

Mini-review

Evolutionary genetics and ecology of sperm-dependent parthenogenesis

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Abstract

Sperm-dependent (or pseudogamous) forms of parthenogenetic reproduction occur in a wide variety of animals. Inheritance is typically clonal and matroclinal (of female descent), but sperm are needed to initiate normal development. As opposed to true parthenogenesis (i.e., sperm-independent reproduction), pseudogamous parthenogenetic lineages must coexist with a 'sperm donor' – e.g., males from a conspecific sexual lineage, conspecific hermaphrodites, or males from a closely related sexual species. Such sperm donors do not contribute genetically to the next generation. The parasitic nature of sperm-dependent parthenogenesis raises numerous ecological and evolutionary questions. How do they arise? What factors help stabilize coexistence between the pseudogamous parthenogens and their sperm donors (i.e., 'sexual hosts')? Why do males waste sperm on the asexual females? Why does true parthenogenesis not evolve in pseudogamous lineages and free them from their dependency on sperm donors? Does pseudogamous parthenogenesis provide compensatory benefits that outweigh the constraints of sperm-dependence? Herein, we consider some genetic, ecological, and geographical consequences of sperm-dependent parthenogenesis in animals.

Introduction

Several asexual (i.e., non-recombinant or clonal) modes of reproduction are found among sperm-dependent parthenogenetic animals. Although sperm-depen-

dent parthenogenesis has been artificially induced in several groups, we restrict the present discussion to naturally occurring cases. Multiple and sometimes confusing names have been used to describe sperm-dependent forms of parthenogenesis (Tab. 1). Pseudogamous parthenogenesis is defined as the initiation of parthenogenetic development by the penetration of a sperm into an ovum, without the sperm genome contributing genetic information to the zygote and syngamy (fusion of egg and sperm pronuclei) and expression of paternal genes typically do not occur. A variety of cytogenetic pathways for producing unreduced ova occur among sperm-dependent parthenogens (Suomalainen et al., 1987), but for the purposes of this discussion, it is only necessary to note that inheritance is matrilineal and clonal.

Gynogenesis (literally meaning 'female descent') often is used as a synonym for pseudogamous parthenogenesis. To activate embryogenesis in their unreduced ova, gynogenetic females need sperm from males of a sexual host. Although this term is appropriate for many cases involving insects and vertebrates, we prefer to use the more general term, sperm-dependent parthenogenesis, to describe such reproduction in hermaphrodites, as hermaphrodites are not strictly of female descent. Other synonyms for sperm-dependent parthenogenesis are listed in Table 1. Androgenesis refers to patrilineal reproduction. It involves elimination of the female pronucleus and syngamy of two sperm cells, or alternatively, fusion of a replicated sperm pronucleus. Androgenesis is only known from the stick insect *Bacillus rossius-grandii* (Mantovani and Scali, 1992) and falls beyond the scope of this text. The term pseudogamy is confusing because it has two meanings. The original (strict sense) definition simply refers to pseudogamous parthenogenesis. However, plant biologists also use the term to describe cases in which embryo formation occurs without fertilization, but pollination is still needed to induce endosperm formation (Asker and Jerling, 1992). The strict sense definition, more often used by zoologists, is confined to fertilization of the egg cell followed by exclusion of the sperm chromosomes. Strict sense pseudogamy is very rare in plants, known only in the potato hybrid *Solanum tuberosum/phureja* (Clulow et al., 1991) and hybrids between *Tripsacum dactyloides* and *Zea mays* (Tsanewaki et al., 1976; De Wet et al., 1984).

Hybridogenesis is a hemiclinal form of sperm-dependent parthenogenesis (Schultz, 1969; Vrijenhoek et al., 1977). Hybridogenetic females (e.g., A^*B) transmit a haploid, nonrecombinant, maternal genome (i.e., hemiclone A^*) to their ova. Diploidy is restored by true fertilization with sperm from males of species B . The hemiclinal A^* genome is paired with new B genome in each generation. Although variation from species B is phenotypically expressed by a hybridogenetic lineage, it is substituted in each generation and is not heritable. It should be noted, however, that hybridogenetic populations often contain multiple hemiclones (e.g., A' , A'' , etc., see Vrijenhoek, 1984b), and differences may exist among hemiclones with regards to their interactions with paternal B genes (Semlitsch et al., 1996; Wetherington et al., 1989).

To complicate matters, some triploid all-female fish and salamanders superimpose elements of hybridogenesis on top of gynogenesis (reviewed by Dawley, 1989). For example, a gynogenetic triploid ($AB'B'$) might occasionally produce reduced ova (AB') that fuse with sperm and generate a new triploid ($AB'B'$). Over time, these replacements may produce triploid lineages that contain none of the original

Table 1. Glossary of sperm-dependent parthenogenesis

Term	Definition
<i>Androgenesis</i>	Development from a fertilized egg followed by disintegration of the maternal pronucleus prior to syngamy so that the zygote possesses only paternally derived chromosomes.
<i>Cryptoparthenogenesis</i>	Synonym of pseudogamous parthenogenesis.
<i>Gynogenesis</i>	Pseudogamous parthenogenesis involving sperm from males of a related sexual species.
<i>Hybridogenesis</i>	A hemiclonal form of reproduction in interspecific hybrids that transmit only a maternally derived chromosome set to ova. The paternal genome is excluded during oogenesis and the hybrid condition is restored each generation by mating with males of a suitable host species.
<i>Parthenogenesis</i> (strict sense)	Virgin birth, or all-female clonal reproduction without the involvement of sperm.
<i>Paternal genome loss</i>	A general term for systems in which paternal chromosomes are eliminated at various developmental stages prior to oogenesis. Pseudogamous parthenogenesis, gynogenesis, and hybridogenesis are special cases.
<i>Pseudofertilization</i>	Synonym of pseudogamous parthenogenesis.
<i>Pseudogamous parthenogenesis</i>	Initiation of parthenogenetic development by the penetration of a sperm into an ovum, without the sperm genome contributing genetic information to the zygote.
<i>Pseudogamy</i> (strict sense)	Synonym of pseudogamous parthenogenesis.
<i>Pseudogamy</i> (broad sense)	A term widely used by plant biologists to refer to the initiation of apomictic (i.e., parthenogenetic) seed production following pollination and fertilization of the primary endosperm.

nuclear genomes (Kraus and Miyamoto, 1990). Such genomic replacements may be responsible for the apparent evolutionary longevity of some gynogenetic *Ambystomatid* salamanders (Hedges et al., 1992; Spolsky et al., 1992), a subject to which we return.

Finally, the term 'paternal genome loss' (Bull, 1983) refers to systems in which males do not transmit paternally derived chromosomes. Elimination of the paternal complement can happen at many different stages in the life cycle. For example, some scale insects (Coccoidea) eliminate the paternal complement during spermatogenesis (Hughes-Schrader, 1948; Nur, 1980). This differs with hybridogenesis in that scale insects are not interspecific hybrids. In some mites, paternal chromosomes are eliminated in one-day old male embryos (Nelson-Rees et al., 1980; Schulten, 1985; Sabelis and Nagelkerke, 1988). Gynogenesis can be considered a special case, as the paternal genome is lost before the first mitotic division of the fertilized egg.

Phylogenetic distribution of sperm-dependent parthenogenesis

Sperm-dependent parthenogenesis is not a common mode of reproduction in the animal kingdom (reviews in Benazzi and Benazzi Lentati, 1967, 1992; Kiestner et al., 1981; Stenseth et al., 1985). Nevertheless, it has arisen independently from sexually reproducing ancestors in 24 genera representative of seven phyla: Rotifera, Platyhelminthes, Nematoda, Annelida, Mollusca, Arthropoda and Chordata (Tab. 2). Sperm-dependent parthenogenesis is frequently (but not exclusively) associated with interspecific hybridization, all-female or hermaphroditic species, and polyploidy. Hybridogenesis appears to be restricted to a few animal taxa of hybrid origin: the stick insect *Bacillus rossius-grandis*; the aquatic frog *Rana esculenta*, and fish in genera *Poeciliopsis* and *Tropidophoxinellus* (Tab. 3). No hermaphroditic hybridogens are known.

Varying levels of evidence exist for sperm-dependent parthenogenesis (Tab. 2). Most older publications are based upon breeding studies, i.e., lack of parthenogenetic reproduction in the absence of a sperm donor, in combination with cytology. More recently, genetic techniques including allozyme electrophoresis and DNA fingerprinting have been applied, but this is still limited to the higher taxa. Controversy exists about the nematode genus *Strongyloides*. Although there are several cytological reports on the existence of sperm-dependent parthenogenesis in this genus, including a recent one by Hammond and Robinson (1994), Viney et al. (1993) provide evidence for genetic exchange in *S. ratti* consistent with normal sexual reproduction. It is unclear whether this discrepancy is due to misinterpretation of the cytology or to the existence of strains with different reproductive modes within the species.

Sperm-dependent parthenogenesis may be more widespread than currently realized, because its detection requires the identification of several, often cryptic, characteristics. The number of hybridogenetic taxa is likely to increase as additional "hybrid species" are discovered and examined with molecular and cytological markers (Bullini, 1994). Most hybridogens have been identified in crossing

Table 2. Incidence of sperm-dependent parthenogenesis in the animal kingdom

Phylum	Order/family	Biotype, or 'species' name	Hybrid	Sex	Ploidy	Self-fertilization	Method	Reference
Rotifera	Monogonta	<i>Keratella quadrata</i> <i>Brachionus urceolaris</i>	no	bisexual	??	possible	B	Rutner-Kolisko, 1969 Birky and Gilbert, 1971
Platyhelminthes	Turbellaria	<i>Polycelis nigra</i> , <i>P. tenuis</i>	no	hermaphroditic	3n, 4n	possible	B, C	Lepori, 1949; 1950 Benazzi, 1961 Benazzi Lentati, 1970
Nematoda	Secernentea	<i>Dugesia benazzi</i> , <i>D. polychroa</i>	no	hermaphroditic	2n, 3n, 4n	no	B, C	Benazzi, 1961 Benazzi Lentati, 1970
		<i>Dugesia goniocephala</i>	yes	hermaphroditic	4n ¹	no	C	Pala et al., 1982
		<i>Herterodera trifolii-schachtii</i>	yes	all-female	3n	no	C	Mulvey, 1958 Triantaphyllou and Hirschman, 1978
		<i>Rhabditis aberrans</i> , <i>R. anomala</i> , <i>R. monohystera</i> (= <i>belari</i>), <i>R. pellio</i> , <i>R. longicauda</i> , <i>R. leptodera</i> <i>Strongyloides ratti</i> ² <i>S. ransoni</i>	no	bisexual	2n	no	B, C	Krüger, 1913 Hertwig, 1920; 1922 Belar, 1923; 1924 Nigon, 1949
			no	bisexual	2n	no	B, C	Nigon and Roman, 1952 Abe and Tanaka, 1965

Coleoptera (beetles)	<i>Ptinus clavipes-mobilis</i> (= <i>latro</i>)	no?	all-female	3n	no	B. C	Sanderson, 1956; 1960
	<i>Ips acuminatus</i>	no	all-female	3n, 4n	no	B. C, G	Moore et al., 1956 Hopping, 1962; 1964
	<i>I. borealis</i>						Smith, 1962
	<i>I. perturbatus</i>						Lanier and Olivier, 1966; Lanier and Kirkendall, 1986
	<i>I. pilifrons</i>						
Homoptera (plant hoppers)	<i>Muellerianella</i>	yes	all-female	3n	no	B. C, G	Drosopoulos, 1976; 1978
	<i>fairmairiei-brevipennis</i>						den Bieman and Eggers-
	<i>Ribatodelphax pungens</i>	no	all-female	3n	no	B. C, G	Schumacher, 1987 den Bieman, 1988a
Lepidoptera (moths)	<i>Luffia lapidella</i>	no	gonochorist	2n	no	C	Narbel-Hofstetter, 1963; 1964
	<i>Alsophila pometricia</i>	no	gonochorist	4n?	no	B. G	Mitter and Futuyma, 1977
	<i>Bacillus rossii-grandii</i>	yes	all-female	2n	no	B. C, G	Mitter et al., 1979
Orthoptera (stick insects)	<i>benazzii</i>	yes	all-female	2n	no		Mantovani and Scali, 1992
	<i>Poecilopsis 2</i>	yes	all-female	3n	no	C	Schultz, 1969; 1977
	<i>monacha-lucida</i>						
	<i>P. monacha-2 lucida</i>						
	<i>P. monacha-viriosa-lucida</i>						
Pisces	<i>Poecilia formosa complex</i>	yes	all-female	3n	no	B. C, G	Hubbs and Hubbs, 1932; Rasch and Balsano, 1989; Turner, 1982; Turner et al., 1983
Chordata							

Table 2 (continued)

Phylum	Order/family	Biotype, or 'species' name	Hybrid	Sex	Ploidy	Self-fertilization	Method	Reference
Amphibia		<i>Menidia clarkhubbsi</i> complex	yes	all-female	2n	no	B, G	Echelle et al., 1989
		<i>Phoxinus eos-neogaeus</i> complex	yes	all-female	2n, 3n	no	B, G	Goddard et al., 1989
		<i>Cobitis</i> complex	yes	all-female	3n, 4n	no	B, C	Vasil'ev et al., 1989
		<i>Carassius auratus gibelio</i> , <i>C. auratus langsdorfi</i>	no	all-female	3n	no	B, C	Cherfas, 1966
		<i>Ambystoma jeffersonianum</i> complex	yes	all-female	2n, 3n, 4n	no	B, C, G	Kobayashi, 1971
		<i>A. laterali-texanum</i> complex						Uzzell, 1964
		<i>A. laterali-jeffersonianum-texanum</i> complex						Bogart, 1989
								Lowcock et al., 1987
								Ellison et al., 1992

The method column refers to the experimental method by which sperm-dependent parthenogenesis was detected: B = breeding, C = cytology and G = genetics.

¹ Other less common ploidy levels including aneuploidy have also been observed.

² Viney et al. (1993) refute pseudogamous parthenogenetic reproduction in *S. ratti* based upon DNA fingerprinting. It is unclear whether the strain that they used differed from the ones used in the earlier cytological studies.

³ The 3n form is male sterile and bisexual lineages are also known.

Table 3. Incidences of hybridogenesis in the animal kingdom

Phylum	Order/family	Biotype or 'species' name	Sex	Ploidy	Reference
Arthropoda	Orthoptera (stick insects)	<i>Bacillus rossius-grandii benazzii</i> and <i>grandii</i>	predominantly female (male sterile)	2n	Mantovani and Scali, 1992
Chordata	Pisces	<i>Poeciliopsis monacha-lucida</i>	all-female	2n	Schultz, 1969; 1971
		<i>P. monacha-occidentalis</i>			Miller and Schultz, 1959
		<i>P. monacha-latidens</i>			
		<i>Tropidophoxinellus alburnoides</i> complex	predominantly female	2n, 3n, 4n	Carmona et al., 1997
	Amphibia	<i>Rana esculenta</i>	predominantly female (male fertile)	2n	Uzzell and Berger, 1975 Uzzell et al., 1980

experiments, but careful use of nuclear and mitochondrial markers can demonstrate hemiclinal patterns of inheritance in natural populations (see for example, Vrijenhoek et al., 1977, 1978; Carmona et al., 1997). Gynogens can be identified by their all-femaleness, strictly clonal inheritance, and most importantly, a requirement for insemination. Detection is relatively difficult in cross-copulating hermaphrodites, as genetic markers are needed both to distinguish mating partners and to establish matroclinal inheritance. If a population is composed of a single clone, such markers are difficult to establish. Detection of sperm-dependent parthenogenesis is even more difficult in selfing hermaphrodites, since lineages are expected to quickly become isogenic, and thus syngamy cannot be ruled out by the same genetic markers. To discriminate this from parthenogenesis and selfing, sperm penetration and lack of pronuclear fusion must be demonstrated cytologically.

Origin of sperm-dependent parthenogenesis

For most described complexes, it has been shown that sperm-dependent parthenogens have recently evolved from sexually reproducing progenitors (e.g. Sanderson and Jacob, 1957; Triantaphyllou and Moncol, 1977; Moritz et al., 1989b; Vrijenhoek 1989a; exceptions are considered below). The discovery of considerable genetic variation among clones of several hybridogenetic and sperm-dependent parthenogenetic taxa (Booij, 1981; Benazzi, 1982; Turner, 1982; Futuyma et al., 1984; Vrijenhoek, 1984b) is consistent with relatively recent and recurrent origins from sexual ancestors. Often, clones are characterized by allozymes and mitochondrial DNA markers that still segregate in sympatric sexual relatives (Christensen et al., 1976; Quattro et al., 1991).

Interspecific hybridization is often invoked as the factor that initiates sperm-dependent parthenogenesis (Hubbs and Hubbs, 1932; Schultz, 1969; reviewed by Lanier and Kirkendall, 1986). Although true for some groups (e.g., fish and salamanders), hybridization is not involved in many invertebrates (e.g., polyploid flatworms, certain bark beetles, and haplodiploid mites; Tab. 2). However, the taxonomic status of putative sexual ancestors may be unclear in some cases, and thus, a hybrid origin cannot be ruled out (e.g., the beetle *Ptinus clavipes* f. *mobilis* and the marine clam *Lasaea*). Alternatively, parthenogenesis may be initiated by polyploidization. Unreduced eggs occasionally produced by sexual diploids may be fertilized to produce triploid progeny. Whether such triploids become stable sperm-dependent parthenogens depends on several factors (Lanier and Kirkendall, 1986): (1) successful development into fertile individuals; (2) a proper chromosome replication mechanism (e.g. endomitotic doubling); and (3) an ability of eggs to exclude sperm chromosomes while retaining sperm stimulation of development.

Sperm-dependent parthenogenesis is frequently associated with hermaphroditism, especially in platyhelminths, nematodes, annelids and molluscs (Tab. 2). Hermaphroditism eliminates the need for a sex-determination mechanism and associated evolution of heteromorphic sex chromosomes, which is believed to provide a barrier to polyploidy in animals (Muller, 1927; Orr, 1990). In turn,

polyploidization may stimulate the origin of parthenogenesis. However, which came first – parthenogenesis or polyploidy – remains enigmatic (Benazzi, 1982; Suomalainen et al., 1987). Some researchers conclude that polyploidy preceded sperm-dependent parthenogenesis (e.g. Benazzi Lentati, 1979; Lanier and Kirkendall, 1986); some argue evidence that sperm-dependent parthenogenesis came before polyploidization (e.g. Schultz, 1969), and finally, some suggest that both evolved simultaneously (e.g. Christensen, 1960). Comprehensive cytological and genetic analyses of gynogenetic *Poeciliopsis* support the “genome addition” hypothesis – i.e., triploid lineages have arisen multiple times by addition of sperm genomes to diploid asexual ancestors (Cimino, 1972; Quattro et al., 1992b). Genome addition appears to be responsible for origin of triploids in other gynogenetic fish complexes – e.g., *Poecilia formosa*, *Menidia clarkhubbsi*, and *Phoxinus eos-neogaeus* (Turner et al., 1980; Echelle et al., 1988; Goddard et al., 1989). Evidence for genome addition also exists in natural populations of the planthopper *Ribautodelphax pungens* (Den Bieman and Eggers-Schumacher, 1987), the oligochaete *Lumbricillus lineatus* (Christensen et al., 1978) and the planarian *Dugesia polychroa* (Beukeboom et al., 1996a). In these latter examples, polyploidy likely arose first through fertilization of occasionally produced unreduced eggs by diploid sexuals, and sperm-dependence for development of eggs was an immediate consequence.

Evolutionary stability of sperm-dependent parthenogenesis

The requirement for sperm forces all-female gynogens and hybridogens into a parasitic relationship with a sexually reproducing host. They cannot escape from, or outcompete, their host without concomitant effect on their own survival (Clanton, 1934). If all else is equal (i.e., niche requirements, fertility, and survival), an all-female lineage should rapidly replace a sexual host that must pay the cost of producing males (Williams, 1975). Thus, the sexual host will decline in numbers and sperm will become limiting. Sperm-limitation appears to mitigate the twofold reproductive advantage of all-female lineages (Moore and McKay, 1971; Kawecki, 1988; Kirkendall, 1990). Strong conspecific mating preferences by sexual males also will limit all-female reproduction, but the conditions for stable equilibrium may be stringent (Moore, 1975, 1976; Stenseth et al., 1985). Additionally, males of a host species may learn to discriminate against common gynogenetic and hybridogenetic clones and this may give phenotypically rare clones a temporary advantage that facilitates the maintenance of clonal diversity (Keegan-Rogers, 1984). Nevertheless, theoretical and empirical studies have revealed that niche separation between sexual and clonal forms may be the major factor that promotes stable coexistence in mixed reproductive complexes (Vrijenhoek, 1978; Kirkendall and Stenseth, 1990). Evidence for clonal niche diversification, and what is called the “Frozen Niche-Variation” model, has been reviewed elsewhere (Vrijenhoek, 1979, 1984a, 1994).

Sperm-dependent hermaphrodites do not require a sexual host species. Although hermaphrodites allocate some reproductive effort to male functions, the cost is not two-fold, as in sexuals; but rather one-and-a-half-fold (Charlesworth, 1980).

Outcrossing hermaphrodites also pay a cost of mate-searching, but selfers do not (Tab. 4). To date, too few sperm-dependent hermaphroditic parthenogens have been studied to allow inferences into factors that promote evolutionary stability. Studies comparing outcrossing hermaphroditic lineages and sperm-dependent parthenogens of the planarian *Dugesia polychroa* found a significant reduction of male allocation and higher fecundity (cocoon production), but lower fertility (number of young per cocoon) in the parthenogens (Weinzierl et al., 1998; unpublished). Such information is necessary to understand the dynamics of coexistence of sexual and asexual lineages, as no evidence for niche separation has been found (Weinzierl et al., unpublished). Similarly, selfing hermaphroditic lineages of the pseudogamous marine clam *Lasaea* exist in sympatry with sexual congeners (O'Foighil and Smith, 1995). Further ecological studies of these anomalous situations are warranted.

Geographical parthenogenesis

True parthenogens have occasionally been characterized as 'fugitive' or 'weedy' species (Wright and Lowe, 1968). They can escape direct competition with their sexual ancestors by colonizing new or marginal habitats. Furthermore, true parthenogens do not bear the costs of producing males or finding mates (Tab. 4) and thus all-female parthenogens have at least a two-fold reproductive advantage that should be favored during colonizing events. The minimum propagule size necessary to establish a parthenogen in a new habitat is one individual. In contrast, the minimum propagule required to establish a biparental sexual species is two (one male and one female), or alternatively, a single pregnant female of a viviparous species, or a single female with stored sperm. The same requirements exist for outcrossing hermaphrodites, but selfers can colonize with a propagule of one. The effective propagule size for sexuals and outcrossing hermaphrodites is likely to be greater, however, due to the difficulties in finding a mate when population density is low. Outcrossing sperm-dependent parthenogens share this problem, but true parthenogens and selfers have 'reproductive assurance' (Baker, 1965).

The putatively superior colonization abilities of parthenogens are often invoked to explain the broad-scale pattern known as 'geographical parthenogenesis' (Vandel, 1928). Parthenogenetic lineages tend to be more frequent in extreme latitudes, at higher altitudes, at the margins of a species range, and in regularly disturbed (i.e., disclimax) communities. Notwithstanding, many researchers invoking the geographical parthenogenesis hypothesis have failed to recognize that a significant proportion of these 'parthenogens' are sperm-dependent. Attempts to explain their geographical distribution must also consider the constraints imposed by sperm-dependence (Vrijenhoek, 1989a). One would expect true parthenogens to be more successful colonists than sperm-dependent forms (Tab. 4).

In the hermaphroditic planarian *Dugesia polychroa*, the sperm-dependent biotype is more widespread than the sexual form (Beukeboom et al., 1996a). A potential advantage that colonizing asexuals have over their sexual counterparts results from protection against inbreeding depression following founder events. The demo-

Table 4. Some costs and benefits of sexual and asexual modes of reproduction

Characteristic	sexual		hybridogenetic	sperm-dependent parthenogenetic		obligate parthenogenetic	
	gonochoristic	hermaphroditic		gonochoristic all-female	hermaphroditic cross-copulating	hermaphroditic all-female self-fertilizing	hermaphroditic
sperm dependence	conspecific males	conspecific males	males of other species	conspecific males	typically males of other species	conspecific males	none
sperm must be compatible	yes	yes	yes	no	no	probably yes	yes
cost of males	yes	yes	no	yes	no	yes ¹	yes ¹
cost of mate searching	yes	yes	yes	yes	yes	yes	no
geographic distribution	limited by other sex	limited by conspecifics	limited by sexual host species	limited by other sex	limited by sexual host species	limited by conspecifics	unlimited by conspecifics
minimum propagule size for establishment of new population	1 male + 1 female, or 1 inseminated female	2 individuals, or 1 inseminated individual	1 individual + exploitable sexual host	1 male + 1 female, or 1 inseminated female	1 individual + exploitable sexual host	2 individuals, or 1 inseminated individual	1 individual
sperm contributes to local adaptation	yes	yes	yes	no	no	no	no
can co-exist genetically with sexual ancestor	not applicable	not applicable	not with maternal ancestor	yes	yes	yes	yes
destabilizing hybridization	not applicable	not applicable	yes	no	no	no	yes ²

¹ Often reduced male allocation.² Sometimes parthenogens are mated by sexuals, resulting in breakdown of clonal reproduction (see Lynch 1984).

graphic value of this protection was demonstrated in a field study involving fish of the genus *Poeciliopsis* (Vrijenhoek and Lerman, 1982; Vrijenhoek, 1989b; Lively et al., 1990). Both the sexual species, *P. monacha*, and the gynogen, *P. 2 monacha-lucida*, suffered local extinction during a severe drought in the headwaters of a small desert stream in Sonora, Mexico. The headwater stream was rapidly recolonized by fish from a more stable refuge about half a kilometer downstream. Although the colonizing gynogens lost no heterozygosity (it is protected by clonal reproduction), the sexual colonists were now homozygous for allozyme markers that segregated in the refuge population. Loss of heterozygosity in the sexual founders was associated with concomitant decreases in developmental stability and competitive ability, and an increase in parasite load, relative to the clone. Translocation of some genetically variable sexuals from the refuge into the headwater area was associated with a recovery of the fitness lost in the founder population. The colonizing sexual population was susceptible to inbreeding depression associated with a founder event. The clone had 'heterozygosity assurance' that provided it with a competitive advantage immediately following the founder events.

Hybridogens and gynogens both require sperm from males of a sexual host species or a conspecific sexual form in order to invade new habitats. If males of a potential host population strongly prefer conspecific females as mates, invasion will be limited. The same is true for sperm-dependent parthenogenetic hermaphrodites, if sexual reproducers can discriminate against parthenogenetic conspecifics. Curiously, the prospects for successful invasion also may be poor if host males are completely promiscuous in their mate choice. With an unlimited supply of sperm, an all-female lineage will rapidly replace its sexual host, and thereby stimulate its own demise. As mentioned above, some degree of sperm-limitation and niche separation appear to facilitate coexistence of sperm parasites and their sexual hosts.

Colonization and sperm compatibility

Invading gynogens would appear to have a colonization advantage over hybridogens, because they may be able to exploit a wider variety of sperm sources (Tab. 4). As syngamy does not occur in gynogens, sperm does not need to be genetically compatible with the egg's genome and thus the range of sperm compatibility can be broad (Sanderson, 1960; Triantaphyllou and Moncol, 1977; Lanier and Kirkendall, 1986). The gynogenetic fish *Poecilia formosa*, can exploit the sperm of males of *P. latipinna* in the northern part of its range and *P. mexicana* in the south (Turner et al., 1983), and *Poeciliopsis* gynogens can be propagated with sperm from different genera (R. J. Schultz, pers. comm.). In contrast, invading hybridogens require genetically compatible sperm since they cannot exploit sexual hosts that are closely related to the maternal hemiclinal genome, a process which would result in the breakdown of hybridogenesis. For example, crossing some *Poeciliopsis monacha*-lucida* hybridogens (* marks the hemiclinal genome) with *P. monacha* males produces *monacha-monacha* progeny with normal Mendelian segregation and assortment (Leslie and Vrijenhoek, 1978). Similarly, crosses of the hybridogenetic

aquatic frog *Rana esculenta* (= *ridibunda**-*lessonae*) with males of *R. ridibunda* produce *ridibunda-ridibunda* progeny (Graf and Polls-Pelaz, 1989). It is not surprising, therefore, that hybridogenetic *Poeciliopsis* and *Rana* do not broadly coexist with their maternal ancestors, a phenomenon broadly subsumed under a phenomenon called 'destabilizing hybridization' (Lynch, 1984).

Some hybridogenetic lineages appear to be relatively old and have diverged mutationally to such a degree that the hemiclinal genome can no longer function in a homospecific genetic background. Some *P. monacha-lucida* lineages produce deformed offspring, dead embryos, or no embryos at all when crossed with *P. monacha* (Leslie and Vrijenhoek, 1980) and a similar phenomenon was observed in *Rana esculenta* (Graf and Polls-Pelaz, 1989). Nevertheless, these hemiclinal genomes function normally when combined with a suitable paternal genome – apparently, they have accumulated mutations that maximize fitness in a hybrid background but are lethal in a homospecific background. Despite the requirement for compatible sperm, hybridogenetic *Poeciliopsis* are much more widely distributed than gynogenetic forms. Gynogenetic forms of *Rana* have not been found. Does paternal gene expression in hybridogens provide adaptive benefits that compensate the reproductive constraints imposed by compatibility? Several potential benefits of hybridogenesis are discussed below.

Local adaptation

Expression of paternal genes may provide invading hybridogens a local adaptive advantage. If a hybridogen *A*B* invades the range of species *C*, its *A*C* progeny co-opt locally adaptive variation that evolved in species *C*. Hybridogens are genetic parasites that borrow and express evolutionary adaptations of their sexual hosts. An elegant example was found in a widespread lineage of *Poeciliopsis monacha-occidentalis* (Bulger and Schultz, 1982). Southern populations in Sonora, Mexico, are relatively intolerant of cold water temperatures. However, northern populations benefit from increased cold-tolerance encoded by the local *occidentalis* genome. Although paternal variation is not heritable for the hybridogen, interclonal selection may favor hemiclones that enhance expression of locally adapted paternal genes.

Evolution of sexual mimicry

If males of a potential host species prefer conspecific females as mates, invading hybridogens may have an immediate advantage over gynogens. Imagine gynogen *AB* and hybridogen *A*B* both invading a region that contains the potential host species *C*. Although both types of females may be equal in their ability to obtain sperm, progeny of the invading hybridogen will become *A*C* and thereby gain partial resemblance to females of species *C* (due to paternal expression). The gynogenetic progeny are still *AB* and do not benefit from sexual mimicry. A broadly distributed hybridogen, *P. monacha-lucidens*, may have arisen by displacement of the *lucida*

genome from a *P. monacha-lucida* ancestor (Schultz, 1966, 1977). It depends on males of *P. latidens*, a widely distributed species, for sperm.

Female genital pigmentation provides cues for mate selection by males of *Poeciliopsis*. The genital pigmentation of some *P. monacha-lucida* lineages closely mimics that of *P. lucida* females (Vrijenhoek and Schultz, 1974). Using laboratory crosses, Lima et al. (1996) found that the best *lucida* mimics have captured and clonally replicated (i.e., 'froze') genomes from *P. monacha* that do not express typical *monacha* pigmentation. The most widespread, and presumably successful, *P. monacha-lucida* lineages in northwestern Mexico are effective *lucida* mimics.

Individual gynogenetic triploid clones of *Poeciliopsis* have narrower distributions. However, elevation of ploidy is another route to sexual mimicry. If gene expression is additive, a triploid *ABB* clone should more closely resemble females of host species *B*, than would a diploid *AB* clone. The triploid gynogenetic biotype, *Poeciliopsis* 2 *monacha-lucida* ($= 2n_{\text{monacha}} + 1n_{\text{lucida}}$), resembles and broadly coexists with the sexual host *P. monacha* (Schultz, 1969). Similarly, *P. monacha*-2 *lucida* ($= 1n_{\text{monacha}} + 2n_{\text{lucida}}$) closely resembles and broadly coexists with *P. lucida*.

Multiple origins and Frozen Niche-Variation

More genetic variation due to multiple origin of hybridogenesis rather than gynogenesis may be another reason for the wider distribution of hybridogenetic lineages in *Poeciliopsis*. Genetic analyses revealed that hybridogens had multiple endemic origins in several tributaries and rivers of northwestern Mexico, whereas gynogenetic origins appear to be highly constrained (Quattro et al. 1991, 1992b). According to the 'Frozen Niche-Variation' model (Vrijenhoek, 1979, 1984a), multiple origins provide genetic variation for interclonal selection, which in turn produces a diverse assemblage of clones that can effectively partition natural resources and minimize niche overlap with the sexual ancestors. The overall numerical success of these all-female populations, relative to the sexuals, is positively correlated with clonal diversity. Perhaps the higher clonal diversity of hybridogens provides greater scope for interclonal selection and the adaptive evolution of these all-female populations.

Paternal substitution and the Red Queen

According to the 'Red Queen' model, microparasites will quickly evolve to exploit the most abundant host genotypes (Van Valen, 1973; Hamilton, 1982). Support for this model was found in a field study of gynogenetic *Poeciliopsis* (Lively et al., 1990); however, hybridogens have not been investigated. Hybridogens may have a strong advantage over gynogens with respect to immunological variation, as hybridogens express paternal variation from the sexual host. However, this prediction remains to be tested. Suitable model systems include *Poeciliopsis*, which provides the only known example of hybridogens, gynogens, and sexuals living together and exposed to the same parasites, and sympatric populations of sexual and pseudogamous parthenogenetic *Dugesia polychroa*.

Why do males waste sperm on sperm-dependent females?

Males that mate with pseudogamous parthenogens or hybridogens waste their sperm. Although hybridogens incorporate and express paternal genes, the entire paternal genome is discarded during the next oogenetic cycle. Selection should therefore favor strong conspecific mating preferences in males of a host species, as choosy males will waste less sperm. McKay (1971) showed that individual males of *Poeciliopsis lucida* are highly selective if given a choice of sexual vs. hybrid females. When in groups, however, *P. lucida* males establish hierarchies, and dominant males guard conspecific females. Denied access to the preferred females, subordinate males will mate with hybrids. Subordinates are not wasting sperm when they have limited access to conspecific females since their indiscretions may be compensated by gaining valuable mating experience.

Mate discrimination against sperm-dependent parthenogenetic females was further found in the salamander *Ambystoma laterale*, in the bark beetle *Ips accuminatus* (Løynning and Kirkendall, 1996) and the planthopper *Ribautodelphax pungens* (den Bieman, 1988a), but not in *Muelleriana* (Booiij and Guldemon, 1984). Mate selection also may occur in the hermaphroditic planarian *Dugesia polychroa*. Sexual and sperm-dependent biotypes are found in sympatry, but sexuals invest more heavily in testicular tissue and sperm than the sperm-dependent parthenogens (Weinzierl et al., 1998). Matings between sexuals and sperm-dependent parthenogens are possible (Benazzi and Benazzi Lentati, 1976) as reciprocal insemination appears to be the rule (Peters et al., 1996). Sexuals should avoid mating with sperm-dependent parthenogens as they will waste sperm and receive fewer (and possibly inferior) sperm in return. Sperm from sperm-dependent parthenogens are incorporated in sexually produced eggs, but the hybrids are typically sexual (Benazzi and Benazzi Lentati, 1976). Thus, paternal transmission by sperm-dependent parthenogens provides no benefits to the parthenogen. In contrast, sperm-dependent parthenogens should favor matings with sexuals because they would receive more sperm which may have nutritional value when digested (Sluijs, 1989). These predictions about mate choice are currently under investigation.

Males of the sailfin molly, *Poecilia latipinna*, do not appear to favor conspecific sexual females (Schlupp et al., 1991). Surprisingly, males may benefit by courting females of the gynogenetic species *Poecilia formosa* (Schlupp et al., 1994). Female *P. latipinna* appear to favor highly active males that are 'consorting' with other females, sexual or clonal. For this species, it pays to engage in courtship, even if the object of a male's attention is a gynogen.

Paternal leakage and the longevity of unisexual lineages

Occasional leakage of genes from a paternal host into sperm-dependent clones may provide a source of adaptive variation and possibly an avenue for the avoidance of 'Muller's ratchet' (Muller, 1964) or 'mutational meltdown' (Lynch et al., 1993). Analyses of nuclear (i.e., allozymes) and mitochondrial genes have revealed no evidence for paternal leakage in hybridogenetic or gynogenetic *Poeciliopsis*, however

(Vrijenhoek et al., 1977, 1978; Avise and Vrijenhoek, 1987; Quattro et al., 1991; Quattro et al., 1992b), even for a lineage that may be more than 100,000 years old (Quattro et al., 1992a). Nevertheless, 100,000 years is relatively young compared to the average longevity of sexual species of *Poeciliopsis* which is on the order of many millions of years (Vrijenhoek, 1993).

In contrast, evidence from mitochondrial sequences suggests that some triploid gynogenetic lineages of *Ambystoma* may be at least five million years old (Hedges et al., 1992; Spolsky et al., 1992) while allozyme evidence revealed that this lineage has undergone complete replacements of its nuclear genomes (Kraus and Miyamoto, 1990), the relevant genomes with respect to sexuality. As mitochondrial genomes have been clonal for more than a billion years, the use of mitochondrial DNA for aging of clonal lineages is likely to be misleading (Maynard Smith, 1992; also see review by Judson and Normark, 1996). Some asexual lineages of the clam *Lasaea* also appear to be ancient (O'Foighil and Smith, 1995) and may have escaped mutational meltdown through occasional outcrossing events. With the appropriate use of nuclear and mitochondrial genes, we suspect that most putatively 'ancient' asexual lineages will show some evidence of paternal leakage or genome replacement. It may be instructive in this regard to contrast estimated evolutionary ages of pseudogamous parthenogens against those of truly parthenogenetic lineages, which theoretically should not experience genomic replacement (but see Moritz et al., 1989a).

Schartl et al. (1995) suggested that paternal leakage may help to stay the course of Muller's ratchet in the gynogenetic amazon molly, *Poecilia formosa*. They reported evidence for leakage of male B chromosomes and genes for black pigmentation. Schartl et al. also hypothesized that such leakage may benefit males as the 'leaky' genes will be replicated more efficiently in all-female offspring. Beukeboom et al. (1995) criticized both arguments. First, it is very dubious whether incorporation of unstable fragments allows for avoidance of Muller's ratchet. The incorporation of whole paternal genomes and elevation of ploidy are more likely mechanisms for shielding against mutational meltdown. Second, the sexual species cannot benefit from transmission of leaky genes to gynogens, unless leaky genes eventually feed back into the sexual gene pool, a phenomenon for which we presently have no evidence. Finally, Lima et al. (1996) argued that gynogens are more likely to be beneficiaries of paternal leakage, because expression of paternal genes may contribute to sexual mimicry, thereby increasing a gynogen's chances of obtaining matings.

Beukeboom et al. (1996b, 1998) reported a high incidence of paternal B chromosomes in two populations of the sperm-dependent parthenogenetic planarian *Polycelis nigra*, although it appears that these B chromosomes likely persist as genomic parasites. Nevertheless, occasional genetic exchange between supernumerary chromosomes and regular autosomes may be possible. Additionally, the frequently observed aneuploidy in *P. nigra* (Beukeboom et al., 1998; Sharbel et al., 1997), the planthopper *Ribautodelphax* (den Bieman, 1988b) and pseudogamous clams of the genus *Lasaea* (O'Foighil and Eernisse, 1988) may have resulted from occasional paternal leakage of autosomes or autosomal fragments, but this hypothesis remains to be tested.

As suggested by the cytological descriptions, fertilized eggs of the pseudogamous parthenogenetic beetle *Ptinus latro* may occasionally allow survival of sperm

chromosomes (Sanderson, 1956), although sex determination in this species should prevent such zygotes from further development. This phenomenon resembles descriptions of cytoplasmic incompatibility in the parasitoid wasp *Nasonia vitripennis* (Ryan et al., 1985, 1987; Reed and Werren, 1995). With incompatible crosses, the paternal chromosome set is typically destroyed in the fertilized egg, but chromosomal fragments may survive. Occasional failures to eliminate paternal chromosomes from the eggs of sperm-dependent parthenogens will result in aneuploidy or elevation of ploidy. Polyspermy (more than one sperm entering an egg) has also been observed in pseudogamous parthenogens, such as in the planarian *Dugesia* (Benazzi Lentati and Deri, 1990), the beetle *Ptinus* (Sanderson, 1960), and the stick insect *Bacillus* (Mantovani and Scali, 1992), and may contribute to elevation of ploidy.

More studies involving cytological and multi-locus genetic markers are needed to refute or confirm paternal leakage in sperm-dependent parthenogens. Both theoretical and empirical work is necessary to test some of the predictions that "a little bit of sex may be as good as a lot" (Green and Noakes, 1995). Even if empirical evidence for occasional paternal leakage is available, it remains to be seen whether this can provide a means to escape the evolutionary path to mutational meltdown and extinction. Additionally, such evidence may illustrate why the evolutionary consequences of pseudogamy in plants ('broad sense', pollen is required to activate endosperm development) should be considered separately from sperm-dependent parthenogenesis in animals. Paternal fertilization of the endosperm alone contributes genetic information neither to the zygote nor to the next generation.

Evolution of sperm-independent parthenogenesis

Given the constraints of sperm-dependence, why does true parthenogenesis not evolve in sperm-dependent lineages? Sperm-limitation should favor mutations that promote true parthenogenesis and remove the constraints associated with finding a sperm donor. Nevertheless, naturally parthenogenetic fish, amphibians and planarians have not been found (Uzzell, 1970; Suomalainen et al., 1987). Alternatively, both pseudogamous and parthenogenetic lineages occur in bark beetles (*Scolytidae*) (Deyrup and Kirkendall, 1983), planthoppers (genus *Delphacodes*) (den Bieman and de Vrijer, 1987), stick insects (genus *Bacillus*) (Mantovani and Scali, 1992), and nematodes (genus *Strongyloides*) (Triantaphyllou and Mocol, 1977). Parasitic females of *Strongyloides ransomi* and *S. papillosus* are mitotic parthenogens whereas free-living forms are pseudogamous parthenogens. Additionally, hybridogenesis may have evolved towards parthenogenesis in *Bacillus whitei* (Mantovani and Scali, 1992).

Are most sperm-dependent parthenogens simply stuck with mechanical requirements for insemination? Are they recent evolutionary accidents that led to functionally suboptimal reproductive modes? Sperm penetration may be required to activate the primary cleavage of eggs in many vertebrates, and in other organisms sperm may provide certain products (e.g. centrioles) that are not contained in the egg (Christensen, 1960; Ward and Zalensky, 1996). An intriguing adaptive explanation for the maintenance of sperm-dependence is given by Grafen (1988). He proposes

that sexual reproduction may have evolved to allow organisms a choice of centrosomes. Nevertheless, purely parthenogenetic systems occur in a wide variety of animal taxa (e.g. reptiles, several insect groups). How do these animals circumvent the need for sperm? Cytological studies of these systems are clearly warranted, as they may provide insights into factors involved in the stimulation and organization of early development in animals. To test the rigidity of sperm-dependence, one could put sperm-dependent parthenogenetic organisms under selection for sperm independent reproduction, as has been done for many sexual organisms with success. Finally, experimental studies to artificially induce egg development in sperm-dependent parthenogens may be informative about the nature of the constraints that fertilization puts on egg development. For example, Elinson et al. (1992) found gynogenesis in *Ambystoma* to be temperature sensitive and gynogenesis induction by temperature shock treatments is commonly practised in aquaculture.

Conclusions

Sperm-dependent parthenogenesis may not be a strictly asexual reproductive mode, as previously believed. With some degree of sperm leakage and genomic replacement, it may turn out to be a means of 'minimal sex'. We have discussed evidence for occasional recombinant (i.e., partially syngamic) processes, but further studies combining crossing experiments with suitable nuclear and mitochondrial markers will be necessary to fully explore this issue. More knowledge about the cytological phenomena, especially the role of the sperm in development of the fertilized egg, will help answer the following question. Should sperm-dependent parthenogenesis be considered as an evolutionary error (i.e., an accident with a suboptimal solution), or should it be interpreted as an advantageous, albeit rare, mode of reproduction?

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