

## Why do parthenogenetic lizards hybridize with sympatric bisexual relatives?

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Received 21 June 1989; 6 December 1989

**ABSTRACT:** A theoretical model is presented to suggest that unisexual lizards are not obligate parthenogens, but rather facultative parthenogens capable of engaging in sex and hybridization with males of sympatric sexual species. Parthenogenetic females may participate in hybrid crosses to acquire elements of a sexual male's genome, which are the product of several generations of recombination and selection in a sexual lineage. Acquisition of new genetic material from a male may allow a parthenogenetic lineage to adapt to a changing environment. The proposed model more fully utilizes existing information on unisexual lizard biology than the traditional evolutionary model. The proposed model argues that sequential hybridization and "genetic piracy" by unisexual lizards is an evolutionary adaptation introducing genetic variation into a clonal line.

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### Introduction

During studies of parthenogenetic lizards in the genus Cnemidophorus (Billy, 1988, 1987, 1986; Billy and Crews, 1986; Moore et al., 1984), I was exposed to several field and laboratory studies that reported findings and observations inconsistent with assumptions or predictions of evolutionary models applied to parthenogenetic animals. In the sections to follow, I propose to outline the generally accepted view on the evolutionary biology of parthenogenetic Cnemidophorus, then present observations at odds with the standard view, and finally propose a new model consistent with the observed biology of Cnemidophorus lizards. This paper presents the hypothesis that hybridization between unisexual and bisexual lizards may be an evolutionary mechanism, of benefit to both parents, that introduces new genetic material into an ongoing clonal line. The proposal to follow will emphasize the biology of lizards in the genus Cnemidophorus, but certain key points are supported with reference to parthenogenetic lizards in the genus Lacerta and other parthenogenetic animals.

Animals reproducing asexually via parthenogenesis have traditionally been described as evolutionary dead-ends and temporally successful as transient or short-lived lineages (Cuellar, 1977a; Mayr, 1970; Maynard Smith, 1978; Uzzell, 1970). Parthenogenetic reproduction is described as an evolutionary liability because meiotic recombination does not occur. Parthenogenesis fixes the degree of genetic variation present in the parent and duplicates it in the next generation. Thus, cytogenetic mechanisms underlying unisexual reproduction produce little genotypic variation over time. While random mutations may increase heterozygosity in a clonal line, several authors have argued that the increased mutational load is deleterious (Felsenstein, 1974; Maynard Smith, 1978; Muller, 1964). Sexual reproduction, however, is perceived as generating new genotypes each generation via syngamy and meiotic recombination. Some of the new genotypes may be better adapted to their environment than other genotypes and possess relatively high fitness and reproductive success. Conversely, parthenogenetic lineages, with essentially unchanging genotypes, are described as being at a competitive disadvantage in adapting to a changing environment compared to sympatric sexual lineages (Cuellar, 1977a; Glesener and Tilman, 1978; Ghiselin, 1974; Jaenike, 1978; Rice, 1983; Slobodchikoff and Daly, 1971). Most evolutionary models comparing sexual and parthenogenetic modes of reproduction assume that parthenoforms are reproductively and ecologically isolated from their sexual relatives and that clonal lineages are narrowly adapted to the environment compared to sexual lineages.

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Evolutionary Theory 9: 225-238 (June, 1990)

The editors thank J.P. Bogart and T. Uzzell for help in evaluating this paper.

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The genus Cnemidophorus consists of 40 species of whiptail lizards including 15 all-female, parthenogenetic species (Darevsky et al., 1985; for taxonomic reviews and discussions, see Cole, 1985; Frost and Wright, 1988; Maslin, 1968; Walker, 1986). Parthenogenetic species of Cnemidophorus have been studied for several decades and considerable information exists on their ecology, reproductive biology, and behavior. Each diploid parthenogenetic species is believed to have arisen in the F<sub>1</sub> generation following a hybridization event between two diploid sexual species. Unisexual taxa may be diploid (e.g. C. neomexicanus) and/or triploid (e.g. C. tessellatus; Fritts, 1969; Parker, 1979 a,b; Parker and Selander, 1976). Triploid parthenoforms are believed to be produced following a back-cross between the diploid parthenoform and one of the sexual parental species (Lowe and Wright, 1966; Wright and Lowe, 1967a, 1968). The important role of hybridization between sexual species, and subsequent back-crossing between parthenogenetic progeny and representatives of a sexual species in generating unisexual lineages has already been well-established in a series of karyological, electrophoretic, histocompatibility, morphological, and mitochondrial DNA studies (reviewed by Darevsky et al., 1985).

Unisexual lizards are considered obligate parthenoforms because of: absence of males in population samples (Cole, 1975; Fritts, 1969; Maslin, 1962; McCoy and Maslin, 1962; Tinkle, 1959; Zweifel, 1965), absence of spermatozoa in the female oviducts (Cuellar, 1968), skin graft histocompatibility within a clonal line (Maslin, 1967), fixed karyological (Lowe and Wright, 1966) or electrophoretic (McKinney et al., 1973; Neaves, 1969; Parker and Selander, 1976) heterozygosity within a clonal line, and virgin reproduction by isolated females in the laboratory (Cole and Townsend, 1977; Maslin, 1971). Parthenogenetic taxa may consist of at least one (as in C. uniparens, Cuellar, 1977b) and up to 13 clonal lines (as in C. tessellatus, Parker and Selander, 1976), with most taxa having 1, 2, or 3 clonal lines. Clonal diversity within a unisexual species has been attributed to multiple initial hybridization events (Parker and Selander, 1976), mutation (Cuellar, 1977a,b), and/or recombination, although the relative importance of each process has not been clarified. Some taxa possess extremely widespread and successful clones (Cuellar, 1976, 1977b; Maslin, 1967; Parker and Selander, 1976).

### The Traditional Evolutionary View of Parthenogenetic Animals

The traditional evolutionary view of parthenogenetic lizard biology (e.g. Cuellar, 1977a) assumes or predicts that: 1) asexual taxa are relatively short-lived phenomena compared to related sexual taxa; 2) parthenogenetic taxa are at a competitive disadvantage and will not be able to coexist with populations of their bisexual relatives; 3) asexual forms possess limited genetic variation, and 4) asexual taxa are obligate parthenoforms.

The first theoretical point cannot be properly addressed as asexual and sexual forms of Cnemidophorus are contemporaneous and have been studied only for approximately 40 years (Duellman and Zweifel, 1962; Maslin, 1962; Minton, 1959; Tinkle, 1959). While parthenogenetic taxa are younger than their sexual relatives as they are the products of hybridization events between existing sexual species (e.g. Lynch, 1984; Uzzell and Darevsky, 1975), there is no evidence to support the argument that unisexual taxa are short-term evolutionary phenomena. However, one study does document evolutionary persistence in an asexual parthenogenetic mollusc, Melanoides tuberculatus, which has persisted and undergone long-term evolutionary changes in parallel to its sexual relatives from at least the Cenozoic era (Williamson, 1981).

While Suomalainen et al (1987) do not accept Williamson's conclusion regarding parthenogenetic M. tuberculatus persisting over time, the point remains open to interpretation. Suomalainen et al (1987) note that parthenogenetic taxa are derived from bisexual taxa and that unisexual taxa do not generate bisexual taxa, so the deduction that M. tuberculatus was parthenogenetic throughout its history seems reasonable. Suomalainen et al (1987) recognize that M. tuberculatus is a variable species with some populations being unisexual while others consist of 20-30% males; and since they accept the concept that "...rare bisexual individuals may promote diversity in some parthenogenetic populations" (p. 173), (whereas the proposed model would imply that this variability may be due to hybridization with a sexual species), the biology of M. tuberculatus still appears to support the proposed model. No evidence exists to indicate that parthenogenetic organisms are short-lived in evolutionary time. While certain models may predict a short existence for parthenoforms, animals do not necessarily have to comply with computer models. The model proposed in this paper implies that a mechanism exists for parthenogenetic animals to persist over time in association with sexual congeners.

The remaining three key features of the traditional evolutionary model can be challenged on the basis of consistent, repeated reports and observations in the existing literature. Such inconsistencies between predicted and actual aspects of unisexual lizard biology suggest revisions may be required in evolutionary models applied to unisexual lizards.

Parthenogenetic species of *Cnemidophorus* characteristically co-exist in close association with sexual congeners (Christiansen, 1969; Cuellar, 1979; Cuellar and McKinney, 1976; Darevsky et al., 1985; Echernacht, 1967; Lowe et al., 1970; Milstead, 1957; Parker and Selander, 1976; Peccinni-Seale and Frota-Pessoa, 1974; Zweifel, 1965). Studies focussing on ecological relationships between asexual and sexual taxa have found that the asexual taxa consistently outcompete or are more successful in certain habitats than related sexual taxa. Unisexual species not only coexist with sexual species, they have also colonized habitats apparently inhospitable to their presumed sexual ancestors (Christiansen, 1971; Cuellar, 1977a, 1979; Darevsky et al., 1985; Maslin, 1968, 1971; Milstead, 1957; Parker and Selander, 1976; Van Denburgh and Slevin, 1913; Wright, 1968; Wright and Lowe, 1965, 1968). Lynch (1984) reviewed arguments against the idea of competitive inferiority in parthenogenetic animals.

Studies focussing on biochemical and morphological characters indicates that the degree of variance is equivalent in parthenogenetic and related sexual species of lizards (in *Cnemidophorus*, Parker, 1979a; in *Lacerta*, Darevsky, 1966). Comparable degrees of variance in asexual and sexual forms argues against evolutionary superiority for sexual forms in a shared environment and indicates that genetic variance in unisexual lineages may arise in a non-traditional manner (i.e. other than regular meiosis and recombination which are apparently absent in clonal lineages). Zweifel (1965) originally speculated that even rare matings between parthenogenetic females and sexual males would significantly increase genetic variation in the next generation.

While isolated unisexual lizards are known to reproduce by parthenogenesis in the laboratory, field and laboratory studies often report that courtship and mating occurs between females of parthenogenetic species and males of sexual species (Cuellar and McKinney, 1976; Lowe et al., 1970; Maslin, 1966, 1971; Neaves, 1971). Indeed, the basic premise underlying the origin of all triploid parthenogenetic lizard species in the genus *Cnemidophorus* is successful courtship, copulation, syngamy, and production of offspring in crosses between a diploid parthenogenetic female and a diploid sexual male. While successful inter-specific hybridization may be a rare event in parthenogenetic lizard biology, it clearly does occur and has important consequences.

The statement that unisexual lizards are obligate parthenoforms should only be abandoned if evidence exists indicating successful sexual reproduction and production of fertile offspring. Studies do indicate that parthenogenetic lizards are capable of clonal reproduction and sexual reproduction; and that crosses between parthenogenetic females and males from sexual species can produce viable, fertile progeny potentially capable of sexual reproduction. Cole (1979) demonstrated that viable hybrid progeny can be produced by mating a parthenogenetic female (*C. sonorae*) with a sexual male (*C. tigris*). This experiment also indicated that inter-specific crosses between animals from different species groups within the genus *Cnemidophorus* (characterized by distinctly different genomes) can occasionally produce viable offspring. At least 52 cases of progeny produced by hybridization between sympatric asexual and sexual species have been reported from field collections (reviewed by Cuellar and McKinney, 1976; Darevsky et al., 1985; Maslin, 1971). Field collections of unisexual *Cnemidophorus* (Taylor et al., 1967) and *Lacerta* (Darevsky, 1966; Darevsky et al., 1978; Uzzell and Darevsky, 1975) have included males that were assigned to presumed unisexual, parthenogenetic species. Billy (1986), Cuellar and McKinney (1976), and Lowe et al., (1970) have argued that these "anomalous males" should be regarded as progeny produced by sex and hybridization. Billy (1986) has also argued that inviable male embryos assigned to parthenogenetic species of *Lacerta* (Danielyan, 1970; Darevsky, 1960, 1966; Darevsky and Kulikova, 1961; Darevsky and Kupriyanova, 1982; Darevsky et al., 1985) should be considered as progeny produced in hybridization events between a parthenogenetic female and a bisexual male.

While most hybrid animals were not tested for reproductive capacity, or possessed reproductive tract deformities (e.g. Maslin, 1971), Neaves (1971) reported a female hybrid with a functional ovary and Fritts (1969) and Maslin (1971) described male hybrids with a normal testes capable of sustaining spermatogenesis. Similarly, Dobrovolskaja (1964) reported that a male animal assigned to a parthenogenetic species of *Lacerta* possessed an apparently functional testis. Saxon (1968) reported that a male hybrid *Cnemidophorus* performed normal copulatory behavior and produced motile sperm, but offspring were not produced in an experimental cross. While no evidence exists to indicate that hybrid progeny are capable of producing viable offspring since sufficient mating tests have not been conducted,

there is evidence that hybrid progeny do occasionally produce viable gametes and engage in normal reproductive behavior.

The scarcity of fertile offspring produced by asexual-sexual crosses should be considered in light of three factors: 1) eggs produced by parthenogenetic lizards normally have low survivability; 2) genomic incompatibility in most hybrid crosses produces many inviable offspring; and 3) difficulties exist in detecting hybrid offspring in field collections.

Parthenogenetic animals generally have lower reproductive rates than their sexual relatives (e.g. Bullini, 1965; Roth, 1974). This reproductive deficiency has been attributed to developmental abnormalities reducing hatching success (e.g. Murdy and Carson, 1959; Roth and Willis, 1956; Templeton, 1979) or to smaller clutch sizes in parthenogens (e.g. Frankel, 1978). Parthenogenetic lizards theoretically have nearly a twofold greater reproductive potential than their sexual relatives as all offspring are reproducing females (Congdon et al., 1978; Maslin, 1971; Wright and Lowe, 1968). This higher reproductive potential for parthenogenetic animals may not be reached (Schall, 1978) because parthenogenetic lizards have a higher rate of errors in embryonic development than their sexual relatives (Billy, 1986; Darevsky, 1966, 1960).

Hatching success in laboratory raised parthenogenetic lizards is lower than in related sexual species and has been reported between 8% and 41% (Billy, 1988; Cuellar, 1984; Maslin, 1966). Cole and Townsend (1977) reported a hatching success of 75% for laboratory-reared *C. exsanguis*, but only eggs oviposited under very specific conditions were collected in this study. A generally low hatching success in parthenogenetic lizard eggs may be due to genomic incompatibility between individuals participating in a hybrid cross which reduces egg viability and causes developmental problems during embryogenesis.

A certain proportion of female hybrids have probably not been detected in field collections because hybrid animals usually resemble the parthenogenetic female parent (e.g. Cuellar and McKinney, 1976). Male hybrid embryos or adults may be easier to detect because of the conspicuous hemipenes. While fertile adult hybrids produced in crosses between a parthenogenetic female and a sexual male are rare, they are produced and are potentially capable of sexual reproduction.

Karyological studies of hybrid offspring presumably produced in crosses between asexual and sexual species of *Cnemidophorus* have reported triploid (e.g. Maslin, 1971; Neaves, 1969) and tetraploid (Cole, 1979; Lowe and Wright, 1966; Lowe et al., 1970; Neaves, 1971) individuals. Hybrid individuals with different ploidy levels supports a key concept underlying the model proposed in this paper. If diploid parthenogenetic species were originally produced in hybridization crosses between diploid sexual species, and subsequent crosses with a sexual male introduces new genetic material into the next generation of parthenogenetic lizards, then hybridization acts as a mechanism which increases genetic variation. The degree of genetic variation introduced into the next generation may be placed along a continuum ranging from no new genetic information (production of inviable offspring) to introduction of considerable new genetic variation (production of new clonal lines and/or taxa). In some inter-specific crosses, hybridization adds a haploid set of chromosomes to the next generation's genome; in other inter-specific crosses, as in the original crosses which produced diploid parthenogenetic species, hybridization does not alter ploidy levels in the next generation. The important variables to consider on the continuum of hybridization consequences are the genetic components regulating the degree of genomic compatibility between parents and factors regulating the insertion of entire chromosomes into a new genotype. If hybridization between species of *Cnemidophorus* is not a reproductive error, it may be an adaptation that allows parthenogenetic animals to acquire elements of a sexual male's genome, increase genetic variation in the next generation, and adapt to a changing environment.

Darevsky et al. (1985) argued that the combination of specific genomes from diploid, sexual species is required to produce diploid, hybrid parthenogenetic progeny. Also, production of hybrid individuals with higher ploidy (triploid or tetraploid) requires an additional one or two hybridization events, respectively, with the required compatibility matches between parental genomes likely to occur in only a few specific crosses. Darevsky et al. (1985) suggested that diploid and tetraploid hybrid offspring would be capable of sexual reproduction if the two genomes from the same parental species synapsed, went through meiosis, and produced haploid gametes. A key concept to consider is that different combinations of parental genomes interacting in different hybridization crosses could introduce varying degrees of genetic variation into the next generation - ranging from no effect to production of a new clonal line to production of a presumably new taxon (either parthenogenetic or sexual). New clonal lines within a parthenogenetic taxon may represent relatively minor genetic inputs from a sexual lineage when no change in ploidy occurs, and relatively major genetic inputs from the sexual lineage when ploidy levels increase to generate new parthenogenetic clonal lines or taxa.

### A Model Based on Facultative Parthenogenesis and Opportunistic Hybridization

Figure 1 outlines the basic proposal that hybridization between asexual and sexual species of Cnemidophorus is an evolutionary adaptation introducing genetic variation into asexual lineages. Figure 1 illustrates different hybridization crosses that can occur between sexual and asexual species and the resultant progeny produced in such crosses. Thus, the model presents the view that unisexual taxa are not obligate parthenoforms but rather facultative parthenoforms capable of asexual reproduction and opportunistic sex and hybridization.

The proposed model assumes that the hybrid Cnemidophorus of yesteryear, which established new lineages with increased genetic variation, are similar to the hybrid Cnemidophorus of today. In both cases, crosses between different sets of parental species presumably produced many inviable embryos, some sterile adults, and occasionally - a rare individual capable of clonal and/or sexual reproduction. Field and laboratory studies indicate that lizards from clonal, hybrid lineages engage in courtship and pseudosex with other unisexual lizards, and engage in courtship and sex with sexual congeners.

The proposed model is based on the following elements of parthenogenetic lizard biology: 1) hybridization occurs between sympatric unisexual and bisexual taxa; 2) hybridization produces viable, parthenogenetic and/or sexual offspring, and 3) hybrid offspring may or may not be characterized by an increase in ploidy levels. An overview of the proposed model indicates that a diploid parthenogen produced through hybridization may generate new clonal lines after additional, future hybridization events. Occasionally, triploid offspring may be generated and future hybridization events may generate additional triploid clonal lines or, rarely, tetraploid individuals. Hybridization may also generate occasional sexual offspring that then breed with individuals from sympatric sexual species. Male hybrids have the option of reproducing sexually with females from sexual or parthenogenetic species. There is no reason to suspect hybrid males to be capable of parthenogenesis. Female hybrids have the option of reproducing parthenogenetically or sexually with a male from another species (or a male hybrid). Clonal reproduction should remain intact in female hybrids since the genes regulating parthenogenesis are not lost in hybridization. The evidence to support the idea that hybrid females possess a combined capacity for sexual and parthenogenetic reproduction is present in existing species of triploid parthenogenetic lizards. Each triploid species originated from a hybrid animal produced through sexual reproduction involving a diploid parthenogenetic female and a diploid sexual male. Since triploid females are known to hybridize with sexual males, and the resultant offspring (of both sexes) are apparently capable of mating and producing viable gametes, then hybrid progeny can potentially mate with individuals from sexual species.

The proposed model is amenable to experimental evaluation by examining progeny produced in laboratory hybridization crosses. Such crosses could be performed by placing females from unisexual species of Cnemidophorus with males from sympatric sexual species or by artificially inseminating females with sperm from a mature male. Hybrid offspring have been detected in several field collections, but have been produced in the laboratory only once.

While the frequency of hybridization events producing viable offspring in nature is unknown, it is clear that hybridization does occur and viable parthenogenetic and sexual offspring are occasionally produced. If one takes the view that hybridization events are not mistakes or errors, but rather a genetic gamble with probable risks and benefits, what are the benefits to individuals participating in this reproductive system? The proposed model assumes that hybridization introduces new genetic material into an asexual lineage with possible favorable genetic consequences to both parents.

The parthenogenetic female parent may benefit from a hybridization event by acquiring genetic material from a successful male in a common environment. Such a male is likely to be the product of several generations of recombination and selection acting on various genotypes that have appeared in the environment. While a parthenoform cannot rapidly generate new genotypes through meiotic recombination, hybridization and "genetic piracy" of a successful genotype could conceivably insert new genetic material into a clonal line. By slightly modifying a successful clonal genotype after sex and hybridization, access to new genetic material may result without disrupting the set of genes coding for parthenogenetic reproduction. Furthermore, this genetic exchange would help prevent establishment of behavioral and morphological barriers to hybridization; a consequence of the model that appears to be supported by field studies of sympatric congeners (e.g. Cuellar and McKinney, 1976). In some cases, certain genetic inputs may override or interfere with parthenogenetic reproduction and produce sterile or sexual offspring.

The sexual male parent may benefit from a hybridization event by inserting his genetic material into a cloning reproductive system. Parthenogenesis will produce many additional copies of the male's genes in the following generations.

The proposed reproductive system combines the benefits of asexual reproduction, which rapidly duplicates a fit genotype and maintains adaptive maternal and paternal gene combinations, with the benefits of prior sexual reproduction, which generates diverse genotypes in a changing environment. The potentially negative costs of hybridization to each parent may be outweighed by possible benefits produced by entering a small proportion of gametes into the genetic lottery of hybridization.

Since parthenogenetic lizards can produce up to two clutches of eggs each season, and since a hybridization event apparently does not necessarily fertilize all the eggs in a female's oviduct (Cole, 1979; Darevsky and Danielyan, 1968), a female could conceivably combine parthenogenetic reproduction with sexual reproduction. Therefore, a single clutch of eggs could consist mostly of unfertilized eggs, which preserve the original clonal line, while a fertilized egg from the same clutch generates a new clonal line. In this system, a parthenogenetic female risks only a proportion of her eggs in a sexual lottery, while still reproducing via parthenogenesis, and a male gambles a proportion of his sperm on a parthenogenetic female while still inseminating sexual females during the mating season. Although a detailed "costs-benefits" analysis of the proposed model is beyond the scope of this paper, such an analysis may help explain the apparent success and high degree of genetic variability present in clonal lines. Such a reproductive strategy would combine the benefits of asexual reproduction while allowing risks to be taken in securing new genetic inputs through hybridization, which may or may not involve compatible parental genomes.

If several hybridization events occur over time, and each one only slightly modifies the original clonal line, a variety of slightly divergent clonal lines would be produced - each with different survival characteristics. An expected consequence of genetic inputs from sequential hybridization is that a single clonal line persisting for several generations could conceivably receive inputs from more than one sexual relative. This consequence of the proposed model has been detected since the genomes of parthenogenetic *C. exsanguis* (Good and Wright, 1984) and the triploid derivative of *C. tessellatus* (Parker and Selander, 1976; Wright and Lowe, 1967B) each consist of elements from three ancestral species, and not just the two parental species. Hybridization apparently can occur between a parthenogenetic female and a sexual male from any sympatric species. Assuming weak anti-hybridization barriers between the parthenoform and its parental species, stronger anti-hybridization barriers should exist between the parthenoform, the two parental species and the more distantly related third sympatric species. And yet, at least two sets of studies indicate that the parthenoform has mated with the third sexual species. The proposed model implies that parthenoforms mate with sympatric sexual species (parental and/or non-parental) and that such matings are not simply cases of mistaken identity. As distributions of sexual species change, parthenogenetic females within a clonal line may be exposed to, and hybridize with, males from different sexual species at different times. While the traditional evolutionary model assumes that triploid parthenogenetic species are produced after a back-cross between a hybrid diploid parthenoform and a male from one of the sexual parental species, the proposed model implies that a parthenoform may incorporate genetic material from any sympatric sexual species with a compatible genome. Furthermore, inter-specific hybridization provides a mechanism to produce multiple clonal lines and/or new taxa by inserting new genetic material into an existing clonal line.

Hybridization between asexual and sexual lizards does not generate progeny intermediate in parental phenotypic characteristics. Several studies have shown that many characters more closely resemble the maternal parent than the paternal parent (Christiansen and Ladman, 1968; Cuellar and McKinney, 1976; Lowe et al., 1970). This is particularly true in cases of triploid hybrids, which possess twice as much genetic material from the maternal parent than from the paternal parent. Other studies emphasize that the expression of certain characters are influenced by non-additive interactions between the parental genomes (epistasis, dominance) resulting in a range of character expressions in different clonal lines (Parker, 1979b). This clonal variation is believed to originate through multiple hybridization events (Parker, 1979b).

The proposed model incorporates certain observed facets of parthenogenetic lizard biology not incorporated by the traditional model. The proposed model implies that weak anti-hybridization barriers, ecological overlap and coexistence will be maintained by on-going inter-specific hybridization between parthenogenetic and sexual species as parthenogenetic species need to maintain contact with sympatric congeners acting as "genetic hosts". To the best of my knowledge, no parthenogenetic species is completely geographically or ecologically separated from a sexually reproducing species.

### Problems with the Proposed Model

A central flaw in both the proposed and traditional models is reference to unspecified genetic mechanisms to insert elements of the paternal genome into the hybrid offspring genome, while not disrupting the maternal genes regulating parthenogenesis (Lynch, 1984 discussed genetic disruptions caused by hybridization). The underlying mechanism associated with an increase in ploidy to produce triploid or tetraploid individuals is the fusion of a haploid sperm with a diploid or triploid parthenogenetically produced egg, respectively (Maslin, 1971; Neaves, 1969). Somatic ploidy is maintained in succeeding generations by chromosomal endoduplication, followed by normal meiosis involving crossing over between identical chromatids (Cuellar, 1971).

The cytogenetic processes that occur following hybridization to incorporate sets of chromosomes or chromosomal elements without altering ploidy levels, as hypothesized for the production of multiple clonal lines in diploid parthenogenetic species of *Cnemidophorus*, are not known. A speculative point presented in this model is that hybridization may produce hybrid offspring without an accompanying increase in ploidy produced by insertion of a complete haploid set of chromosomes from the sexual male parent. To date, hybrid identification has relied heavily on detecting the haploid set of chromosomes contributed by the male parent. Consequently, offspring exhibiting an increase in ploidy are defined as hybrids, while offspring not exhibiting an increase in ploidy are defined as non-hybrids. If entire haploid sets of male chromosomes can be incorporated into a genome following hybridization, could the same mechanism incorporate smaller elements of the male genome? If such genetic exchange mechanisms exists, then hybridization between a parthenogenetic female and a sexual male could generate multiple clonal lines without changing ploidy levels or disrupting parthenogenesis. At present, I am speculating that the genomic consequences of hybridization lead to disruption of meiosis and occasional exchanges between paternal and maternal genomes through crossing-over between chromosomes. Different hybridization events may insert varying amounts of the sexual male's genome into the offspring's genome - thus producing a range of possible genetic outcomes - from slight modification of the clonal genotype to the addition of an entire set of chromosomes.

While the proposed model is speculative, it is more consistent with documented parthenogenetic lizard biology than the traditional evolutionary model. Furthermore, while the proposed model requires an undefined cytogenetic mechanism to incorporate male genes into the unisexual female genome, it invokes essentially the same undefined cytogenetic mechanism accepted by the traditional model to generate multiple clonal lines and increased ploidy levels following hybridization. Incorporation of elements of a sexual male's genome into facultative parthenogenetic lineages may represent an evolutionary adaptation that allows clonal taxa to adapt to a changing environment.

If such a mechanism exists to produce variation in the amount of chromosomal material incorporated in different hybrid crosses, then surveys of parthenogenetic taxa showing distinct karyotypes in different regions (as in Peccinini-Seale and Frota-Pessoa, 1974) could be interpreted as examples of hybrid progeny from different hybridization events incorporating different elements of the male parental genome. Peccinini-Seale and Frota-Pessoa (1974) reported five geographically distinct karyotypes for diploid *C. lemniscatus* characterized by different chromosome numbers and configurations. This observation argues that considerable genomic compatibility exists between hybridizing species and new clonal lines may be occasionally generated depending on interactions between maternal and paternal genomes.

At present, it is not possible to specify factors regulating genomic compatibility and genomic interactions in inter-specific hybridization. In general, a relatively high degree of genomic compatibility is indicated by the finding that certain bisexual species are implicated in the hybrid origin of more than one unisexual species (e.g.s *C. tigris*, *C. inornatus*, *C. septemvittatus*, *C. gularis*; reviewed by Darevsky et al., 1985). Thus, while hybridization is invoked to generate new clonal lines and/or taxa, the cytogenetic mechanism regulating genomic compatibility, paternal gene expression within a clonal line, and changes in ploidy level have not been studied in depth. Nevertheless, existing evidence implies that the paternal genetic contribution is variable and ranges from no contribution because of genomic incompatibility to the production of new diploid clonal lines without altering ploidy levels, to the contribution of an entire haploid set of chromosomes to produce triploid or tetraploid progeny. Even when an entire set of chromosomes is added to a genome, it is not known to what degree the paternal contribution is expressed. It is conceivable that only a small proportion of the paternal genes are activated and expressed while the remainder are held in a "genetic reservoir". Furthermore, it is also possible that different triploid clonal

lines in a parthenogenetic taxa may be expressing different sets of genes although no evidence exists to support or contradict these speculations.

While the meiotic mechanisms underlying reproduction in several parthenogenetic animals have been studied (reviewed by Uzzell, 1970; for *C. uniparens*, see Cuellar, 1971), no studies have examined the possibility of variation within the established mechanism. While hybridization can greatly disrupt genomic stability (Lynch, 1984), no studies have specifically examined the consequences of hybridization on subsequent egg development in parthenogenetic lizards. The paternal genetic contribution to the hybrid genome may range from zero to the contribution of an entire haploid set of chromosomes and not be restricted to just the two extreme possibilities. The concept of variable paternal genetic contributions into the hybrid genome was considered and dismissed by earlier workers. Wright (1968) considered an "intergrading clones" model that implied genetic material could be transferred from one clone to another by either occasional males of a unisexual species, males of a bisexual species, or by males produced in hybrid crosses. Wright (1968) dismissed the idea of males inserting new genetic material into clonal lines based on an analysis of three sympatric species that preserved separate morphological identities without producing intergrading clones. While the initial model and Wright's analysis assumed intergrading clones would be characterized by morphological intermediacy between two distinct forms, the possibility remains that the male genetic input may be more subtly expressed. This point is important particularly since other studies indicate that multiple clonal lines within a parthenogenetic taxa, which were attributed to multiple hybridization events, were characterized by the maternal genomic contribution being much more obvious than the male genomic contribution (e.g. Christiansen and Ladman, 1968; Cuellar and McKinney, 1976). Other studies also recognized the presence of a significant male genetic input (particularly in the formation of triploid clonal lines or new taxa) that are not characterized by distinct morphological intermediacy. Thus, the possibility of detecting variable male genetic inputs into a hybrid genome should remain as a possible factor in parthenogenetic lizard biology until the question is specifically examined in experimental studies.

The statement that apparent all-female vertebrate taxa are not obligate parthenogens has recently been supported by studies of salamanders in the genus *Ambystoma*. In striking parallel to the biology of *Cnemidophorus* lizards, hybridization between diploid species of *Ambystoma* is believed to have generated diploid, triploid, and tetraploid all-female taxa that presumably reproduce via parthenogenesis (Downs, 1978; Kraus, 1985 a,b; Uzzell 1970,1969) or gynogenesis (Morris and Brandon, 1984; Uzzell, 1964; Uzzell and Goldblatt, 1978). In *Ambystoma*, unisexual and bisexual taxa are sympatric, hybridize frequently, and produce hybrid female progeny characterized by low egg viability (Bogart and Licht, 1986) and, in triploid female progeny, by a greater similarity to the female parent than to the male parent (Uzzell, 1964). Bogart and Licht (1986) have determined that presumed parthenogenetic *Ambystoma* actually required sperm to produce viable offspring and that the resultant progeny sometimes incorporate genes from the paternal genome, thus precluding obligate parthenogenetic and gynogenetic modes of reproduction. While Bogart and Licht (1986) did not specify whether the sperm came from a male of one of the parental species or from a male hybrid, either source could be utilized in the propagation of the hybrid female's genes.

While *Cnemidophorus* and *Ambystoma* differ in that parthenogenesis has been confirmed only in unisexual *Cnemidophorus*, both genera apparently share the characteristic that sex and hybridization contribute to the maintenance of all-female taxa.

Similarly, sex and hybridization is necessary for propagation of diploid and triploid all-female lines of fish in the genus *Poeciliopsis* (Angus and Schultz, 1979; Kawecki, 1988; Leslie and Vrijenhoek, 1980; Schultz, 1977, 1973, 1971; Vrijenhoek, 1979, 1978; Vrijenhoek and Schultz, 1974). Again, as in *Cnemidophorus*, hybridization between diploid sexual species of *Poeciliopsis* has produced diploid progeny that reproduce via hybridogenesis. In this mode of reproduction, sperm from a male of a sympatric sexual species fertilizes the female's eggs and elements of the male genome are expressed in the all-female progeny. Utilization of paternal genes is believed to have allowed hybrid *Poeciliopsis* to extend its range and utilize new habitats (Bulger and Schultz, 1982; Schultz, 1971). Usually, only the maternal genome is present in eggs produced by the hybrid female and sperm is once again required for egg activation to produce the next generation (Angus, 1980; Schultz, 1961, Vrijenhoek et al., 1977). In this hybridogenetic system, paternal genes are presumably expressed in a single generation and then are replaced by a new set of paternal genes when the progeny hybridize with another sexual male. Crossing over or mixing between maternal and paternal genomes apparently does not occur. In each generation, the maternal genome is transferred intact to the eggs and is essentially cloned from one generation to the next. In the hybridogenetic system, and in the proposed model for unisexual *Cnemidophorus*, elements of a



successful male genome (produced through sex, recombination, and selection) are incorporated into the hybrid genome (short-term utilization by one generation, no genetic exchange, in Poeciliopsis; potential long-term utilization by several generations, with proposed genetic exchange, in Cnemidophorus). One hybridogenetic species of Poeciliopsis has switched paternal host species while extending its range; indicating a plastic genetic mechanism underlying incorporation of paternal genetic material and considerable genomic compatibility between related forms (Moore et al., 1970; Schultz, 1969). The proposed model for Cnemidophorus implies that clonal lines may acquire genetic material from more than one related sexual species over time. Gynogenetic Poeciliopsis have persisted long enough to accumulate mutations at several loci, indicating that such clonal lines are not necessarily short-lived (Angus and Schultz, 1979; Leslie and Vrijenhoek, 1980) and may indicate that utilization of elements of the male's genome facilitates success and persistence of the clonal line.

Comparisons between different complexes of unisexual and bisexual taxa involving hybridization, as in Cnemidophorus, Ambystoma, and Poeciliopsis, may lead to insights into the population dynamics and evolutionary significance of such complexes. Each system may represent variation on the theme of ongoing hybridization as a means of incorporating elements of the genome from a male of a sexual species into the genome of an individual from an all-female taxon. Each system exploits elements of a successful male genome, albeit in different ways, to facilitate success and persistence in unisexual taxa.

The proposal that unisexual species of Cnemidophorus are facultative parthenogens utilizing opportunistic sex and hybridization to incorporate elements of a male genome into an ongoing clonal line is a departure from orthodox evolutionary theory, which requires unisexual lizards to be obligate parthenogens. Recognition of hybridization as a regular feature of the population dynamics of unisexual lizards more fully utilizes the available information on unisexual lizard biology than the traditional evolutionary model. Specifically, the proposed model suggests that unisexual and bisexual species coexist in interacting complexes in a shared environment, hybridization occurs regularly as anti-hybridization barriers are maintained in a poorly developed state because of genetic inputs from the sexual species; viable hybrid progeny incorporate varying degrees of genetic input from the paternal genome - ranging from none to an entire set of chromosomes; and clonal lineages can adapt to a changing environment by incorporating genes from a sexual lineage that has undergone several generations of recombination and selection. The model presented in this paper suggests that in unisexual species of Cnemidophorus hybridization serves as a mechanism to acquire new genetic material and increase the amount of genetic variation in a clonal lineage.

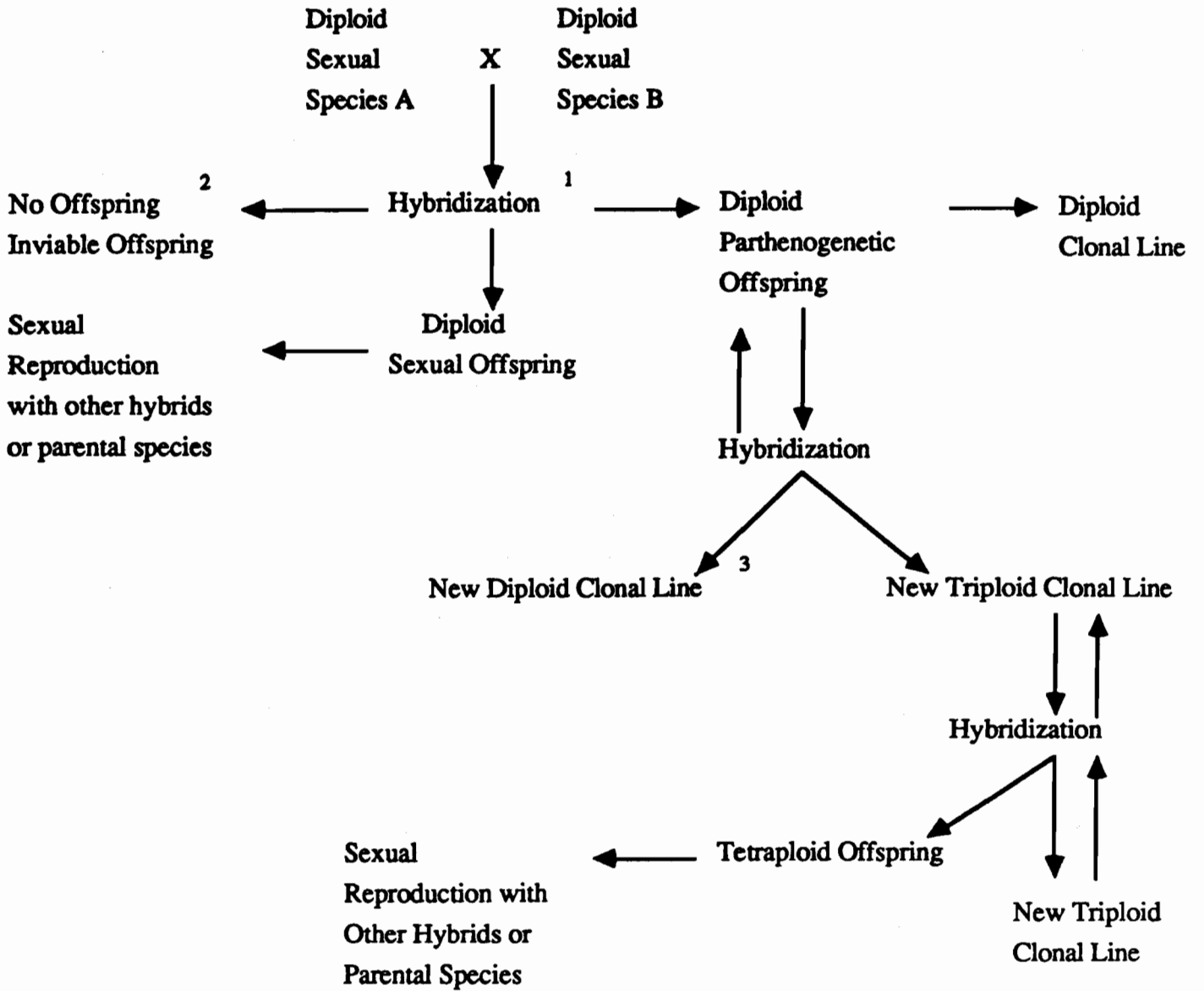
### Acknowledgements

I thank N.R. Liley, C. Shaw, and D. March for valuable discussions and comments on earlier versions of this manuscript.

### Figure 1

#### The Consequences of Sequential Hybridization between Unisexual and Bisexual Species of Lizards

- <sup>1</sup> Hybridization normally involves a diploid sexual species.
- <sup>2</sup> No offspring, inviable or sterile offspring are possible consequences in every hybridization event illustrated in the figure.
- <sup>3</sup> No distinction is made between the production of a new clonal line and the production of a new taxon.



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