and 0 for males, yielding an average of $\frac{1}{8}$ instead of the $\frac{1}{4}$ expected from within-type matings. The diploid/paternal "grandmother" is not being related to what would otherwise be her grandsons. Relative gains for the haploid/paternal genotype from this asymmetric pattern of inheritance, the type of built-in advantage associated with the production of haploid males, may account for the establishment of some haploid/paternal populations.

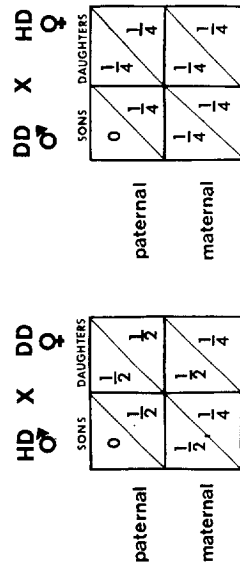


FIG. 1. Gain for haploids resulting from between-type matings. This principle is illustrated by relationship of offspring from between-type crosses to their paternal and maternal grandmothers as shown by genes shared i.b.d. Expected relationships are derived from the results of within-type matings and realized relationships from between-type matings.

Mating patterns in this qualitative model can also be used to develop a quantitative model that will allow estimation of the strength of selection for the haploid/paternal trait in a panmictic population. The spread of the character coding for the production of haploid males depends on the frequency of between-type matings. Let H represent alleles coding for diploid/paternal behavior and H' for the parthenogenetic production of males. For simplicity, parthenogenetically produced males are treated as diploids in which all genetic information is maternally derived (as if there was postmitotic doubling); these males produce the same sperm as haploids. Diploidy in males should have no effect on the spread of the haploid allele and is similar to the genetic system of the soft scales *Lecanium putmani* and *L. cerasifex* (Nur, 1972).

The frequencies of genotypes in each sex are assumed to occur in Hardy-Weinberg proportions but then are modified by a system of recursion equations (Tables Ia and b) that transform gene frequencies in relation to the type of offspring expected to be produced from the various mating combinations. Probabilities of each mating combination are determined in a nine-member matrix where matings occur at random; a represents the probability of each type of pairing.

TABLE Ia

H' AS DOMINANT

$H'H'_{m,k+1} = a_{11} + a_{22}/2 + a_{21}/2 + a_{12} + a_{13} + a_{23}/2$
$H'H_{m,k+1} = a_{13} + a_{33}/2$
$HH_{m,k+1} = a_{21}/2 + a_{22}/2 + a_{32}/2 + a_{33}/2 + a_{33}$
$H'H'_{f,k+1} = a_{11} + a_{12}/2 + a_{21}/2 + a_{32}/4$
$H'H_{f,k+1} = a_{13}/2 + a_{13} + a_{21}/2 + a_{22}/2 + a_{23}/2 + a_{31} + a_{32}/2$
$HH_{f,k+1} = a_{22}/4 + a_{23}/2 + a_{33} + a_{33}/2$

TABLE Ib

H' AS RECESSIVE

$H'H'_{m,k+1} = a_{11} + a_{12} + a_{13} + a_{21}/2 + a_{22}/2 + a_{22}/4$
$H'H_{m,k+1} = a_{22}/2 + a_{23}/2 + a_{33}/2 + a_{31} + a_{21}/2$
$HH_{m,k+1} = a_{22}/4 + a_{23}/2 + a_{32}/2 + a_{33}$
$H'H'_{f,k+1} = a_{11} + a_{12}/2 + a_{21}/2 + a_{22}/4$
$H'H_{f,k+1} = a_{13}/2 + a_{13} + a_{21}/2 + a_{22}/2 + a_{23}/2 + a_{31} + a_{32}/2$
$HH_{f,k+1} = a_{22}/4 + a_{23}/2 + a_{33} + a_{23}/2$

Males

	Females	HH	HH'	H'H'
HH		a_{11}	a_{21}	a_{31}
HH'		a_{12}	a_{22}	a_{32}
H'H'		a_{13}	a_{23}	a_{33}

The success of the mutant allele over any number of generations can be computed by iteratively assigning probabilities to each mating combination and then using the expected proportions for each of the kinds of matings to predict frequencies of genotypes in the succeeding generation (Table IIa and b).

The rate of the H' allele has been considered for both dominant and recessive cases for an initial frequency of 0.01 and the results are shown in Figs. 2a and b. The dominant mutant rapidly rises in frequency to 0.9 in 86 generations after which the rate if increase drops off and only reaches 0.985 after 500 generations. This leveling off in the rate of increase is due to H'H' $\times$ H'H male-female matings in which the frequency of H' is typically lowered as compared to a similar mating where meiosis is unaffected. The recessive H' increases at a slow

TABLE IIa
DOMINANT

Type of mating		Offspring									
		Female					Male				
		H'H'	H'H	HH	H'H'	H'H	H'H	HH	H'H	HH	H
♀	♂										
H'H' × H'H'	H'H' × H'H'	1	0	0	0	0	0	0	1	1	0
*H'H' × H'H'	H'H' × H'H'	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	$\frac{1}{2}$
HH × H'	H'H' × H'	0	1	0	0	0	1	0	0	0	0
H'H' × H'H	H'H' × H'H	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	0	1	$\frac{1}{2}$	0
H'H' × H'H	H'H' × H'H	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	0	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	0
HH × H'H	H'H' × H'	0	1	0	0	0	0	0	1	0	0
H'H' × HH	H'H' × H'	0	1	0	0	0	0	0	1	0	0
H'H' × HH	H'H' × H'	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0
HH × H'H	H'H' × H'	0	1	0	0	0	0	0	1	0	0
HH × H	H'H' × H	0	1	0	0	0	0	0	1	0	0
HH × H	H'H' × H	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0
HH × H	H'H' × H	0	1	0	0	0	0	0	1	0	0

TABLE IIb
RECESSIVE

Type of mating		Offspring									
		Female					Male				
		H'H'	H'H	HH	H'H'	H'H	H'H'	H'H	HH	H'H	H'
♀	♂										
H'H' × H'	H'H' × H'	1	0	0	0	0	0	0	0	1	1
H'H' × H'	H'H' × H'	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{2}$	0	0	0
HH × H'	H'H' × H'	0	1	0	0	0	1	0	0	0	0
H'H' × H'H	H'H' × H'H	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	0	0	0	1	1
H'H' × H'H	H'H' × H'H	$\frac{1}{4}$	$\frac{1}{4}$	$\frac{1}{2}$	$\frac{1}{4}$	$\frac{1}{4}$	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0
HH × H'H	H'H' × H'	0	1	0	0	0	0	0	0	0	0
H'H' × H'H	H'H' × H'H	1	0	0	0	0	0	0	0	1	1
H'H' × H'H	H'H' × H'H	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{2}$	$\frac{1}{2}$	0	$\frac{1}{2}$	0	0	0
HH × H'H	H'H' × H'	0	1	0	0	0	0	0	0	0	0
H'H' × HH	H'H' × H'	0	1	0	0	0	0	0	0	1	1
H'H' × HH	H'H' × H'	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0	0	$\frac{1}{2}$	$\frac{1}{2}$	0	0
HH × HH	H'H' × H'	0	1	0	0	0	0	0	0	1	1

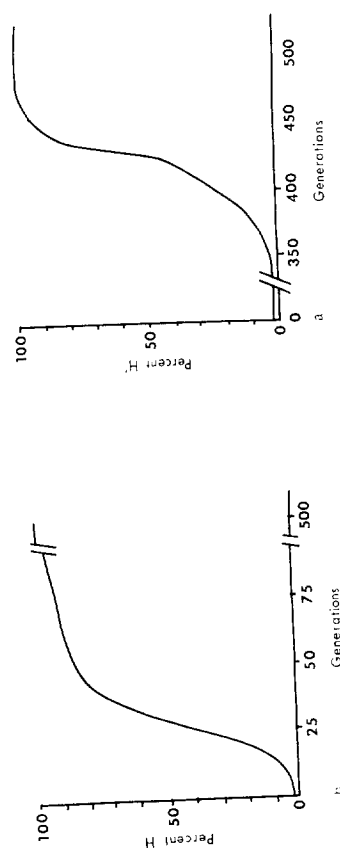


FIG. 2. (a) Results of simulation showing the spread of the dominant H' allele.
(b) Results of simulation showing the spread of the recessive H' allele.

rate initially and then rapidly rises toward fixation. The slow start-up here is due to the low frequency of expression of the recessive allele. As that allele increases in frequency, it is expressed more and more often and the opportunity for gain from between-type matings increases dramatically. In both cases, the rate of change is entirely determined by the frequency of the genotypes in the preceding generation. Substitution of other, higher initial frequencies for the H' allele will follow an abbreviated course similar to the one described in Figs. 2a and b.

Two important assumptions of this model must be considered before we can weigh its relative importance as a factor explaining the evolution of male haploid systems. We have treated haploid males and diploid males as if they are of the same quality. In earlier discussions, it was shown that haploids can generally be expected to be inferior, at least when they are first produced. Following the approach used by Hartl and Brown (1970), who assume that some low level of unfertilized eggs exists in the population, there is a context that allows for the selective improvement of haploid males. Over time the haploids should approach the selective improvement of haploid males. Moreover, through the appearance of an H' mutant, which causes its bearer to produce an increased fraction of haploid sons, eventually the exclusive production of haploids should spread as in the above simulation. Perhaps the greatest difficulty with a hypothesis relying on gains from producing parthenogenetic males is in finding sex-determining systems in antecedent diploid populations that are compatible with the proposed pattern of transition to haplodiploidy. If this pattern of transition were to occur in a population where males were initially heterogametic, important changes would seem to be necessary to generate the typical haplodiploid pattern of sex determination. There are two possible routes by which such a transition might occur. The first involves females that develop the ability to override the effect of sex determination of heterogametic males. This may occur for a few generations, but severe problems arise in the offspring of heterogametic females, since they will produce

male and female zygotes without X chromosomes. This may be unimportant if the X's carry little more information than a switch to control maleness and femaleness, but if effective development cannot proceed without an X chromosome, the mortality of these zygotes is likely to outweigh any gains from the production of haploid males.

Females who selectively kill sperm without X's could produce haploid males and diploid females with great ease. Mothers need only increase the fraction of haploid males in order to produce a balanced sex ratio. Although this appears a simple solution, there are reasons to suspect that it may not be effective. Any attempt by females to kill non-X sperm would place a strong selective pressure on sperm to escape whatever detection mechanism is used. For example, non-X sperm might mimic the appearance of X-bearing sperm. Though I know of no case where differential sperm killing is effective, its success would be dependent on use of some character that is not easy to conceal. It may be possible that differential killing can go on long enough so that haploid males, who produce only X-bearing sperm, would out compete diploids in multiply mated females in whom none of the sperm of haploids are killed, while one-half of those of diploids are killed. The replacement of diploid by haploid males would eliminate the need for sperm killing and might occur before non-X sperm could develop sufficient genetic changes to avoid these effects. Dominant Y systems with heterogametic males seem to present even more problems and will not be considered here.

Perhaps a simpler pathway to haplodiploidy transition may occur where females are heterogametic. An XO female need only allow X-bearing gametes to begin development before being fertilized in order to produce an unbiased sex ratio. Presumably, the already developing embryo would resist fertilization and retain its haploid autosome plus an X chromosomal complement. Non-X eggs which begin development only after being fertilized develop as females since all sperm from males contains the X chromosome. Such a system does not allow females the simple means of varying sex ratios evidently used in some species. Nevertheless, in outbreeding populations, such control is not necessary and its presence has not been established in a large number of haplodiploid species.

There appear to be few haplodiploid groups where closely related diploid species have heterogametic females. However, in the case of parahaploid coccids, sex determination follows a pattern similar to what would be expected if females were the heterogametic sex. Selective elimination of paternal genetic information in eggs of germ line cells implies the presence of genetic or cytoplasmic cues derived from the mother. Visible color differences in eggs that develop as males and females in some scale insects (Brown and Bennett, 1957) support the notion of sexual predetermination by the female. Kerr (1974) describes several mechanisms in bees in which females appear to be heterogametic. Although these systems have probably developed long after the advent of haplodiploidy, their presence suggests some lability in sex-determining systems.

B. Resistance to Driving Chromosomes

The tendency for one of a pair of homologous chromosomal elements (including sex chromosomes) to appear in a greater than random proportion of zygotes is known as meiotic drive. Unrestricted drive may lead to the loss of the nondriving element, and unchecked drive involving sex chromosomes of the heterogametic sex may lead to severe sex ratio deprivations and the extinction of one sex and ultimately the population (Hamilton, 1967, describes these events in detail). Females able to produce haploid males may be able to override the effects of driving sex chromosomes in their sons. These genotypes should spread because of their ability to produce the sex in short supply.

The relative success of haplodiploidy as a solution to driving sex chromosomes depends on the system of sex determination. For heterogametic females, male haploidy provides no obvious solution because abatement of drive can occur only in males. Therefore, only in initially heterogametic males can such a model be effective. This is restricted further to cases where there is no strong Y chromosome, since females cannot provide Y chromosomes and all genetic information is maternally derived. Drive of either the X chromosome or of sperm containing no X could enhance selection for male haploidy, but two factors suggest that driving X's are a more likely case. First, there is no chromosomal element that stands to gain directly from driving non-X-bearing sperm. Selection at all levels should oppose this kind of chromosomal behavior. In the case of the driving X, at least some elements in the sex chromosome have an opportunity for short-term gain. Second, a driving X chromosome will cause an overproduction of females and a shortage of males. Haplodiploid females can produce males who will be subject to a reduced level of sexual competition for an excess of females. These conditions suggest that haploid males that are weak relative to diploids may still enjoy a reasonable level of mating success.

Brown (1964) described a model based on chromosomal drive, somewhat different than the one discussed above, in which haplodiploidy was proposed as a solution to driving chromosomal elements throughout the genome. Driving chromosomes were considered to carry disadvantageous characters in addition to their tendency to spread. Haplodiploidy provided a potential barrier to this form of drive. However, Brown discounted drive as a factor in haplodiploid evolution, stating that "adaptations to homozygosity must precede the evolution of male haploidy and similar systems. Meiotic drive would presumably be less apt to occur in species so adapted since inbreeding per se would tend to eliminate heterozygosity on which drive depends."

Although this observation is correct in most cases, for the specific instance I have discussed, that of driving sex-chromosomes, experience shows that heterozygosity based on sex chromosome dimorphism need not be lost by inbreeding. Hence, contrary to Brown's argument, inbreeding may not only have little effect on the tendency for drive to occur but might also assist in

increasing the mating success of haploid males, and by shielding them from competition with diploids, enhance their ability to compete sexually.

Assessment of the ultimate value of haplodiploidy as a potential block to drive is dependent on estimates of the frequency at which driving sex chromosomes occur, likelihood that haploid males will be present in the populations, and prospects for successful matings by the haploids. Only a small proportion of the populations with driving chromosomes will lead to establishment of haplodiploid populations. Even, so, given sufficient time, benefits provided by haplodiploidy in blocking drive may contribute to instances of transition to haplodiploidy.

EVALUATING MODELS OF HAPLODIPLOID EVOLUTION

A. *Elimination of Deleterious Recessives and Protection of Haploid Males*

In varying degrees, the models presented here allow haploid males to escape the problem of expressing disadvantageous recessive alleles. Populations with close inbreeding are preadapted for the survival of haploids because disadvantageous alleles have been expressed and eliminated. Haploid males produced in response to sperm shortage may have more difficulty, since they are more likely to carry disadvantageous recessives. Yet because males are produced at little or no added cost to their parents, they should continue to be made even if they obtain only infrequent matings. The presence of haploids may reduce the proportion of recessive alleles, but the importance of this effect is dependent on the level of success among these haploid males. Successful matings by haploids should commonly increase the frequency of alleles which allow haploids to survive. This may not occur in all cases, such as when alleles disadvantageous as homozygotes are maintained by advantage in heterozygotes. Low levels of success by haploid males may be insufficient to counteract gains for these alleles in heterozygotes.

Removal of disadvantageous alleles is very much related to the "protection" of haploid males. Haploids in inbred populations are not forced into direct competition with diploids, except when occasional outbreeding occurs. With no direct competition, problems of dosage compensation and other effects likely to reduce absolute fitness may be unimportant if the males can inseminate their sisters. Genotypes producing haploid males under conditions of the sperm shortage model are not directly protected from this type of competition. Although the continued persistence of haploids is not likely to be strongly affected by their success in mating, success is necessary to enhance their production and eventually lead to the replacement of diploids. Small differences in the quality of males may lead to large differentials in productive success (see Williams, 1975) so the improvement of haploid males may occur very slowly.

Strongly driving sex chromosomes may place haploid males in situations where

they are not forced to compete directly with diploid males. This is similar to the conditions created by close inbreeding. Even minimal ability to survive and mate may allow the spread of male haploidy but it must be established over a relatively short time. Unlike inbreeders, however, haploids in initially outbreeding populations where drive is occurring are likely to express detrimental recessive alleles. Where chromosome drive is less strong the establishment of viable haplodiploid males is less rapid, but there is a corresponding reduction in gains for haploid males, because there are more diploid male competitors.

B. *Sperm Shortage and the Evolution of Parahaploid and Related Systems*

Models which require sperm shortage cannot operate in cases where females use sperm to initiate development of male zygotes. These include models proposed by Brown (1964) and Hartl and Brown (1970) and my own involving mother-son mating. Sperm is required to produce males in some coccids (see above) and in mites of the families Dermanyssidae and Phytoseiidae (reviewed by Oliver, 1971, 1977). It is possible that gynogenetic and related systems arose from haplodiploid instead of diploid origins. Nur (1972) showed that the paternal genetic information in some parahaploid male coccids is expressed. These males may be of higher fitness than comparable haploid males. Gynogenetic production of males may have the effect of assisting the development of eggs. However, the complexity of conditions necessary to produce haplodiploid systems implies that these are unlikely routes for the origins of parahaploid-like systems. For such an evolutionary pathway to operate, the problem of sperm shortage which led to haplodiploidy must have been alleviated before the transition to these sperm-requiring patterns of reproduction could have occurred. Thus the intermediate pregynogenetic haploid males must be of sufficient quality to replace diploids, but also of sufficiently low quality that there is some advantage in a change to a sperm-requiring form of reproduction.

C. *Sex Determination*

Of the problems associated with haplodiploid evolution, those related to sex determination are among the most difficult to evaluate. The system of sex determination in diploids most likely to lead to haplodiploidy in all but one of the models discussed here has not been shown to exist in any diploid species. No sex-determining systems have been demonstrated among diploids in which only the number of X's accounts for sex differences. White (1973) in a summary of his discussion of sex-determining systems, states:

It is fairly obvious that sex determination must depend on genetic balance rather than on a dominant Y throughout those groups where many of the species are XO in the male sex. Thus the great majority of the species in the orthopteran insects (i.e., roaches, mantids, phasmantids, and Orthoptera (Saltatoria), including the crickets, tettigoniids and grasshoppers, and Odonta

(dragonflies)) have XO males and all other types of sex-determining mechanisms in these groups are obviously derivative and in a recent evolutionary sense. We must accordingly conclude that sex determination throughout at least one or two main branches of the phylogeny of winged insects was originally, and remains in most all other species, of the *Drosophila* type, depending on the balance between female-determining X-chromosomes and male-determining autosomes. (*italics added*)

However, this problem may be of little real significance if one considers the very small number of systems in which sex determination is really understood. For example, unless tested by changes in ploidy or in organisms that vary the number of X's, the XO system proposed above for outbreeding diploids would be identical to the *Drosophila* system White discusses. The sex-determining system suggested here as a prerequisite to most models of haplodiploid evolution cannot be excluded on the basis of what is known about the vast majority of most XO sex-determining systems. The inherent simplicity of this supposed pattern of transition in sex determination from diploid progenitors to haploids should not allow the absence of sufficient data on sexual systems to significantly diminish the importance of the proposed models. For the remaining model, based on gain from the parthenogenetic production of males, there are two patterns of sex determination that would allow the evolution of male haploidy. These are: (1) an XO female heterogametic sex-determining system, or (2) female override of the existing chromosomal system with sex determination based on induced cytoplasmic differences. There is little evidence of haplodiploid evolution in groups where progenitor females are known to be heterogametic. However, in sperm-requiring species that produce haploid males, sexual pre-determination either by chromosomes or by cytoplasmic factors may occur. James (1937) has described highly variable sex ratios in some sperm-requiring scale insects and Beardsley and Gonzalez (1975) interpret this as a possible instance of cytoplasmic sex determination. If sex is determined by maternally controlled cytoplasmic factors, then evolution of haplodiploidy via benefits from the parthenogenetic production of males may be effective in sperm-requiring species.

CONCLUDING REMARKS

It should be clear that there appears to be no easy solution to the problem of how haplodiploidy evolved. All models proposed so far have important difficulties that limit their effectiveness as general explanations of how diploid populations become haplodiploid. Some of the questionable aspects of these theories may be resolved when more information is collected about such things as the control of sex ratios.

Even with its limitations the inbreeding context seems the most likely

situation for the evolution of haplodiploidy because it resolves three important problems. Two of these have been alluded to above. Sheltering of weak males from sexual competition allows them to function with little or no loss to the selective unit. The potential twofold advantage provided by avoiding costs of sexuality, which seems an almost automatic result of haplodiploid reproduction, provides a strong force to overcome some of the barriers to the evolution of male haploidy. A third consideration is that this model provides an explanation for the prevalence of male haploidy and the absence of female haploidy. In inbred populations the fitness of reproductive units is highly dependent on the fecundity of females. Thus in contrast to males, inbreeding females are never buffered from factors that influence fitness. For this reason the inbreeding models would never predict the evolution of female haploidy.

Even though inbreeding models seem to provide the best general explanations for the evolution of male haploidy, in specific instances pathways to male haploidy specified by outbreeding models may be important. The multiple origins of haplodiploid and haplodiploid-like systems make it possible that this kind of genetic system may have evolved in many different ways. For each instance of transition to haploidy different models must be considered to determine which is most likely. In this paper I have attempted to outline some of the models which might be considered in such analyses and discuss some of the problems each such pathway poses for the transition to haplodiploidy.

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The Stationary Distribution of an Asymmetrical Model of Selection in a Random Environment

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The stationary distribution for the asymmetrical form of the SAS-CFF model of selection in a random environment is presented. Also presented are the conditions for the stable coexistence of K alleles. These conditions are the same as the conditions obtained from the classical constant-fitness model with the formal substitution of geometric mean fitnesses for the constant fitnesses of the classical model. Two examples are explored. In the "equally spaced" example, increases in the degree of asymmetry raise the homozygosity, which is accompanied by loss of alleles from the population. In the "best allele" example, increases in the degree of asymmetry raise the homozygosity without the loss of alleles. In both cases the frequency spectra are altered by the changes in the degree of asymmetry.

INTRODUCTION

The multiallele stationary density for the symmetric SAS-CFF model of natural selection in a random environment was provided by Gillespie (1977a). In the present paper this result will be extended to the asymmetric case.

The SAS-CFF model was developed to simultaneously account for observations on the quantitative genetics of fitness traits and on enzyme polymorphisms. The model incorporates a stochastic additive scale (SAS) that is a stochastic process reflecting spatial and temporal fluctuations in the environment as well as the additive nature of enzyme activity in heterozygotes, and a concave fitness function (CFF) that maps the stochastic additive scale onto fitness. More formally, we can describe the one-locus model by a series of postulates:

(I) Each homozygous genotype is characterized by a random variable, $Y_i(n, T)$, which will be called the enzyme activity of the genotype. The enzyme activity will generally fluctuate at random in both time and space, the arguments referring to the n th patch in the T th generation. The i refers to the i th allele.

(II) The enzyme activity of a heterozygote is exactly intermediate between the activities of the two associated homozygotes. If we refer to the activity of the