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Quarterly Review of Biology, Volume 59, Issue 3 (Sep., 1984), 257-290.

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Quarterly Review of Biology
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DESTABILIZING HYBRIDIZATION, GENERAL-PURPOSE GENOTYPES AND GEOGRAPHIC PARTHENOGENESIS

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ABSTRACT

The ecological and genetic correlates of parthenogenesis are clarified by focusing upon two of the major challenges that confront a newly arisen parthenogen: the genetic disruption that results from backcrosses with sexual relatives, and the evolution of a highly generalized genotype. Both of these factors have been ignored in previous theories of the evolution of reproductive systems. Yet, the geographic ranges, ecological characteristics, elevated ploidy levels, and hybrid origins of many parthenogens, as well as the widespread suppression of recombination in automicts, are consistent with expectations derived from the destabilizing hybridization and general-purpose genotype hypotheses. Whereas the support for these hypotheses is broad, much of the evidence is circumstantial; experimental tests would allow an evaluation of the proposed hypotheses and the more traditional alternatives based on differential colonization, competitive, and coevolutionary abilities. An appreciation of the stringent requirements for a successful transition to parthenogenesis may help to explain its uneven phylogenetic distribution. The relevance of parthenogenesis to the biological control of pest species also requires attention.

INTRODUCTION

CHARLES BONNET'S (1745) critical experiments with aphids conclusively demonstrated that the propagation of offspring from unfertilized eggs (parthenogenesis) can occur in animals. Even then, however, many thought that parthenogens were masquerading as hermaphrodites or that they were aberrant individuals reproducing themselves vegetatively, as do plants. August Weismann's cytological work laid these arguments to rest at the end of the 19th century. Since then, numerous parthenogenetic species have been identified in phylogenetically diverse groups of animals. For example, nearly fifty species of obligately parthenogenetic vertebrates have been discovered in the past fifty years. As White (1973) has emphasized, virtually all well-studied animals (including humans) show

some potential for parthenogenetic reproduction; many cases probably remain to be discovered.

In the majority of cases, parthenogenesis is thelytokous with all asexually produced progeny being females. However, haplodiploid insects utilize an arrhenotokous parthenogenetic system. In this case, unfertilized eggs develop into males, whereas fertilized eggs give rise to diploid females. Unless otherwise noted, my discussion will concentrate on obligate thelytoky.

Parthenogenesis is rare in comparison to sexuality (amphimixis), but it is not simply a pathological aberration, although in many cases it may originate as such. Species that employ this reproductive strategy are of theoretical as well as of practical interest. Early research centered on the cytological mechanisms that allow parthenogens to replicate but, more recently, ecologists and

evolutionary biologists have focused on the question of how asexual organisms persist in evolutionary time. Whereas considerable controversy still exists over the adaptive significance of sexual versus asexual reproduction (Ghiselin, 1974; Williams, 1975; Maynard Smith, 1978; Bell, 1982; Shields, 1982), there is general agreement that newly arisen asexual lines are confronted with many ecological and evolutionary problems.

Limitations associated with the genetic systems of asexual organisms have earned them labels of evolutionary dead ends, blind alleys, and no-hopers (Darlington, 1939; Stalker, 1956a; Mayr, 1970; Uzzell, 1970; Uzzell and Barry, 1971; Smith, 1971; White, 1973; White Cheney, and Key, 1963; Maynard Smith, 1978). To many, it has seemed reasonable to assume that the level of genetic variance and the rate at which it is produced are reduced in asexual organisms, because they do not undergo meiotic recombination. This restricted reservoir of genetic variance is expected to render asexual lineages exceptionally sensitive to environmental perturbations and to encumber them in their coevolutionary interactions with sexual organisms (Selander and Hudson, 1976; Glesener and Tilman, 1978; Jaenike, 1978; Hamilton, Henderson, and Moran, 1981; Rice, 1983). It has often been suggested that heterozygosity will ultimately increase in an asexual lineage, but the accumulation of mutations is generally perceived as a deleterious process (Muller, 1964).

Despite these disadvantages, there are many parthenogenetic species that appear to be remarkably successful by most standards. An understanding of why these species persist would help to dispose of the evolution-of-sex controversy and would also provide insight into numerous biological problems that are best studied in clonally reproducing organisms. The few notable searches (Vandel, 1928, 1931; Suomalainen, 1950; White, 1973, 1978; Cuellar, 1977a; Glesener and Tilman, 1978) that have been made for general patterns among parthenogenetic species have not for the most part offered satisfying explanations for the observed patterns (Bell, 1982). This shortcoming has been primarily a consequence of the paucity

of good population genetic and ecological data for parthenogenetic species (White, 1973). Over the past decade, however, enough progress has been made in this area to pose specific hypotheses for the distribution, behavior, and genetic properties of obligate parthenogens and their sexual parental species. Although this review is confined to animals, perhaps botanists will recognize parallel evidence in their own subjects. In fact, the concept of the general-purpose genotype, which I will address in detail, was first offered by Baker (1965) as an explanation for the geographic distribution of weedy plants.

GEOGRAPHIC PARTHENOGENESIS

As defined by Vandel (1928), the term "geographic parthenogenesis" simply refers to the fact that parthenogens tend to occupy ranges different from those of their close, sexually reproducing relatives. Although Vandel emphasized that parthenogenetic species have more northerly distributions, he was careful to point out cases of geographic parthenogenesis that are unrelated to latitude. He also recognized instances of coexistence of parthenogenetic and sexual races. Later, Vandel (1940) suggested that polyploidy was involved, but he did not give a mechanistic explanation for the geographic patterns he observed.

More recently, such an explanation has been offered by Ghiselin (1974), Levin (1975), Glesener and Tilman (1978), and Hamilton, Henderson, and Moran (1981), who have noted that, compared to their sexual relatives, parthenogens often occur at higher altitudes, on islands or in island-like habitats, in xeric environments, or in disturbed habitats. The hypothesized common denominator of these environments is a reduced incidence and diversity of biotic interactions. The greater species and genotypic diversity in the opposite set of environments is expected to provide a significant element of environmental uncertainty that can only be sustained, in the long run, by sexual reproduction of genetically variable progeny.

An alternative hypothesis that has been strongly advocated by Bell (1982) is the "tangled bank" model, which states that

sexual lineages are dominant in spatially complex environments because they produce genetically diverse progeny that are capable of occupying a variety of the available niches. On the assumption that clonal populations have a narrower ecological range than their sexual relatives, Bell (1982) has concluded that obligate asexuals will tend to be displaced except in environments that are kept in a permanently undeveloped state by frequent disturbances.

As is true of nearly all hypotheses that relate to the evolution and maintenance of sex, neither the biotic-uncertainty nor the tangled-bank models has been empirically tested. Both models undoubtedly contain elements that are important factors in explaining the evolutionary maintenance of sex but, for several reasons, they do not provide a satisfactory explanation for the geographic distribution of parthenogenesis. Unless one is willing to invoke the "cost-of-producing males" argument, which has almost certainly been exaggerated (Bell, 1982; Shields, 1982; see below), neither model explains why most sexual lineages have failed to expand throughout the range occupied by asexual-sexual complexes. Moreover, they do not adequately account for the numerous striking examples of coexistence between obligate parthenogens and their sexual ancestors. These two models, and indeed virtually all evolution-of-sex models, critically rest upon two assumptions: that incipient parthenogens are reproductively isolated from their sexual parental species, and that clonal lineages are narrowly adapted in comparison to sexual populations. Neither of these assumptions is consistent with the existing data reported in the literature on parthenogenesis.

Two alternative and interactive hypotheses may be proposed to account for geographic parthenogenesis: the destabilizing hybridization hypothesis; and the general-purpose genotype hypothesis. Cases of disjunct distributions are often likely to be a consequence of the deleterious genetic effects of hybridization between parthenogens and their sexual relatives, rather than a result of inferior competitive or coevolutionary ability of the parthenogens. Coexistence of sexual and asexual forms becomes possible

when interference mechanisms that result from hybridization are absent. In addition, there is evidence that parthenogens often have less restrictive habitat requirements (i.e., possess more generalized genotypes) that allow them to occupy more extreme environments and broader geographic ranges than their sexual relatives (when destabilizing hybridization is not a problem). Whereas the general significance of destabilizing hybridization for geographic parthenogenesis has received scant attention, the general-purpose genotype hypothesis is not an entirely new idea. Indeed, Vandel (1940) expressed a similar conclusion, as did some later reviewers (Suomalainen, 1950; White, 1970; Williams, 1975; Maynard Smith, 1978).

GENETIC INTERFERENCE AND DISJUNCT DISTRIBUTIONS: THE DESTABILIZING HYBRIDIZATION HYPOTHESIS

The assumption of complete reproductive isolation between sexual and asexual lineages appears to be so well accepted among theoreticians that it is almost never explicitly stated. Yet any violation of this assumption would be serious enough to invalidate most existing hypotheses for the evolution and maintenance of sex, since virtually all of these hypotheses assume two distinct gene pools that interact only through their competition for resources. Bell (1982) recognized the importance of the reproductive isolation requirement for evolution-of-sex theory, and especially for the tangled-bank model, but concluded (p. 355) that ". . . a strong correlation between parthenogenesis and polyploidy . . . leads to the crucial consequences that thelytokous and amphimictic populations of the same species will commonly experience complete reproductive isolation, even if they are sympatric." However, the few existing empirical investigations of the genetic consequences of mixing asexual and sexual genomes, as well as a large descriptive literature, indicate that several powerful interactions can result in the rapid displacement of parthenogenesis by sexuality (or vice versa) when males are indiscriminate in areas of sympatry. Six potential mechanisms of destabilizing hybridization are outlined below.

Dominance of Genes Coding for Sex

White (1973) suggested that males from sexual strains might introduce into parthenogens dominant "bisexuality genes" that would result in an immediate breakdown of parthenogenesis. There are no definitive examples of any such simple mechanism, although results from crosses between aneuploid parthenogenetic and diploid sexual forms of the tick *Haemaphysalis longicornis* are suggestive (Oliver, Tanaka, and Sawada, 1973). Work with experimentally established parthenogenetic lines of *Drosophila* has repeatedly demonstrated that the capacity for parthenogenesis is immediately lost upon backcrossing, but this is for very different reasons than those envisioned by White (Templeton, 1982, 1983).

Expression of Genes Coding for Parthenogenesis Dependent on Their Genetic Background

Experiments on hybridogenetic and gynogenetic fish of the genera *Poeciliopsis* and *Poecilia* provide support for the conversion of unisexuality to bisexuality via the introgression of a bisexual genome by more complex mechanisms. Hybridogenesis, known only from *Poeciliopsis* and the European frog *Rana esculenta*, is a form of unisexual propagation in which an all-female population depends on the donation of spermatozoa from a bisexual host species for the fertilization of its haploid eggs. Both maternal and paternal genomes are expressed in the all-female progeny, but only the maternal genes are transmitted through the eggs. With this mode of inheritance, the maternal haplotype remains intact from generation to generation. Gynogenesis is similar to hybridogenesis except that spermatozoa from the host species simply activate cleavage of the eggs; hence offspring are genetically identical to their mothers (with the possible exception of paternally derived mitochondrial genes, T. Uzzell, pers. comm.).

In the sense that gynogenesis is a form of propagation by means of unfertilized eggs, it can be considered to be a special form of parthenogenesis. On the other hand, hybridogenesis requires fertilization and is therefore not a form of parthenogenesis. Nonetheless, since hybridogenesis involves the propagation of all-female lines through

the eggs, it bears a certain resemblance to parthenogenesis, and so I have chosen to include it in my discussion. Note also that since gynogens and hybridogens are functionally parasitic on a closely related sexual species for sperm, the sperm-donating species is referred to as a host.

Three species of hybridogenetic fish occur in the genus *Poeciliopsis*. Each is a diploid hybrid between two diploid parental species (Vrijenhoek, 1979). The normal host species of *P. monacha-lucida* (a hybrid of *P. monacha* and *P. lucida*) is *Poeciliopsis lucida*. All offspring of such matings, with rare exceptions, are diploid hybridogens; the *monacha* haplotype is inherited intact (Schultz, 1977). When the contributing paternal genotype is *P. monacha*, however, the progeny are no longer hybridogenetic but are fully fertile males and females. If those offspring are allowed to interbreed or to backcross with *P. monacha*, they produce bisexual progeny (Schultz, 1969; Leslie and Vrijenhoek, 1980). The reconstitution of the *monacha* genome by this type of hybridization in part explains the reconversion to bisexuality. But there is more to this case than a simple conversion to bisexuality. Even with artificial insemination, a large proportion of the crosses produce either no progeny or inviable progeny, and most F₁ clutches are dominated by one sex. This may be a consequence of the complex sex determination system found in most cyprinodont fishes (White, 1973).

The other two hybridogenetic *Poeciliopsis* (*P. monacha-occidentalis* and *P. monacha-latidens*) also contain a *monacha* haplotype. In neither case is *P. monacha* the host species, although *P. monacha-occidentalis* is capable of switching to *P. lucida* (Leslie and Vrijenhoek, 1980). This situation suggests that there is something special about the *monacha* genome, such that when it is placed in a heterospecific background there is an alteration of normal meiotic activity. Restoration of bisexuality by backcrossing in this case is therefore not a consequence of the dominance of bisexuality genes but of the dependence of *monacha* genome expression on its genetic background. Inasmuch as the detection of progeny of hybridogen \times *P. monacha* crosses in the field is nearly impossible, nothing is

known of the frequency of such events in natural populations. The implications are clear, however, and it is of interest to note that *P. monacha-lucida* and *P. monacha* coexist only in limited areas of western Mexico, where the latter has exclusive use of headwaters (Schultz, 1971; Vrijenhoek, Angus, and Schultz, 1978).

Gynogenetic systems appear to be more refractory to the introgression of foreign genomes. The spermatozoa of several different conspecifics will activate the eggs of gynogenetic *Poeciliopsis* (Schultz, 1969) and *Poecilia* (Haskins, Haskins, and Hewitt, 1960; Turner, Brett, Rasch, and Balzano, 1980). This is also the case in the marine oligochaete *Lumbricillus lineatus* (Christensen, Jølnes, and Berg, 1978). Occasional crosses between members of other species pairs do result in a return to bisexuality, however. For example, when the diploid gynogen *Poecilia formosa* was mated to distantly related *P. vittata*, the F₁ progeny were fully fertile males and females (Haskins, Haskins, and Hewitt, 1960). Crosses between the F₁ offspring produced progeny indistinguishable from *P. vittata*, as did backcrosses to *P. vittata*, but backcrosses to *P. formosa* produced mixed broods of gynogens and bisexuals. When the two species were maintained in large pools for several months, sexual reproduction began to displace gynogenesis. It is important to point out, however, that some crosses between *P. formosa* and *P. vittata* produced only normal gynogenetic progeny. These results suggest that the barrier between gynogenesis and sexual reproduction is a fine one whose penetration depends on the genomes of both host and gynogen. Once this barrier has been broken, backcrosses of the F₁ with the gynogenetic form may result in a rapid conversion to bisexuality. The potential for such genetic disruption may be particularly strong in the case of poeciliids, since subdominant males are often indiscriminate in their choice of mates (Moore and McKay, 1971).

Simultaneous Conversion to Odd Ploidy Level and Sexuality

Hybridogenesis and gynogenesis are really rather rare and exceptional unisexual

systems. When genes from a male of a sexual race introgress into a normal (host-free) asexual genome, a frequent and equally important consequence will be an elevation of the hybrid's ploidy level by one. White (1973) was fully aware of this possibility, since he posed his hypothesis (above) as a mechanism for the inhibition of the origin of polyploid clones. Should the new hybrid be sexual and of odd ploidy level, chromosomal imbalance in the sex-determining mechanism could result in developmental abnormalities in the sex organs. Even if that did not occur, successful reproduction very likely would be hampered by problems during meiosis, by production of aneuploid gametes, or by production of mosaic progeny. The frequency of these hybridization events and the relative population sizes of parthenogenetic and sexual races will determine whether such an interference mechanism will result in the local exclusion of either race. Selection for prezygotic isolating mechanisms (including habitat isolation) in both races could also occur.

Polyploidization and subsequent sterilization may be responsible for the geographic separation of the diploid parthenogenetic grasshopper *Warramaba virgo* from its unnamed diploid parent species, P169 and P196 (White, Contreras, Cheney, and Webb, 1977; White and Contreras, 1979). Despite the fact that *W. virgo* may have originated 50,000 to 100,000 years ago, the parthenogens readily mate with sexuals in the laboratory. All offspring are triploids, however; the males are invariably sterile, and the females have visibly abnormal ovaries, largely sterile eggs, and extremely limited parthenogenetic capacity. Further support for the importance of genetic disruption in this system is obtained from Atchley's (1978) demonstration that significant character displacement exists in areas of close proximity of *W. virgo* and P196.

Another example of this mechanism of destabilizing hybridization is provided by four parthenogenetic races of the rock lizard, *Lacerta*, found in the Caucasus. Each asexual race is thought to have originated by interspecific hybridization more than 5,000 years ago (Uzzell and Darevsky, 1975), and except for a few narrow zones of contact, the

distribution of the parthenogen is largely disjunct from that of the parental forms. The parthenogenetic females exhibit some courtship behavior (Darevsky and Kulikova, 1964; Darevsky, 1966), and hybrids between the parthenogens and sexuals are relatively common in areas of parapatry. Although the hybrid offspring do express some male secondary sex characteristics, they are always sterile triploid females. Their ovaries are abnormal and extremely reduced in size, and there is no maturation of their oocytes. Darevsky and Danielyan (1968) have experimentally demonstrated the significance of destabilizing hybridization by releasing males of the sexual species, *L. saxicola*, into isolated populations of parthenogenetic *L. armeniaca* and *L. unisexualis*.

Cases of natural hybridization between diploid parthenogenetic whiptail lizards (*Cnemidophorus*) and their diploid, sexual parental species have also been widely reported in the southwestern United States, where several successful triploid parthenogenetic races are known to occur (Maslin, 1971). The consequences of hybridization in this group appear to be variable, however. Although some taxonomic confusion and interpretative differences exist (Taylor and Medica, 1966; Wright and Lowe, 1967; Maslin, 1971; Cuellar, 1974), crosses between *Cnemidophorus neomexicanus* (a diploid parthenogen) and one of its diploid parental species, *C. inornatus*, appear to provide another example of conversion to polyploid sexuality with resultant sterilization of progeny. Hybrid *neomexicanus-inornatus* are triploid and of both sexes. Although the possibility of some functional sperm production by hybrid males has not yet been satisfactorily ruled out, most males that have been examined have atrophied testes, incomplete spermatogenesis, or abnormal spermatozoa (Taylor and Medica, 1966; Christiansen and Ladman, 1968). *C. inornatus* is unusual among *Cnemidophorus* species in that it co-occurs with its daughter species or occupies adjacent habitat (Cuellar, 1977a, 1979). The exact mechanism for this phenomenon has not been verified, but Wright and Lowe (1978) have suggested that *C. neomexicanus* is expanding its range at the expense of *C. inornatus*.

Conversion to a New Polyploid, Parthenogenetic Race

There is no inherent reason why sexual gene systems should completely dominate those coding for obligate parthenogenesis. Therefore, an asexual \times sexual cross could result simply in the production of a new clone with elevated ploidy level. The consequences of this type of hybridization would depend on the relative competitive abilities of the parental populations and the newly synthesized clones. Nevertheless, allopolyploid parthenogens are common, and this fact provides compelling evidence that such hybridization events are important modes of origin for parthenogenetic races. Of the 63 parthenogenetic weevils that have been discovered, all but three are triploid or of higher ploidy (Takenouchi, 1981). All of these species are apomicts and have high levels of heterozygosity (Suomalainen, Saura, and Lokki, 1976), characteristics that argue strongly against an autopolyploid origin by fusion of multiple meiotic products. Presumably the polyploid asexuals originated from crosses between established parthenogenetic species and diploid males of a sexual species. Other examples exist for which genetic evidence strongly supports the origin of a new triploid parthenogenetic race by means of the fusion of a haploid sperm with a parthenogenetically produced egg: salamanders of the genus *Ambystoma* (Uzzell, 1964; Downs, 1978), members of the *Cnemidophorus tessellatus* complex (Neaves, 1969; Maslin, 1971), and certain gynogenetic clones of the *Poeciliopsis monacha-lucida* and *Poecilia formosa* complexes (Schultz, 1977; Rasch, Prehn, and Rasch, 1970; Turner, Balsano, Monaco, and Rasch, 1983). The genetic basis of many other triploid parthenogens has been evaluated to a less satisfactory extent: the gekko *Hemidactylus garnotti* (Kluge and Eckardt, 1969), the goldfish *Carassius auratus gibelio* (Cherfas, 1965), several dipterans including *Cnephia mutata* (Basrur and Rothfels, 1959), *Lundstroemia parthenogenetica* (Porter, 1971), and *Ochthiphila polystigma* (Stalker, 1956b), the spider beetle *Ptinus clavipes* f. *mobilis* (Sanderson, 1960), the chrysomelid beetle *Adoxus obscurus* (Suomalainen, 1965), the cockroach *Pycno-*

scelus surinamensis (Roth and Cohen, 1968), the tick *Haemaphysalis longicornis* (Oliver, Tanaka, and Sawada, 1973), the terrestrial isopod *Trichoniscus pusillus* (Vandel, 1928; Christensen, 1979), the root-knot nematode *Meloidogyne incognita* (Triantaphyllou, 1981), and the marine oligochaete *Lumbricillus lineatus* (Christensen, Jernes, and Berg, 1978).

*General Incompatibility between Gene Complexes
Coadapted to Parthenogenesis and Sexuality*

Sudden one-sided results of asexual \times sexual crosses may be rather exceptional. As with poeciliids, the genetic basis for reproductive systems in other animals appears to be complex and polygenic. From crosses between males of the diploid moth *Luffia lapidella* and its parthenogenetic relative *Luffia ferchaultella*, Narbel-Hofstetter (1962) obtained parthenogenetic offspring (perhaps unfertilized eggs), a large number of intersexes of all degrees, and a few functional male and female sexuals. Similar results have been obtained from crosses between amphimictic and gynogenetic flatworms (Benazzi-Lentati, 1966). In crosses between genetically marked thelytokous (female-producing parthenogenetic) and arrhenotokous (male-producing parthenogenetic) races of the hymenopteran *Aphytis mytilaspidis*, Rössler and DeBach (1972) found that fertilized eggs produced both types of female progeny. Selection for parthenogenetic lines of *Drosophila* (Stalker, 1954; Carson, 1967; Templeton, 1979) and for male fertility in synthesized tetraploid sexual strains of the silkworm *Bombyx* (Astaurov, 1972) proceeds gradually. That fact further indicates that the barrier between parthenogenesis and sexuality is polygenic.

Asexual \times sexual hybridizations frequently result in disruptions of sex determination, sexual development, and gametogenesis (i.e., a general breakdown in the reproductive integrity of the hybrid progeny) but hybrid inferiority may often be more than a simple consequence of imbalance in genes coding for reproductive systems. In laboratory strains of *Drosophila mercatorum*, genomic incompatibilities between incipient asexual strains can result in a severe reduction in the parthenogenetic

capacity of their parthenogenetically produced hybrid offspring (Templeton, 1979; Templeton, Sing, and Brokaw, 1976). (In this case, the reproductive systems of the two hybridizing strains were identical.) Frequently there are also abnormalities in the fundamental developmental processes of such progeny. In *D. mercatorum* parthenogenesis is almost entirely by fusion of two genetically identical cleavage nuclei, so that the reproductive transition to parthenogenesis is extremely selective; only those thelytokous genomes that are viable in a totally homozygous state are promoted. Apparently, such genomes can arise in a variety of mutually incompatible ways.

In light of the polygenic basis for the underlying cytological mechanisms of parthenogenesis and the intense selection for reproductive efficiency that must operate on newly arisen clones (Templeton, 1982, 1983), it seems likely that successful parthenogens may frequently possess radically different genetic constitutions from their bisexual relatives. Some deleterious mutations that accumulate in parthenogenetic lines may only be fully expressed when reinserted into a sexual genetic background (Leslie and Vrijenhoek, 1980). Thus, the incompatibility between genomes coadapted to parthenogenesis and those coadapted to sexuality may be in large part responsible for many of the known cases of reproductive incompetence of hybrids from asexual \times sexual crosses. This is, of course, frequently the case in interspecific hybridization of sexual species.

*Conversion of Sexuality to Asexuality by
Parthenogenetically Produced Males*

In all of the asexual-sexual interactions considered so far, sexual males have actively contributed to hybrid progeny. A different sort of hybridization, suggested by both Jaenike and Selander (1979) and by Hebert (1981), is one in which asexuality genes are spread by parthenogenetically produced males in zones of overlap with sexual relatives. If a mutant gene or gene complex that confers parthenogenetic ability upon its carrier does not suppress the production of functional males, a contagious spread of asexuality might occur, the rate depending

on the magnitude of the short-term advantages of sex. Jaenike proposed this model to explain the spread of parthenogenesis in hermaphroditic earthworm populations, while Hebert invoked it as a possible mechanism for the displacement of cyclical by obligate parthenogenesis in *Daphnia*. An equally effective barrier to coexistence might occur if spermatozoa transmitted by a parthenogenetic race resulted in the sterilization or production of sterile offspring by sexual females. Such a mechanism has been offered as an explanation for the disjunct distribution of tetraploid and diploid *Lumbricillus lineatus* (Christensen, Jernes, and Berg, 1978). As yet, however, there is no direct evidence for the operation of either of these mechanisms.

In addition to the unlikelihood of a simple genetic basis for parthenogenesis or of genomic compatibilities of asexuals and sexuals, a major barrier to the operation of "contagious parthenogenesis" is the evolution of a cytological mechanism that enforces the parthenogenetic production of female progeny without disrupting male production and spermatogenesis. Clearly, cyclical parthenogens and arrhenotokous species have been able to accomplish this, but the production of functional male gametes by obligate parthenogens is extremely rare. Abnormalities in spermatogenesis in thelytokous earthworms (White, 1973; Christensen, Jernes, and Berg, 1978) reduce the likelihood of "contagious parthenogenesis" in this group. Parthenogenetic *Lacerta* produce a few male progeny, but they are invariably teratological (Darevsky, 1960, 1966). Moreover, parthenogenetically produced male *Cnemidophorus* also appear to be sterile (Maslin, 1971). Thelytokous invertebrates for which rare but nonfunctional males have been reported include the freshwater snails *Melanoides lineatus* and *M. tuberculatus* (Jacob, 1957), the isopod *Trichoniscus pusillus* (Vandel, 1928), the millipedes *Proteroiulus fuscus* (Rantala, 1974) and *Nemasoma varicorne* (Enghoff, 1976a), the tick *Haemaphysalis longicornis* (Bremner, 1959), the cockroach *Pycnoscelus surinamensis* (Roth, 1967), and the fruit fly *Drosophila mangabeirai* (Carson, 1962). Although it is possible that loss of male function was not coincident with the

evolution of obligate thelytoky in all of these cases, the fact that all parthenogenetically produced males are sterile in newly synthesized clones of *Drosophila mercatorum* (Carson, 1967) and *Drosophila parthenogenetica* (Stalker, 1954) argues against this interpretation.

Only a few unequivocal demonstrations of functional male production by an obligate parthenogen are known, and in none of these cases do such males promote asexuality. Gynogenetic strains of the flatworm *Dugesia lugubris* (Benazzi-Lentati, 1966) and the fish *Poecilia formosa* (Darnell and Abramoff, 1968) rarely produce competent males. Smith (1955) found that the thelytokous sawfly *Pristiphora erichsonii* occasionally produces haploid males from eggs that fail to diploidize, and that these in turn are capable of fertilizing haploid eggs. Rare males produced by *Artemia parthenogenetica* are capable of fertilizing females of sexual races, but the progeny are never parthenogenetic (Bowen, Durkin, Sterling, and Clark, 1978).

In summary, notwithstanding the barriers to "contagious parthenogenesis," there are many plausible genetic mechanisms that can lead to a breakdown in the integrity of either parthenogenetic or sexual populations, or of both, in zones where they overlap; there are mechanisms that can result in the genetic assimilation of one race by the other. Most of the mechanisms have been thoroughly supported by laboratory studies, and their operation in the field has been verified. All of the proposed interactions between sexual and asexual types result in progeny that are qualitatively different from and frequently reproductively inferior to one or both parents. One of the major reasons that asexual \times sexual hybridization occurs in areas of overlap may be the inclusion of genes for female attractiveness, mate receptivity, and other sexual characters in newly arisen clones (Seiler, 1960; Darevsky and Kulikova, 1964; Roth, 1967; Downs, 1978). Destabilizing hybridization is therefore hardly a phenomenon that can be ignored in attempts to explain the evolution and ecology of parthenogenesis. Moreover, its widespread existence introduces a considerable nonadaptational element into the evolution-of-sex controversy, and suggests the possibility that asexuality is rare in higher orga-

nisms simply because of the frequent existence of genomic incompatibility between sexual species and their parthenogenetic derivatives.

Since one of the most stringent requirements for the establishment and maintenance of a parthenogenetic line will be the avoidance of backcrosses with sexual ancestors, incipient clones that tend to use habitats not normally occupied by the parental species will have an initial selective advantage over other clones. Thus, the frequent association of parthenogenesis with marginal habitats may be more a consequence of the difficulty of maintaining the genetic integrity of such a reproductive system in a habitat occupied by sexual ancestors, rather than a result of any inherent adaptive value of parthenogenesis per se in marginal habitats. Geographic isolation may be further sharpened during the initial establishment of parthenogenesis by strong selection, acting on one or both species, for habitat avoidance. The genetic impediments to coexistence will eventually be lifted, however, as more permanent reproductive barriers evolve (such as mating reluctance or loss of accessory sexual structures in the parthenogens). These evolutionary changes will arise naturally as a direct response to destabilizing hybridization or as a pleiotropic effect of adaptive divergence. The regressive evolution of sexual characters is expected to occur in parthenogens even in the absence of sexual parental species as a consequence of the mutational degradation of a trait no longer selected for (Muller, 1949; Carson, Chang, and Lyttle, 1982). Several examples of the evolution of reproductive barriers in parthenogens will be provided later in this paper. Others may be found in Bell (1982).

COMPETITIVE ABILITY AND COEVOLUTIONARY POTENTIAL OF PARTHENOGENS

Even after the establishment of absolute reproductive isolating mechanisms, competition between a parthenogenetic population and its sexual parental species could subsequently result in the exclusion of one of the races or in the reinforcement of parapatric distributions. Many authors (Slobodchikoff and Daly, 1971; White, 1973; Ghiselin, 1974; Cuellar, 1977a; Glesener

and Tilman, 1978) have speculated on the competitive inferiority of parthenogens. Indeed, if one ignores destabilizing hybridization, competitive exclusion appears to be one of the few viable hypotheses of geographic parthenogenesis. Other than Williams (1975), Uzzell and Darevsky (1975), and in a very restrictive sense, Bell (1982), few persons have admitted there might be any possibility of a competitive edge for parthenogens. White (1973), at least, has acknowledged that the empirical basis for making any generalizations about the competitive prowess of parthenogens is exceedingly weak.

There are, nonetheless, compelling reasons to doubt that extant parthenogens are in general competitively inferior to their sexual conspecifics. The existence of gynogenesis in numerous phylogenetic groups clearly establishes the potential for the coexistence of unisexuals and their close bisexual relatives. In no instance is there any evidence of mutualism between gynogen and host. In the case of *Poeciliopsis* there is evidence that extant clones have been in existence long enough for the accumulation of mutations at numerous loci (Angus and Schultz, 1979; Leslie and Vrijenhoek, 1980), a situation that demonstrates that gynogenetic clones are not necessarily exceptionally short-lived.

A tendency on the part of many investigators to overstate the domain of the competitive exclusion principle may be partially responsible for the widespread view that asexuals will be outclassed in competition by their sexual relatives in areas of overlapping distribution. The critical assumptions of competitive exclusion have been neatly outlined by Armstrong and McGehee (1980), who have also pointed out that the internal dynamics of competitive systems can promote coexistence among competitors that overlap highly in resource utilization (as is expected in asexual-sexual complexes). In theory, partitioning of resources is not a necessary condition for coexistence even in a completely deterministic environment, so long as the inherent characteristics of the interacting species result in fluctuations in the amounts or availability of resources that favor the different species at different times.

It is also significant that an inefficient generalist can coexist with an otherwise similar specialist if the generalist's exclusive resources are not too scarce. This has been empirically demonstrated by Dykhuizen and Davies (1980) and is particularly relevant here, as I will argue later that generalized strategies may be prevalent among parthenogens. The salient point is that, in addition to often-cited resource partitioning and rarefaction of competing species, other mechanisms do exist that allow very closely related species to coexist.

There is one type of competition that could be disadvantageous only to the sexual population—i.e., sperm robbing. Under some circumstances parthenogenetic females might restrict the availability of spermatozoa by copulating with males from the sexual population. This mechanism has been suggested at least four times (Clanton, 1934; Suomalainen, 1969; White and Contreras, 1979; Browne, 1980), but as yet there is no direct evidence that it operates in nature. Clearly, it requires that males are in limited number and are indiscriminate in their choice of mates.

Few empirical attempts have been made to compare the competitive abilities of reproductively isolated populations of parthenogens and sexuals. The two of which I know do not wholly support the generalization that unisexuals are inferior. Browne (1980) found that parthenogenetic strains of the brine shrimp *Artemia salina*, when kept under low food conditions in the laboratory, out-competed sexual populations in 2 out of 8 trials. In six of the seven laboratory experiments I have performed with an obligately asexual clone of the cladoceran *Daphnia pulex*, other cyclically parthenogenetic clones were excluded. In the remaining case the two clones continued to coexist. Wilbur (1971) found that triploid gynogenetic *Ambystoma* were more adversely affected by their diploid bisexual hosts than vice versa, but his study was restricted to the larval stage.

Although limited in scope, these results are really not so surprising. Disjunct distributions are known for many asexual-sexual complexes, but there are also many exceptions, and there is still no direct evidence for

competitive exclusion. The coexistence of clones with their sexual relatives on a microgeographic scale has been noted several times (Vandel, 1928; Jahn, 1941; Seiler, 1961; Stefani, 1956, 1959; Milstead, 1957; Basrur and Rothfels, 1959; Takenouchi, 1968; Enghoff, 1976a; Cuellar, 1979; Fussey and Sutton, 1981). Coexisting races of obligately and cyclically parthenogenetic *Daphnia pulex* are found in virtually all central Illinois ponds that have been studied in detail (Lynch, 1983, and unpub.; Weider, 1984). Thus, it is clear that coexistence of closely related sexual and clonal forms is not peculiar to gynogenetic complexes. Further empirical work is necessary, however, to determine whether the observed cases of coexistence are transient or stable.

One could still argue, as Ghiselin (1974) and Glesener and Tilman (1978) have done, that over evolutionary time the sexuals will develop more and more efficient genotypes and will thereby outcompete the parthenogens, which are unable to evolve as rapidly; i.e., that any competitive advantage enjoyed by an asexual population would be transient. The relative evolutionary rates of asexual and sexual populations is a problem that has been extensively investigated with single-locus models (Muller, 1964; Crow and Kimura, 1965; Felsenstein, 1974; Williams, 1975; Maynard Smith, 1971, 1976, 1978) and more recently from a polygenic perspective (Lynch and Gabriel, 1983). The conclusions of these studies vary somewhat depending on the assumptions (in respect to population size, fitness interactions between alleles and loci, and temporal aspects of the selection process), but the extreme view that asexual lineages are evolutionary dead-ends is clearly untenable. Mutation will act as a continuous source of genetic variation for any asexual line. When the intensity of selection is roughly constant, an equilibrium level of genetic variance will eventually be reached, at which point the input by mutation is balanced by the output due to selection. If the population arises from a single asexual genotype, equilibrium will almost always be reached within a few hundred generations. Although this equilibrium will be lower than that for an otherwise similar sexual population (Lynch and Gabriel,

1983), the question remains open whether the genetic systems of parthenogens and amphimicts differ with respect to recombination only. In addition to mutation, a variety of other variance-generating mechanisms are available to parthenogens. These include mitotic recombination, intra-cis-tronic recombination, mitotic nondisjunction, endomeiosis and endomitosis, transposition of regulatory genes, heterochromatization, and polyploidization. All of these mechanisms are subject to genetic modification and may be modified by selection under parthenogenesis.

The existence of extensive genetic variation for mutator activity (Thompson and Woodruff, 1978) suggests that some parthenogens may compensate for low recombinational rates of production of genetic variance by adopting elevated mutation rates. Mutator activity is frequently released by hybridization (Woodruff and Thompson, 1980), which in turn is a source of origin for many parthenogens (see below). For polygenic characters with an additive genetic basis, an obligate apomict could match the rate of phenotypic evolution of its sexual counterpart by elevating its rate of mutation by the factor $2N$, where N is the number of segregating factors for the character in the sexual population (Lynch and Gabriel, 1983).

The precise genetic mechanisms remain unknown, but considerable evidence does exist that the evolutionary rate of some clones may be substantial (especially during the initial transition to parthenogenesis) even in the complete absence of sex. Work with incipient parthenogenetic lines of *Drosophila* has repeatedly demonstrated a rapid evolutionary change in parthenogenetic capacity, degree of sexual receptivity, and in the cytological mechanism of parthenogenesis itself (Henslee, 1966; Carson, Chang, and Lyttle, 1982; Templeton, 1982, 1983). This capacity for evolutionary change can be anticipated to occur in all incipient parthenogens that have made the initial transition to parthenogenesis with a recombinational automictic mechanism. Under such conditions there may be a much more rapid response to selection than could ever occur under the restrictions of sexuality.

Progressive evolution has also been

demonstrated in some well-established asexual species that lack cytological mechanisms that permit recombination. Successful attempts at artificial selection for the tendency to produce alate progeny (Cognetti, 1962), the number of caudal hairs (Pagliai, 1967), and insecticide resistance (Beranek, 1974; Beranek and Berry, 1974) have been reported for parthenogenetic lines of aphids, although Blackman (1979) has presented contrary results and has disputed most of the existing evidence. Badino and Robotti (1975) have presented more convincing evidence in a demonstration that genetic variants for feeding morphology are generated asexually in the rotifer *Asplanchna sieboldi*. But perhaps the most dramatic examples for the generation of genetic variants in parthenogenetic lines are from Banta's (1939) work with cladoceran clones. From initially uniclonal lines maintained at 200 to 400 individuals, he was able to select within 50 to 200 generations for substantial changes in reactivity to light, degree of intersexuality, and head shape. Selection was not successful in every experimental line (as would be expected for a solely mutational source of variance), nor were most traits completely penetrant. But the performance of adjunct experiments and the apparent care with which Banta performed his work strongly support the interpretation of a gradual genetic change in his clones. It is extremely unlikely that Banta's variants were generated by automictic recombination, since all existing accounts verify the absence of recombination in parthenogenetic cladocerans (Hebert, 1978; Lynch, 1983). Finally, it is of interest that a remarkably complete set of fossil data for the late Cenozoic era indicates that *Melanoides tuberculata*, one of the few known parthenogenetic molluscs, has undergone evolutionary transitions just as dramatic as have sexual species of molluscs (Williamson, 1981). Verification of the long-term existence of parthenogenesis in this species would be of great interest.

Descriptive evidence of the potential for evolutionary change in natural populations of parthenogens can also be found in the several field studies that have identified substantial levels of variance at the biochemical as well as at the morphological level within

ances that likely had a monophyletic origin. In an extensive biometrical survey of the grasshopper *Warramaba virgo*, Atchley (1977a, b, 1978) found that levels of phenotypic variance for morphometric and reproductive characters are generally as high in the parthenogens as they are in related sexual populations. Parker (1979a) reached a similar conclusion in the comparison of growth-related characters of *Cnemidophorus* clones with those of sexual populations, and data for *Haemaphysalis longicornis* are suggestive (Oliver and Herrin, 1976). Fairly strong evidence exists for allelic or karyotypic evolution within unisexual lines of *Poecilia* (Leslie and Vrijenhoek, 1980), *Cnemidophorus* (Parker, 1979a), weevils (Suomalainen, 1961; Saura, Lokki, Lankinen, and Suomalainen, 1976), the chrysomelid *Adoxus obscurus* (Lokki, Saura, Lankinen, and Suomalainen, 1976), the dipteran *Lonchoptera dubia* (Ochman, Stille, Niklasson, Selander, and Templeton, 1980), the moth *Solenobia triquetrella* (Lokki, Suomalainen, Saura, and Lankinen, 1975), the nematode *Meloidogyne incognita* (Triantaphyllou, 1981), and the snail *Thiara balonnensis* (Stoddart, 1983).

PARTHENOGENESIS AND ECOLOGICAL
GENERALISM: THE GENERAL-PURPOSE
GENOTYPE HYPOTHESIS

Even if sexual populations are, in general, competitively and coevolutionarily superior, neither hypothesis explains why sexuals fail to spread to peripheral areas and displace the parthenogens. To account for this, almost all investigators have argued that parthenogens have superior colonizing ability. One clear advantage of asexuality is the potential to start a new population with a single colonist. Non-hermaphroditic sexual species obviously require two colonists of the appropriate sexes, except when fertilized females act as colonizers. Another frequently mentioned advantage for colonizing parthenogens is the release from the cost of producing males. All other things being equal, asexual populations, because all of their progeny are females, can increase twice as rapidly as sexual ones that have balanced sex ratios. What has not been appreciated until recently, however, despite the existence of substantial data, is that with respect to re-

production all other things are generally not equal between parthenogens and sexuals (Lamb and Willey, 1979; Bell, 1982).

Although cases have been recorded in which the two-fold cost of producing males is fully recovered under parthenogenesis (Robertson, 1966; Congdon, Vitt, and Hadley, 1978), parthenogens most often appear to have lower reproductive rates than their sexual relatives, in many cases less than the 50% necessary for equal rates of increase (Roth, 1974; Bullini, 1965; Enghoff, 1976b). Frequently, this lower rate stems from the poor hatching success of eggs resulting from developmental abnormalities of progeny (Roth and Willis, 1956; Stalker, 1956a; Murdy and Carson, 1959; Darevsky, 1966; Templeton, 1979); but some parthenogens also produce fewer eggs than their sexual relatives. Enghoff (1976b) has noted that the thelytokous race of the millipede *Nemasoma varicorne* produces fewer than half the number of eggs of sexual females. The two gynogenetic forms of *Ambystoma* produce 60 to 70 per cent as many eggs as do the sexual forms (Uzzell, 1964). In the case of featherwing beetles of the genus *Ptinella*, parthenogenetic *P. errabunda* individuals produce only 65 per cent as many eggs, and with only 65 per cent of the hatching success, of two similar sexual species (Taylor, 1981). Parthenogenetic *Trichoniscus pusillus* individuals produce significantly smaller clutches than sexual females of the same size (Frankel, 1978). The situation is certainly worse in the case of newly arisen parthenogens (Stalker, 1954; 1956a; Roth and Willis, 1956; Carson, 1967; Vrijenhoek and Schultz, 1974; White, Contreras, Cheney, and Webb, 1977; Templeton, 1979).

There is no denying that differential colonization has played a role in many instances of geographic parthenogenesis (Roth and Willis, 1956; Winterbourn, 1970; Gates, 1972; Takenouchi, 1978). A critical question remains, however. Is the exclusive occupation of marginal areas by parthenogens solely a byproduct of their exceptional abilities as fugitive species or is it a result of the acquisition of additional adaptations to such environments by asexual lineages subsequent to (or coincident with) their origin? Given that parthenogenetic lineages can

evolve, we would be mistaken not to consider the latter possibility. It has been suggested that a higher rate of increase may act as an adaptation in itself, by enabling parthenogens to crowd out their sexual relatives in marginal areas (Cuellar, 1977a). This seems unlikely, however, not only for the reasons given above, but also because there is no necessary relationship between the intrinsic rate of increase and competitive ability (Ricklefs, 1979; Roughgarden, 1979).

I have suggested above that the frequent association of parthenogens with marginal habitats (at least in the early stages of the transition to parthenogenesis) may be an effect that is correlated with the need to avoid backcrosses with sexual relatives. This is not to say that all incipient parthenogens are preadapted to life in marginal environments. But the subset of lineages that successfully make the transition to parthenogenesis is likely to be biased in that direction by selection against destabilizing hybridization.

The fundamentally different manner in which selection shapes the genetic structure of asexual and sexual populations provides a more general reason for expecting parthenogens to be exceptionally well adapted to extreme environments. Over evolutionary time, clonal selection will favor those asexual lineages with the greatest geometric mean fitness. As the environment changes in time, different clones will be favored in different generations, but in the long run the most successful clones will be those with the lowest temporal variance in fitness. To take the extreme case, among a subset of clones in which no mutations have arisen, each surviving clone must have had a tolerance (positive fitness) to the full range of environmental conditions to which it has been exposed since its incipience. Relatively specialized clones will surely arise (perhaps frequently), but they will only survive as long as the narrow niche to which they are adapted remains available. Therefore, in the long term, clonal selection will promote the evolution of highly generalized (or general-purpose) genotypes, which are characterized by both broad tolerance ranges and low fitness variance for relevant physical, chemical, and biotic gradients. The genetic variance necessary for the successful selection of

general-purpose genotypes will arise continuously through polygenic mutation, and in some cases the variance may be augmented by the polyphyletic origin of clones.

It is my contention that highly generalized genotypes that are acquired as adaptations by parthenogens will promote a more generalized use of habitat and resources, but I recognize that generalist strategies exist in sexual populations as well. Depending on the grain of the environment and the magnitude of the differences between patches, sexual populations certainly may evolve in the direction of specialization or generalization (Levins, 1968). Nevertheless, two consequences of recombination—the cohesiveness of gene flow and the opportunistic nature of selection—constrain the extent to which generalist strategies can evolve in amphimicts.

Whereas selection necessarily perceives clones as complete linkage groups and acts upon the composite properties of the genotype (including interactions within and between loci), in sexual populations alleles are selected primarily for their average additive effects. Selection will favor the survival of those individuals with gene complexes most coadapted to the prevailing conditions but, when they reproduce, a single episode of outcrossing may destroy such genic associations. Thus, while a broadly adapted parthenogen will produce only broadly adapted progeny, a broadly adapted parent of the sexual type will produce few if any such progeny. It is well known that sexual individuals with extreme phenotypic values for complex characters tend to produce progeny that regress toward the population mean (Falconer, 1981).

A second consequence of the frequent rearrangement of genetic structure is that the genomes of sexual reproducers will carry a smaller record of the past, and therefore tend to be more closely adapted to the immediate environment than will those of parthenogens (Lynch and Gabriel, 1983). Within sexual populations, mutations that were advantageous in the past, but later become less favorable because of a change in environment will be purged from the gene pool by recombination, syngamy, and selection, and will be replaced by more favorable al-

leles. On the other hand, any new mutation that arises in a clone will be carried for the life of that clone (except in the case of back or secondary mutations), although its effects may eventually become masked by balancing mutations on accompanying genes (Lynch and Gabriel, 1983). This dichotomy between the response to selection in asexual and sexual lineages will be accentuated if philopatry and inbreeding are as significant in sexual organisms as Shields (1982) suggests.

Depending on the importance of destabilizing hybridization, the relative efficiencies of the two races on shared resources, and the spatial and temporal scale of resource availability, the evolution of asexual generalists will have varied consequences for geographic parthenogenesis. Because of their exclusive use of extreme resources, highly generalized parthenogens will be buffered from complete competitive exclusion by their more specialized sexual relatives. If, however, the evolution of parthenogenesis and generalism entails a significant cost in terms of the efficiency of utilization of resources appropriated by the sexual species (Lynch and Gabriel, 1983), and if the exclusive resources of the parthenogen are in insufficient supply within the range of the sexual species, the parthenogen may be confined to marginal habitats by competitive interactions. The critical distinction between the general-purpose genotype hypothesis and other hypotheses for the geographic distribution of parthenogenesis is that in the former the exclusive use of extreme environments by parthenogens is a byproduct of physiological or morphological adaptations acquired through selection for generalism rather than a simple consequence of enhanced colonizing ability. The general-purpose genotype hypothesis further predicts that the exclusion of sexual species from extreme environments will be partially attributable to their inferior fitness in such settings.

The idea that ecological generalism is common among obligate parthenogens is not new. In 1965, Baker presented evidence that weedy plants (many of which are apomicts or selfers) are so successful because they have evolved "general-purpose" genotypes. Since then many other investigators

have extended this idea to particular animal groups (Maslin, 1968, 1971; Schultz, 1971; Selander and Hudson, 1976; Parker, Selander, Hudson, and Lester, 1977; Parker, 1979a; Angus and Schultz, 1979; Jaenike, Parker, and Selander, 1980). The broad implications of this idea for the phylogenetic, cytogenetic, and geographic aspects of obligate parthenogenesis have not yet been examined, nor has the hypothesis been rigorously tested.

Much of the support for the general-purpose genotype hypothesis is descriptive or circumstantial, as little experimental work has been done with asexual-sexual complexes. I am by no means convinced that citing from the descriptive literature is a final means of testing and falsifying mechanistic hypotheses, because the data are often open to multiple interpretations. This point is made especially clear when one considers that several of the cases that I cite in support of the destabilizing hybridization and general-purpose genotype hypotheses have been previously invoked as support for the biological-uncertainty hypothesis (Glesener and Tilman, 1978) or the tangled-bank model (Bell, 1982). The most one can do in this situation is to examine thoroughly the literature for the presence of glaring inconsistencies and to make a subjective judgment as to whether one's hypothesis warrants a serious test by more formal experimental means. The ecological information available for the most thoroughly investigated complexes of parthenogens and amphimicts (see below) is strikingly consistent with expectations under the joint operation of destabilizing hybridization and selection for asexual general-purpose genotypes, certainly enough so to warrant their erection as formal hypotheses. I emphasize, however, that these hypotheses remain to be thoroughly tested experimentally.

One additional impediment to deriving an ecological interpretation for geographic parthenogenesis needs to be pointed out. In the absence of detailed information about the genetic structure of asexual populations, it is impossible to verify whether a widespread distribution of a parthenogen has resulted from the dispersal of a single (or several) highly generalized clone(s) or from the joint

distribution of many locally adapted clones. The latter interpretation has been fostered by several investigators, including White (1973), and several electrophoretic surveys point to the potential significance of multiple, ecologically unique clones. Microgeographic variation has been noted for *PGM/PGI* genotypes of *Trichoniscus pusillus* in different litter types (Christensen, 1979) and for the intertidal position of clones of different ploidy level in *Lumbricillus lineatus* (Christensen, 1980). Tetraploid asexual *Solenobia triquetrella* populations also consist of multiple clones (Lokki, Suomalainen, Saura, and Lankinen, 1975). These clones are highly variable in the Alps, and show no consistent patterns between populations; but in Finland one clone dominates throughout the west and another dominates in the east. Several clones of the tetraploid parthenogenetic weevil *Otiorrhynchus scaber* have distributions that are closely associated with the major biotic zones of northern Europe (Saura, Lokki, Lankinen, and Suomalainen, 1976). The grasshopper *Warramaba virgo* (Webb, White, Contreras, and Cheney, 1978), the snail *Campeloma decisa* (Selander, Parker, and Browne, 1978), and the South American whiptail *Cnemidophorus lemniscatus* (Peccinini-Seale and Frota-Pessoa, 1974) are all multiclonal, but local populations are either monokaryotypic or electrophoretically homogeneous. Unfortunately, information regarding the ecological requirements of these different clones is lacking.

These examples provide convincing evidence that the broad distributions of some asexual species are at least partially a consequence of the joint distribution of several differentially adapted clones. The extent to which the ecological diversity of clones in these cases is a product of a polyphyletic background, as opposed to adaptive divergence, is less clear. Some degree of local adaptation is clearly to be anticipated (Lynch and Gabriel, 1983), but in no way does this vitiate the general-purpose genotype hypothesis, which is concerned with the way the variance in fitness over environmental gradients contrasts between asexual and sexual genotypes.

The vast majority of local populations of parthenogens are multiclonal (Parker,

1979b; Bell, 1982), and many individual clones (at least in so far as clones can be distinguished by electrophoretic, karyotypic, and histocompatibility analyses) are geographically widespread. The triploid chrysomelid beetle *Adoxus obscurus* (Lokki, Saura, Lankinen, and Suomalainen, 1976) provides a striking example. This species exists only as an apomictic parthenogen in Eurasia, where it extends from Europe through Siberia to Japan. It is an active flier, and 80 per cent of the individuals identified throughout Scandinavia were found to be identical at 16 structural gene loci. *Lonchoptera dubia*, which consists of four chromosomal races of parthenogens (Stalker, 1956a), provides another example. Race 1 is spread through the northeastern and midwestern United States and extends into the Rocky Mountains. Race 2 has a similar distribution, but is also found in California. Races 3 and 4 are found in the Appalachian Mountains as well as in Canada. Thus, all four races are fairly widespread, and coexistence is common (all four are found in Rochester, New York). Stalker was unable to detect any ecological differences between the races, although future research on a finer scale might indicate otherwise, since the karyotypic races are now known to be comprised of several electrophoretically distinct clones (Ochman, Stille, Niklasson, Selander, and Templeton, 1980). Similarly, the only known naturally parthenogenetic drosophilid, *Drosophila mangabeirai*, has a constant karyotype, yet occupies a considerable range of habitats in Central America from sea level to 4000 feet (Carson, 1962). Finally, tissue graft analysis has verified that several haplotypes of the hybridogenetic *Poeciliopsis monacha-lucida* are widespread throughout the range of their complex (Angus and Shultz, 1979).

With the above caveats in mind, I shall next examine the available information on the geography and ecology of asexual-sexual complexes with respect to expectations that follow from the joint operation of the general-purpose genotype and destabilizing hybridization hypotheses. As previously discussed, there are compelling reasons to believe that genomic interference mechanisms prevent the coexistence of parthenogenetic

Lacerta with their sexual parental species (Darevsky and Kulikova, 1964; Darevsky and Danielyan, 1968). The distributions may best be described as parapatric. Nevertheless, where parthenogenetic species do occur, they generally occupy an intermediate elevational range relative to their two parental species (Uzzell and Darevsky, 1975). There is also considerable elevational overlap. For instance, the altitudinal range of asexual *L. rostombekovi* encompasses that of both its parental species. Three of the four parthenogenetic species are found in more arid areas than their sexual relatives, and a higher tolerance to desiccation has been demonstrated for the eggs of parthenogens. Among the parthenogens, *L. dahli* is exceptional. Its individuals occupy habitat that is intermediate between the parental habitats with respect to humidity and tree cover. Uzzell and Darevsky suggested that the characters of the parthenogens are products of the sexual parental characters at the time of origin (which is suspected to be the exceptionally arid hypothermal period). If this is true, the asexuals' ability to occupy arid areas may be relict to some degree. The sexual species, since the complex's formation, may have evolved a greater competitive ability in more humid areas at the expense of their adaptation to arid environments.

As noted above, individual *Cnemidophorus* clones are often very widespread, occasionally to the point of covering the entire range of the parthenogenetic complex (Maslin, 1967; Cuellar, 1976, 1977b; Parker and Selander, 1976). The existing data imply that a broader ecological tolerance (perhaps to physical factors) enables the parthenogens to occupy a more diverse array of habitats (Maslin, 1968; Parker, 1979a). *C. tessellatus*, which consists largely of one clone (Parker and Selander, 1976), has been able to spread far north of its two parental species. Zweifel (1965) describes the microgeographic distribution of this species as unpredictable. It is often found in riparian and roughland habitats, but in some areas it occurs on plains. Within a particular area it is generally restricted to a specific habitat. Sexual individuals may not be so flexible, however. Milstead (1957) noted that whereas asexual *C. tessellatus* and *C. exsanguis* often coexist

with sexual *C. inornatus* in plains habitats, only the latter avoids the roughlands. Cuellar (1979) found that sexual *C. tigris* actively avoids the habitat of parthenogenetic *C. uniparens*, even when all individuals of the latter are removed. Thus, as Milstead (1957) has suggested, active habitat selection may be responsible for the coexistence of the sexuals and asexuals, although an ecological basis for such habitat selection has not been found. Parthenogens and sexual individuals consume the same food types and exhibit no aggression towards each other. Since sterile hybrids have been collected (see above), it is reasonable to consider the possibility that these species are avoiding genetic disruption.

Jaenike, Parker, and Selander, (1980) have used the hypothesis of general-purpose genotypes to explain the widespread distribution of two clones of the parthenogenetic earthworm *Octolasion tyrtaeum* through a diversity of habitats in three U.S. states. An unambiguous interpretation of their data is impossible, however, without similar information on related (preferably the parental) sexual species. Jaenike and Selander's (1979) claim that litter and decaying logs are occupied solely by parthenogens does not appear to be substantiated, although it is true that most species of *Bimastus* (11 of which are parthenogenetic) show a strong preference for such habitats (Reynolds, Clebsch, and Reynolds, 1974). It is noteworthy, however, that Reynolds, Clebsch, and Reynolds (1974) found that 70 per cent of the sexual earthworm species in Tennessee were restricted to fewer than 20 counties, whereas 69 per cent of the parthenogens were found in 21 to 94 counties. In his 1952 review, Muldal stated that within their genera "the polyploid parthenogens are all the most successful and widespread species" (p. 73). In Iceland, Bengtson, Nilsson, Nordstrom, and Rundgren (1975) found that, although all lumbricid species utilized a variety of environments, only the parthenogens *Dendrobaena octaedra* and *Dendrobaena rubida* were distributed across all natural and man-made habitats. Competition does not appear to be a severe problem for earthworms, as it is not uncommon to find as many as three congeners coexisting in the same soil horizon (Rundgren, 1975).

Phylogenetic, biogeographic, and ecological studies of earthworms are fraught with interpretative difficulties that result from the tremendous amount of human transport that has occurred in the last 500 years (cf. Gates, 1972, 1973). The fact that many lumbricids are globally distributed, however, underscores the ecological generalization of members of this group. One of the most thorough earthworm studies (Reynolds, Clebsch, and Reynolds, 1974) indicated that an eclectic use of microhabitats is not peculiar to parthenogenetic clones, but rather is characteristic of lumbricids in general. The exceptional ecological flexibility inherent in sexual earthworms may facilitate the relatively common transition to parthenogenesis in this group (Omodeo, 1955; Gates, 1972, 1973). Of the 26 species identified in Tennessee by Reynolds, Clebsch, and Reynolds, (1974), only 10 were sexual.

A number of surveys have been done on geographic parthenogenesis in European millipedes, but as yet no information is available regarding the genetic structure of the asexual races. The ecogeographic data that exist for three species are consistent with the idea that generalized parthenogens have evolved from sexual parental species. *Proteroiulus fuscus*, a widespread parthenogen in Europe, ranges from the Mediterranean to Iceland, whereas two other related sexual species have extremely limited distributions on the Iberian peninsula (Enghoff, 1978a). Parthenogenetic populations of *Polyxenus lagurus* are much more widespread than sexual populations, which are restricted to four isolated areas in Europe and the Middle East (Enghoff, 1978a). Within Denmark, the parthenogens occur throughout the country, whereas the sexual form is restricted to islands and to southeast Jutland (Enghoff, 1976a). Both forms live associated with tree bark or stones, but only the parthenogens have been found in houses. The parthenogenetic form of *Nemasoma varicorne* is distributed in a ring around the range of its sexual relatives and therefore has a broader geographic distribution (Enghoff, 1976b, 1978b). In a few limited areas the two forms coexist, and they may even be found under the same piece of bark. Since the spermathecae of the thelytokous females are either

vestigial or lacking entirely, there would appear to be little chance for genetic interference between the two forms or for sperm-robbing by the parthenogens. Enghoff (1976b) has argued that the largely disjunct distributions result from each species' competitive superiority in its own area. Such an interpretation is consistent with the notion that asexuals have more broadly adapted phenotypes at the expense of their competitive ability within the sexual race's range.

The terrestrial isopod *Trichoniscus pusillus* was one of the earliest species to be studied with respect to geographic parthenogenesis (Vandel, 1928), but there is still little information on the clonal structure of the asexual race. The triploid parthenogens, which extend into colder as well as drier areas, are clearly more widely distributed than the sexuals, however. The parthenogens extend nearly as far south in Europe as do the sexuals. The former are rare in damp areas of this region, but they alone have been able to colonize arid regions (Vandel, 1940). The parthenogens have been found by Frankel (1979) to achieve greater autumn and winter growth than the diploid sexuals, a fact that suggests a greater degree of cold tolerance in the asexuals. Northern Europe is heavily dominated by the parthenogenetic race (Vandel, 1928), and the diploid sexuals are found only in isolated areas with a particularly favorable habitat that contains an abundance of decaying matter and moisture throughout the year (B. Christensen, pers. comm.). The parthenogens are much commoner than the sexuals in Ireland, where the latter are dominant only in Carboniferous limestone areas (Fussey and Sutton, 1981).

There are areas in central and southern France (Vandel, 1928), Ireland (Fussey and Sutton, 1981), and England (Frankel, 1978) where the two forms of *Trichoniscus* coexist on a very fine scale. In fact, in the Toulouse area Vandel never sampled any sites in which both forms were not present. Coexistence in this area is apparently facilitated by the complete absence of copulations between the diploid males and the triploid parthenogens (Vandel, 1928). That diploid males from southern France copulate freely with parthenogens from Toulouse is a fact that suggests that the coexisting races of central

France have evolved premating isolating mechanisms, while the more disjunct southern populations have not. Nor do Toulouse males copulate with more northerly parthenogens. Thus, the general failure of the sexual race to become well established in northern Europe cannot be a consequence of its inability to immigrate, of sperm robbery, or of genetic disruption.

Among the Lepidoptera, obligate parthenogenesis has been thoroughly documented in only seven species, five of which are members of the Psychidae, a family characterized by apterous females. Despite the restricted mobility of females in *Solenobia triquetrella*, however, the parthenogenetic forms have been able to disperse broadly beyond the range of the diploid parent species while also coexisting in a wide area of sympatry (Seiler, 1943, 1946, 1961). The sexual form is sporadically distributed throughout the Alps and in a few neighboring unglaciated areas, but the parthenogens extend farther east, west, south, and north. The few sexual populations in Switzerland are estimated to contain fewer than 100 individuals (Lokki, Suomalainen, Saura, and Lankinen, 1975). This scarcity prompted Seiler (1961) to suggest that the sexuals are on the verge of extinction. The extreme reduction in the size and distribution of the sexual populations may be a consequence of genetic disruption that is favoring the asexuals. Thelytokous females exhibit some courtship behavior (Seiler, 1960), and males will readily fertilize tetraploid females from transition zones. The resultant progeny are triploid intersexes. Unfortunately, the significance of such hybridization events for the dynamics of natural populations is unknown. It is of interest to note, however, that parthenogens from more distant areas (presumably older lineages) have undergone an evolutionary reduction in their copulatory organs. Fewer of their eggs are fertilized in crosses with males, and those that are fertilized result in triploid intersexes. These offspring are more like males than are hybrid progeny from transition-zone matings.

Another parthenogenetic psychid, *Luffia ferchaultella*, is generally sympatric with its presumed sexual parent, *L. lapidella*, although the sexuals may have exclusive use of

the southern part of the range. The two species separate out on a microhabitat scale (Narbel-Hofstetter, 1963). Both forms depend on the alga *Pleurococcus* for food, but while *L. ferchaultella* is generally found in humid microhabitats on branches with high densities of algae, *L. lapidella* is restricted to drier areas (generally on walls or rocks) with fewer algae. Again, the ultimate reason for habitat segregation may be the genomic incompatibility of the two races. Narbel-Hofstetter (1962) has shown that males do not discriminate between the two female types and that hybridization events result in a near doubling in the mortality of the progeny, as well as in the production of a large number of sterile and intersexual offspring. A few apparently intact sexuals are produced, but backcrosses of these with the parental species have not been studied. The fact that intersexes have been found in nature verifies the potential significance of genetic interference (Narbel-Hofstetter, 1963).

Obligate thelytoky is relatively common in the Curculionidae (weevils) and in all known cases is apomictic. The geographic distribution of the component species of most complexes has not been accurately determined, nor has much comparative ecological work been done. Nevertheless, in the carefully studied cases, parthenogenetic races have a much broader distribution and occasionally coexist with sexuals (Jahn, 1941; Suomalainen, 1950, 1969; Suomalainen and Saura, 1973; Suomalainen, Saura, and Lokki, 1976; Takenouchi, 1968, 1970, 1976, 1981). In a few cases where only polyploid parthenogenetic races are known, the sexual parent species have perhaps become extinct. There is some indirect evidence for a broader ecological tolerance in asexuals of *Otiorrhynchus dubius*, in which the tetraploid parthenogens can maintain activity at lower temperatures than diploid sexuals can (Lindroth, 1954).

Dybas (1978) has studied the ecology of bog-inhabiting featherwing beetles. Males of North American *Ptiliopycna moerens* are known only from the northern part of its range; the parthenogens are much more widely dispersed and overlap with the sexuals. In Volo Bog (Illinois) parthenogenetic

P. moerens are distributed across all seral stages and parthenogenetic *Acrotrichus* sp. are evenly distributed across 2 of 4 stages, whereas sexual *Pteryx* #4 appears to be concentrated in one seral stage. Furthermore, the two parthenogens can be found throughout the year, but the sexual species is restricted to the summer months. Another member of the Ptiliidae, *Ptinella mekura*, is widely distributed as a parthenogen throughout Japan, the Mediterranean, and the United States, and is found in a diversity of habitats including forest floors, grasslands, and agricultural areas. Two parthenogenetic species that have immigrated to the British Isles, *Ptinella errabunda* and *Ptinella cavelli*, have been able to spread throughout the country in less than 100 years. Indigenous sexual *Ptinella aptera* is confined to relict areas of mature woodland, and a sexual immigrant, *Ptinella taylorae*, has spread slowly (Taylor, 1981).

The parthenogenetic fungus beetle *Cis fuscipes* is the most common and widespread of the North American Ciidae. It occurs throughout the United States (except in the arid West), and in British Columbia and eastern Canada. It is also found in Cuba, Hawaii, and perhaps in Siberia (Lawrence, 1967). A morphologically indistinguishable sexual race is found only on the periphery of the North American range of the complex, and the most northerly populations are sexual. Males will not fertilize parthenogenetic females, and there are broad areas of overlap of the two races. The parthenogens are usually associated with other sexual *Cis* species, and according to Lawrence (1967) they appear to compete successfully with foreign species that inhabit the same fungi.

The evidence is particularly strong that the coexistence of *Warramaba virgo* with its sexual relatives is prevented by genomic incompatibility (see p. 000). Nonetheless, despite its apterous condition, *W. virgo* has been able to extend its range to eastern Australia. In contrast, both its sexual parent species and all other congeners are restricted to western Australia (White and Webb, 1968). Where the parthenogens and sexuals are contiguous, their fecundities are approximately equal (White and Contreras, 1979). Evidence for a generalized strategy in

W. virgo comes from observations that individuals gathered over a north-south gradient have a relatively constant fecundity, whereas there is a considerable cline in reproductive and body-size characters for sexual P196 taken over a similar gradient.

Another extremely widespread parthenogen is the cockroach *Pycnoscelus surinamensis*, which is found on every continent and is generally associated with human activity. *P. surinamensis* is karyotypically and electrophoretically diverse (Roth and Cohen, 1968; Parker, Selander, Hudson, and Lester, 1977), a condition that suggests multiple origins of clones, but 3 of the 10 composite genotypes identified by Parker, Selander, Hudson, and Lester (1977) have been able to spread to more than one continent. Many sexual cockroaches are also geographically widespread (Roth and Willis, 1961), but the sexual parent form of *P. surinamensis* (*P. indicus*) is restricted to Indo-Malaysia, Hawaii, and a few islands off the coast of Australia. The parthenogenetic and sexual races coexist only in Indonesia and Hawaii. *P. indicus* males will copulate with the parthenogenetic females, but there is little chance of genetic interference, since none of the apomictically produced eggs are fertilized (Roth, 1967). Rare males produced by *P. surinamensis* will copulate with both types of females. In neither case, however, does fertilization occur. Thus, while the two races are clearly reproductively isolated, it is possible that sperm-robbing by *P. surinamensis* occurs in areas of sympatry. Although Parker, Selander, Hudson, and Lester (1977) have argued that the general-purpose genotype hypothesis explains geographic parthenogenesis in this complex, the work essential for determining the relative importance of sperm-robbing, differential colonizing ability, and ecological tolerances has not yet been done. Roth and Cohen (1968), however, have clearly demonstrated that the reproductive rates of *P. surinamensis* clones are often substantially less than that of *P. indicus* because of high egg mortality.

The embiid *Haploembia solieri* provides an example of a species that has adapted to a biotic selective agent not by increasing its recombination rate but by switching to parthenogenesis (Stefani 1956, 1959). Asexuals

are widespread throughout Mediterranean Europe, where they coexist with the sexual race on some islands as well as in some mainland areas. The parthenogens are the sole occupants of Sardinia. Males are often sterilized by a parasitic protozoan, and there is a strong positive relation between the incidence of parasitism and the proportion of thelytokous females in a population.

More inferential evidence for the association of general-purpose genotypes with obligate thelytoky can be drawn from Mockford's (1971) review on psocids. No information on the clonal structure of their parthenogenetic races is available, but these bark lice provide some of the most dramatic examples of how restricted the ranges of sexual species can be relative to those of their asexual derivatives. In all cases, the sexual races tend to occur either on the periphery of the range of the species complex or in ecologically unusual areas. For example, in the eastern United States, thelytokous *Echmep-teryx hageni* are widely distributed, whereas sexual populations are found only in two isolated areas. Where the forms coexist in southern Illinois, the sexuals are found on rocks, whereas the parthenogens inhabit trees. Asexual forms of *Caecilius aurantiacus* are also wide-ranging. Sexual individuals are less commonly found, and most of their populations are within the range of the parthenogens; however, the most northerly (Alaska) as well as the most southerly (Mexico) populations are sexual. Similarly, in *Peripsocus quadrifasciatus*, *Trichadenotecnum alexanderae*, and *Psocidus pollutus*, the parthenogenetic races have broad geographic ranges, within which a few isolated sexual populations are found.

A similar case is that of the tick *Haemaphysalis longicornis*, a serious disease vector (Oliver, Tanaka, and Sawada, 1973). The triploid parthenogenetic race is more widely distributed in Japan than are the diploid sexuals. The two are able to coexist in some areas, and experiments indicate that crosses between them are unlikely.

Finally, in a recent analysis of an ostracod community (McLay, 1978), two of the four species studied (*Herpetocypris reptans* and *Cyprinotus carolinensis*) were parthenogens.

These two species numerically dominated the community, had niche breadth measures 3 to 4 times higher than those of the coexisting sexual species, and their behavioral repertoires were more diverse than those of the sexuals.

NARROWLY ADAPTED PARTHENOGENS

Most data on the ecology of parthenogens are consistent with the general-purpose genotype hypothesis, but there are several cases in which parthenogens are more specialized than their sexual ancestors. Each of these cases is a gynogenetic system. For example, widespread gynogenetic clones of the *Poeciliopsis monacha-lucida* complex, despite their hybrid origin, appear to be more narrowly adapted to certain environmental parameters than are their sexual relatives (Angus and Schultz, 1979). Each of the two known clones of *P. monacha-2 lucida* has a superior thermal tolerance at one end of the temperature scale and an inferior tolerance at the other extreme (Bulger and Schultz, 1979). Two dominant clones of *P. 2 monacha-lucida* are morphologically and behaviorally adapted for very different modes of feeding: clone 1 scrapes rocks, and clone 2 browses on filamentous algae and detritus (Vrijenhoek, 1978). The host species, *P. monacha*, is significantly more generalized in its feeding preferences than either clone. Indirect evidence suggests that gynogenetic forms of *Ambystoma* are more specialized with respect to the use of resources than are their sexual hosts. In detailed enclosure experiments, Wilbur (1971) found that the diploid sexual larvae are less adversely affected by the presence of the triploid gynogens than vice versa, an observation which indicates that the sexuals may have some exclusive resources. Gynogenetic clones of the fall cankerworm *Alsophila pomataria* are significantly more restricted with respect to habitat utilization and emergence time than their sexual host population is. Furthermore, the different clones are specialized on different trees (Mitter, Futuyma, Schneider, and Hare, 1979). The gynogenetic spider beetle *Ptinus clavipes* form *mobilis* is found only in warehouses, whereas its sexual host extends to some natural habitats (Sanderson, 1960).

On the other hand, an enhanced level of specialization may not be universal among gynogenetic species. Turner, Brett, Rasch, and Balsano (1980) noted that the gynogenetic fish *Poecilia formosa* is more broadly distributed than either of its sexual parental (and host) species. The gynogenetic race of *Luffia lapidella* is found at virtually all locations that contain its sexual host (Narbel-Hofstetter, 1964). The tetraploid gynogenetic race of *Lumbricillus lineatus* appears to have a much broader niche than the diploid sexuals (Christensen, Jelnes, and Berg, 1978).

Despite these exceptions, it seems noteworthy that all clear examples of specialized parthenogens are from gynogenetic systems. Why should gynogens be more narrowly adapted than their sexual hosts? Clanton (1934), Uzzell (1964), and Kiester, Nagylaki, and Shaffer (1981) have all pointed out the precarious nature of gynogenetic systems. When gynogens and their hosts are ecologically identical and males are indiscriminate in their choice of mates, the gynogens will function as sperm robbers and will eventually force the extinction of the sexual population and hence of the gynogens. Density-dependent mate preference can stabilize such systems in a purely deterministic environment (Moore and McKay, 1971), but stochastic variation in the density of males could strongly influence the survivorship of the gynogenetic line. Since reproduction by a gynogen is absolutely dependent upon the presence of a sexual host, it is clearly in a gynogen's best interest to influence the density of its host as little as possible and in a way that does not insure its own demise through competition for critical resources.

One possible means of accomplishing this goal is for the gynogen to adopt a niche that is inclusive within that of its host species. Such an adaptation facilitates coexistence as long as the gynogen is more efficient in using its own resources while insuring sufficient resources are available to support its host. All of the examples here given for specialized gynogens are consistent with this mechanism. Furthermore, it is of interest to note that two of the apparently broadly adapted

gynogens, *Poecilia formosa* and the tetraploid *Lumbricillus lineatus*, have multiple hosts. Under these conditions, narrowly adapted gynogenetic genotypes may be unnecessary.

POLYPLOIDY, NONSEGREGATIVE AUTOMIXIS, AND HYBRID ORIGIN OF PARTHENOGENESIS

The extreme rarity of polyploidy among sexual animals is well known and has been the subject of a great deal of speculation (Muller, 1925; Vandel, 1940; Stebbins, 1950; Bungenberg de Jong, 1957; Astaurov, 1969; White, 1973; Cavalier-Smith, 1978; Lewis, 1980). Reasons that have been suggested for the conservation of diploidy in sexual animals include (1) the inevitable disruption of a balancing sex-determination system that would result from the segregation of sex chromosomes in polyploids; (2) the production of sterile, aneuploid gametes by individuals of odd ploidy levels; (3) the remote possibility of any newly arisen, fertile polyploid individual locating a fertile mate of the same level of ploidy; (4) the dependence of adaptive developmental programs on the nuclear DNA content; and (5) the inevitable disruptive consequences of backcrossing with the diploid parental species.

Only the last two situations offer potentially significant barriers to the establishment of polyploidy under most systems of obligate parthenogenesis. As has been already discussed, genetic disruptions are of potential importance regardless of the level of ploidy. Therefore, it is not surprising that polyploidy is more common among asexual than sexual populations. What is striking is the extreme frequency of polyploidy and the relative rarity of diploidy among parthenogens (Suomalainen, 1950; Omodeo, 1955; White, 1973; Lokki, 1976a; Lokki and Saura, 1979; Takenouchi, 1981).

One clear advantage of polyploidy accrues to asexual lineages that are subject to the effects of Muller's (1964) "ratchet." The greater the ploidy level, the slower the rate at which deleterious recessive mutations will accumulate in the "homozygous" state (Lokki, 1976b; Rasch, Cassidy, and King, 1977). In addition to this possible protective role, polyploidy may play a critical constructive part in the adaptive differentiation of a par-

thenogenetic race by providing a substrate for multiple pathways to the evolution of general-purpose genotypes. To the extent that intra-cistronic recombination is important (Watt, 1972), polyploidy will enhance the rate at which new alleles are produced by an automictic system. Polyploidization also provides the simplest route to freeing large amounts of DNA for mutational experimentation without disrupting committed loci, a consequence that has been generally recognized in studies on the adaptive divergence of duplicate genes (MacIntyre, 1976). Although it seems reasonable to expect that multiple, functional products of individual loci would enhance the range of conditions under which an organism can survive and reproduce, we need not rigidly subscribe to this viewpoint. The evolutionary advantage of polyploidy in parthenogenetic organisms simply lies in the additional sites that it supplies for the production of novel alleles, some combinations of which may lead to a more broadly adapted phenotype than could ever be obtained in diploidy. The positive influence that an increase in ploidy level alone can have on the rate of adaptive evolution in asexual populations has been empirically demonstrated with haploid and diploid isogenic strains of yeast (Paquin and Adams, 1983).

In many sexual organisms whose germ line remains diploid, for the reasons given above, the ploidy level of somatic tissues is elevated (Bungenberg de Jong, 1957; White, 1973; Cavalier-Smith, 1978). This condition strongly suggests that there are advantages to polyploidy in addition to those that relate to the genetic system. As is the general case in plants, most polyploid parthenogenetic animals are larger than their diploid sexual and parthenogenetic relatives (Suomalainen, 1950; Muldal, 1952; Bungenberg de Jong, 1957). Some exceptions do exist in the urodeles and the orthopteran *Saga pedo*. Growth and developmental rates are also affected (Cavalier-Smith, 1978), and other subtle morphological, physiological, and behavioral changes may also accompany polyploidy.

One advantage to an increase in size, particularly in the case of poikilotherms, may be a parallel increase in fecundity, although

conspicuously larger size may also bring about greater attention from predators. Given that destabilizing hybridization that results from backcrosses with sexual relatives is a major barrier to the successful establishment of a new parthenogenetic lineage, an increase in body size by polyploidization may be the most rapid and least developmentally damaging means for a parthenogen to establish a prezygotic isolating mechanism. Such a cytogenetic event might provide a significant enough phenotypic change in the parthenogen to reduce attention from males without inducing other negative pleiotropic effects. Moreover, it is possible that polyploid eggs are less penetrable by sperms. This notion has received little attention, and it is not supported by Astaurov's (1972) experimental work on induced polyploidy and parthenogenesis in silkworms. Nonetheless, the ultimate consequences of backcrosses to a parthenogenetic lineage will undoubtedly depend on the level of ploidy. For instance, in the case of *Solenobia triquetrella* the fertilization of diploid parthenogens results in their immediate conversion to functional sexuality, whereas fertilized tetraploids produce largely sterile triploid intersexes (Seiler, 1936, 1942, 1969).

The cytogenetic properties of egg production by most parthenogens also appear to be consistent with predictions of the general-purpose genotype hypothesis. Automictic parthenogens that employ homozygosity-enforcing mechanisms are extremely rare (Nur, 1971; White, 1973; Stille and Davring, 1980). Even though most obligate parthenogens exhibit meiotic activity prior to egg formation, in almost all known cases premeiotic duplication, crossingover suppression, or fusion of nonsister pronuclei insure that automixis will be functionally equivalent to apomixis, and that offspring will be genetic replicates of their mothers, barring mutation (Uzzell, 1970; White, 1973). Yet the fact that a segregative automictic (heterozygosity-eroding) system represents the minimal deviation of a parthenogenetic mechanism from normal gametogenesis and fertilization suggests that such cytogenetic systems must be common among newly derived clones. This view is clearly sup-

ported by experimental work with *Drosophila* (Templeton, 1982, 1983). The extreme genetic inflexibility that results from the complete homozygosity that is ultimately imposed by segregative automixis will undoubtedly provide strong selection for cytogenetic modifications that maintain heterozygosity and the integrity of coadapted gene complexes (Templeton, 1982, 1983). It is of interest that most of the extant parthenogens that utilize homozygosity-enforcing mechanisms have evolved from haplo-diploid species, whose genotypes have presumably been selected in the past for their homozygous qualities (Nur, 1971).

Because of the prevalence of nonsegregative automixis and apomixis among parthenogens, it is not surprising that most asexual races exhibit enhanced levels of heterozygosity compared to their sexual relatives (White, 1970; Lokki, 1976a, b; Vepsäläinen and Järvinen, 1979). It is equally noteworthy, however, that the elevated heterozygosity of many parthenogenetic lineages is also a result of their hybrid origin. There are cytological reasons for expecting that interspecific hybridization will promote the capacity for parthenogenesis (White, 1973; Cuellar, 1974). Indeed, several successful syntheses of clones by means of a hybridization of sexual species have been accomplished in the laboratory (Harrison and Peacock, 1926; Astaurov, 1967, 1969, 1972; Schultz, 1973; Vrijenhoek and Schultz, 1974; White, Contreras, Cheney, and Webb, 1977; O'Rourke, 1979). Many natural parthenogens are suspected of having hybrid origins on morphological or electrophoretic grounds. In fact, there is no strong evidence that any extant vertebrate parthenogen has arisen by any mechanism other than hybridization. Nevertheless, hybridization is by no means the only possible route to parthenogenesis (Cuellar, 1974).

Why do such a large proportion of successful parthenogens owe their origin to interspecific hybridization? Again, this is a prediction to be expected from the general-purpose genotype hypothesis. Through a hybrid origin, a parthenogen may gain access to both of its parents' environments. Whether it also gains access to new habitats will depend upon the function of novel genic

combinations. Clearly, not all newly arisen parthenogenetic hybrids will be so adapted. The mere production of a reproductively competent parthenogen, regardless of its ecological characteristics, must be an extremely rare event. But this is also undoubtedly true of uniparental origins (Templeton, 1982, 1983). Another reason for the increased success of clones of hybrid origin may be their reduced vulnerability to backcross matings with the parental species. Whereas most newly arisen clones of uniparental origin will bear an extreme resemblance to their parent species and hence will attract a great deal of attention from males, parthenogens of hybrid origin may appear sufficiently different from either parent species to allow for some discrimination by males.

The expected characteristics of the genetic system of an obligate parthenogen can be summarized as follows: (1) polyploidy should be common among parthenogens; (2) homozygosity-enforcing automictic systems should be rare among parthenogens; (3) interspecific hybridization should be a common mode of origin of successful parthenogens (Table 1).

CONCLUDING COMMENTS

The hypotheses that I have raised are meant to provide insight into the ecology and evolution of parthenogenesis, which is a special form of asexuality. Since parthenogenesis is in all known cases derived from sexuality, it is by no means clear that studies on the constraints and correlates of parthenogenesis have any bearing on the more fundamental issues of how and why sex evolved. Investigations of parthenogenesis certainly are pertinent to the problem of the maintenance of sex. But even here a complete answer cannot be expected, since the interactions between parthenogens and their sexual relatives will often be very different from those of clones employing other forms of propagation. For example, obligate vegetative reproduction provides a complete release from the constraint of destabilizing hybridization.

If one accepts the validity of the destabilizing hybridization and general-purpose genotype hypotheses, one need not also reject dif-

TABLE 1

Expected characteristics of the genetic system of an obligate parthenogen under selection for a general-purpose genotype and for reproductive isolation from its sexual parental species

| Genetic Corollaries of the General-Purpose Genotype (G-PG) and Destabilizing-Hybridization (DH) Hypotheses | | |
|---|------|----|
| | G-PG | DH |
| 1. Polyploidy should be common among parthenogens | X | X |
| 2. Homozygosity-enforcing automictic systems should be rare among parthenogens | X | |
| 3. Interspecific hybridization should be a common mode of origin of successful parthenogens | X | X |

ferential competitive, coevolutionary, and colonization abilities as factors that influence the geographic and phylogenetic distribution of parthenogens. Many persons who have become embroiled in the evolution-of-sex controversy have subscribed to the philosophy that a hypothesis with broad explanatory power is always preferable to one with a narrower domain. Bell (1982) goes so far as to use this as a criterion for rejecting several alternative hypotheses in favor of his own "tangled-bank" model. Hypotheses with broad predictive capabilities are indeed useful, but it does not follow that they are actually correct. Biological systems are complex and probabilistic. The ecological and genetic constraints placed on one set of organisms may be very different than those on another. We may therefore find different mechanisms regulating the incidence of parthenogenesis in different phylogenetic groups.

I have attempted to focus attention on the stringency of the ecological and evolutionary challenges that a newly arisen parthenogen faces. It is my contention, as well as that of Templeton (1982, 1983), that we need a deeper understanding of the barriers to parthenogenesis and of the evolutionary dynamics of the transitional process, rather than a simple consideration of the ecological correlates of extant species. Only then can we develop a comprehensive theory for the distribution of parthenogenesis. The geographic distributions, ecological properties, and genetic attributes of most well-studied obligate parthenogens are consistent with the expectations derived from the destabilizing hybridization and general-purpose geno-

type hypotheses. Yet virtually all existing evolution-of-sex theory makes the assumptions, a priori, of the complete reproductive isolation and narrow adaptation of parthenogens.

The direct evidence for destabilizing hybridization as an influential factor in the establishment of parthenogenesis is so overwhelming that it is surprising that it has not received previous attention in the evolution-of-sex controversy. Existing hypotheses, such as the "biotic uncertainty" and "tangled-bank" models, interpret the frequent isolation of parthenogens in extreme, peripheral, or undeveloped habitats as a consequence of an inferior competitive or coevolutionary ability. It should now be clear that destabilizing hybridization is an equally likely candidate in many cases. Empirical investigations are needed in which parthenogens are released within the range of their sexual relatives, or vice versa (as in Darevsky and Danielyan, 1968) in order to illuminate this question.

The direct support for the general-purpose genotype hypothesis is less substantial than that for the destabilizing hybridization hypothesis, but the former idea is supported by population genetic theory, and there is considerable circumstantial evidence for it. It should also be noted that the alternative ecological hypotheses for geographic parthenogenesis, which are based on arguments regarding colonization or competition, are also without direct empirical support. In several of the examples that have been cited, the restricted range of sexual species relative to their parthenogenetic derivatives is clearly not a consequence of any lack of colonization

opportunities for the sexuals. Moreover, many parthenogenetic races have less restrictive habitat requirements than their sexual relatives do, and also a broader geographic range which includes that of the sexuals. These facts seem inconsistent with the claim that competitive inferiority is a general property of asexual lineages.

For many of the asexual-sexual complexes discussed, it should not be difficult to design experiments that are capable of discriminating between alternative ecological hypotheses for geographic parthenogenesis. For example, although the general-purpose genotype hypothesis does not fail to recognize that asexual individuals can have a higher probability than sexuals of colonizing a marginal habitat, this hypothesis is unique in its prediction that the long-term establishment of parthenogens in such environments will be facilitated because they possess generalized phenotypes. Artificial introductions of sexual populations and clones into extreme environments would shed considerable light on this point. More general tests of the general-purpose genotype hypothesis could also be performed by measuring the respective fitness response or tolerance of clones and of sexual individuals to environmental gradients. If parthenogens do show a reduced sensitivity of fitness to environmental change, then the general-purpose genotype hypothesis would be supported. Moreover, when information regarding the response of fitness to the environment becomes available for a large number of genetically marked clones, an explicit test of the hypothesis can be performed by growing the clones in a mixed culture in a temporally variable environment and monitoring the resultant succession.

Other than rampant speculation, based on biogeographical data, that most parthenogenetic races are post-Pleistocene in origin (Suomalainen, 1950; White, 1973), there are virtually no empirical estimates of the ages of clonal reproducers in comparison with their sexual relatives. Even approximate estimates of clonal ages that are based on well-founded assumptions would provide a great deal of information about the evolutionary tenacity of the more successful parthenogens. Recent developments in elec-

trophoretic and immunological distance analysis, in DNA hybridization, and in recombinant DNA technology could all be exploited to do this. The potential utility of such work is illustrated by a recent study by Abreau-Grobois and Beardmore (1982). In an electrophoretic survey of the genus *Artemia*, these authors were able to estimate the age of the parthenogenetic race to be $\sim 10^6$ years. In a broader context, particularly for establishing the rates of clonal origin, extinction, and evolution, long-term studies are badly needed on the clonal dynamics of obligate parthenogens. Other than the limited data of Hebert and Crease (1980), Ochman, Stille, Niklasson, Selander, and Templeton (1980), and Lynch (1983), there is virtually no information available regarding the temporal dynamics of obligate parthenogens.

Another major challenge is to develop a theory for the phylogenetic distribution of parthenogenesis. The striking frequency of parthenogenesis in such groups as the enchytraeid and lumbricid oligochaetes, parasitic nematodes, rotifers, cladocerans, ostracods, aphids, and curculionid weevils contrasts with its complete absence among birds and mammals and its extreme rarity in the molluscs. This uneven phylogenetic distribution of thelytoky suggests that some groups may have a predisposition for the transition to parthenogenesis. Many factors, which include cytogenetic barriers and the social and spatial structure of populations, are probably involved. Given the significance of a generalist strategy for the survival of an asexual lineage, however, the ecology of a taxon must have a great deal of influence upon its likelihood of producing a successful parthenogenetic lineage. Sexual populations that are tolerant of only a narrow range of ecological conditions would be unlikely to spawn many long-lived clones.

It is in this light that the characteristic immobility of many parthenogens (White, 1973; Lokki and Saura, 1979) takes on new meaning. For instance, parthenogenesis is relatively rare among the Lepidoptera, whose adults are fairly mobile. Of the seven known asexual species in the order, five of them (*Solenobia fennicella*, *Solenobia lichenella*, *Solenobia triquetrella*, *Luffia lapidella*, and *Apterona helix*) are psychids, one (*Orgyia dubia*) is a

lymantriid, and one (*Alsophila pometaria*) is a geometrid. All seven species are characterized by wingless females. The only known parthenogenetic mantid, *Brunneria borealis*, is almost completely apterous (White, 1948). Both of the well-known parthenogenetic orthopteran, *Saga pedo* and *Warramaba virgo*, are also exceptionally sedentary, and most of the parthenogenetic weevils are wingless, or at least flightless. Immobile organisms may be ecologically preadapted to make the transition to parthenogenesis because they are unable to select specific habitats actively and to seek out refuges from adverse climatological and biological conditions. This view is contrary to the opinion of White (1973), who has suggested that parthenogens and immobile organisms in general are extremely specialized.

The absence of parthenogenesis in extant birds and mammals is puzzling, especially when one considers that both groups exhibit a rudimentary potential for the spontaneous development of unfertilized embryos (Beatty, 1967). By analogy with the above argument, homeothermy would seem to be a preadaptation to parthenogenesis because it reduces dependency on the external environment. When one considers the large number of lizard species that have made the transition to parthenogenesis (Cole, 1975), it does not seem likely that the cytogenetic or developmental barriers to parthenogenesis are exceptionally stringent in the amniotes. Complete parthenogenetic development has been experimentally obtained in turkeys, although all transitional individuals have been males (Olsen and Mardsen, 1954; Olsen, 1965). It is worth considering that destabilizing hybridization resulting from the relatively high degree of mobility and the opportunistic breeding of birds and mammals could provide an insurmountable barrier to the long-term establishment of parthenogenesis in these groups.

Finally, a thorough understanding of the evolution and ecology of parthenogenesis may take on added significance in the future in the area of pest management (DeBach,

1969; Templeton and Rankin, 1978). Many recently developed pest-control techniques, such as the use of sex attractants and the release of sterile males (International Atomic Energy Agency, 1971) attempt to reduce economically important insects by interfering with their reproductive strategies. One clear consequence of such practices will be strong selection for parthenogenetic modes of reproduction among pest species. Whether a response to such selection will actually occur remains to be seen, but it is worth noting that several significant parthenogenetic pests are already known to exist. These include a number of nematodes, ticks, spider beetles, and mealy bugs, the larch sawfly and the European spruce sawfly, the fall cankerworm, the cockroach, the rice weevil, and the black vine weevil. The importance of selection for parthenogenesis is underscored when one considers the formidable pest that might result should the transition to parthenogenesis be accompanied by the evolution of a highly generalized genotype. On the other hand, it is conceivable that an equally formidable control agent might be developed from research on parthenogenetic races of the parasitic Hymenoptera (DeBach, 1969).

ACKNOWLEDGMENTS

An appointment in the University of Illinois Center for Advanced Study provided me with the time needed to complete this review. Discussions and correspondence with B.-L. Brett, B. Christensen, J. Lokki, U. Nur, J. Oliver, A. Saura, E. Suomalainen, A. Templeton, A. Triantaphyllou, and T. Uzzell helped clarify a number of points in this paper, as did many useful comments on the manuscript by R. Crozier, T. Uzzell, A. Weis, and M. Willson. I am especially grateful to Graham Bell for extensive criticism of my ideas and for writing his own book. Although our interpretations of the existing data are radically different in many respects, we both agree that closer attention to biological detail will greatly facilitate our understanding of evolution-of-sex problems. Future research will reveal which of us, if either, is correct.

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