THE EVOLUTIONARY ECOLOGY OF GYNOGENESIS

Ingo Schlupp
Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019; email: schlupp@ou.edu

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Abstract Most metazoans engage in recombination every generation. In theory this is associated with considerable cost, such as the production of males, so that asexual organisms, which do not pay this cost, should be able to invade populations of sexuals. Some asexuals depend on sperm of sexual males to trigger embryogenesis, a reproductive mode called gynogenesis. The genetic information of males is typically not used. Theory predicts that such mating complexes are short-lived and highly unstable. Sperm dependency is not only the defining feature of the biology of gynogenetic metazoans, it is also a major puzzle in evolutionary biology. Organisms that apparently combine disadvantages of both sexuality and asexuality are a serious challenge to theory. A number of questions about these systems are still unresolved.

CONCEPTUAL BACKGROUND: WHY SEX?

The evolution and maintenance of sexual reproduction is still one of the major unresolved problems in evolutionary biology (Redfield 1994, West et al. 1999). Once evolved, recombination must persist against invading asexuals (Doncaster et al. 2000), which do not show meiosis and recombination. During sexual reproduction any given individual pays a cost: It reduces the number of genes passed on to the next generation by half [cost of meiosis (Williams 1975)]. Additionally, for sexual reproduction two sexes are needed to restore the parental state, mostly diploidy. Hence, females have to produce males [cost of males (Maynard Smith 1978)] and mate with them. The costs also include finding a mate and risks associated with mating, like sexually transmitted diseases or increased predation. This contrasts with clonal reproduction in which the whole genome is transmitted unchanged and only females are produced. Parthenogenesis should be the more successful strategy—at least in the short term. In the long run, clonal organisms also appear to pay a cost: They accumulate deleterious mutations that cannot be purged without recombination and rare beneficial mutations cannot be combined in the same individual (Muller 1964, Williams 1975). Several theories have been proposed to explain the persistence of sexual reproduction in spite of the costs (Kondrashov 1993, West et al. 1999), but no single theory has unanimous support. Currently, one of the most widely accepted, and arguably best supported, ideas to explain
the maintenance of recombination is the Red Queen hypothesis (Hamilton 1980, Ladle 1992, Van Valen 1973). It proposes that recombination results in genetically diverse offspring which, contrary to the uniform offspring of asexuals, are difficult targets for parasites and diseases (Bell 1982).

Essentially, we still lack an understanding of how sexual organisms can keep asexuals at bay given the hypothesized short-term advantages of asexuality (Agrawal 2001, West et al. 1999). One approach to this problem is to directly compare closely related sexual and asexual species. Such animals are unsuitable to study the origin of recombination, but questions concerning the maintenance of sex can be addressed.

WHAT IS GYNOGENESIS?

Parthenogenesis in metazoans is the development of an adult organism using only maternal genetic information. Parthenogenesis is not uncommon in metazoans and, in many species, parthenogenesis and sexual reproduction coexist. They may alternate throughout the life cycle as in water fleas (Daphnia) (Suomalainen et al. 1987), or exist simultaneously as in hymenopterans, which produce males from unfertilized eggs and females from fertilized eggs (Suomalainen et al. 1987). In the related phenomenon of androgenesis, eggs develop after the disintegration of the maternal chromosomes, using only the remaining paternal genes. Natural androgenesis is extremely rare [for example, in Bacillus rossius, a stick insect (Mantovani & Scali 1992)]. Natural parthenogenetic development can be spontaneous or it may need to be induced by sperm. This is called pseudogamy, or gynogenesis (Figure 1). The “correct” ploidy, often diploidy, of the organism is achieved either by absence of meiosis (apomixis) or by one of several mechanisms that restore ploidy after meiosis. A common mechanism is fusion of the egg cell with one of the polar bodies (Suomalainen et al. 1987). In gynogenesis, the sperm serves

![Figure 1](Schematic representation of sexual reproduction, parthenogenesis, and gynogenesis. M refers to maternal contributions; P to paternal contributions.)
solely to trigger embryogenesis, but further contribution of the sperm is usually absent (for exceptions, see below).

In hybridogenesis, another form of sperm-dependent clonal reproduction, haploid egg cells are formed, which fuse with the sperm nucleus. During gametogenesis, the male chromosomes are removed from the egg and only the clonal part of the genome is passed on. This is called hemiclonal because only the maternal half of the genome is clonal. Hybridogenesis is found in several vertebrates and invertebrates (Beukeboom & Vrijenhoek 1998). Examples from vertebrates include the waterfrog complex (*Rana esculenta*) (Hellriegel & Reyer 2000, Reyer et al. 1999, Tunner 1979), and a group of fish (*Poeciliopsis* complex) (Vrijenhoek 1994, 1998).

Gynogenesis differs from sexual reproduction because the female genome is passed on unchanged. It is similar to sexual reproduction because it also requires males. For sperm-dependent unisexuals this means they need to use sperm from a heterospecific male. Due to this physiological dependency, gynogenesis has been called “sperm parasitism” (Hubbs 1964). Gynogens are interesting models because they combine disadvantageous traits from both sexuality and asexuality. Understanding how they evolve is especially revealing. Gynogenesis is being investigated at three levels: (a) the level of genetics because organisms without recombination have to deal with genetic decay, (b) the level of ecology to understand how stability in associations of sexuals and gynogens evolves and is maintained, and (c) the level of behavior because mating decisions of the associated males may be crucial to the stability of such mating systems.

**EVOLUTIONARY ORIGINS OF GYNOGENESIS**

Gynogenesis occurs in a number of taxa. Gynogens are not species in the sense of the biospecies concept (Mayr 1967), leading to difficulties in taxonomy (Cole 1985). On the one hand, they do not reproduce sexually in the sense of the definition, but on the other hand, they are usually morphologically, ecologically, and genetically distinct. Nonetheless, knowing the number of gynogenic (or parthenogenetic) species is difficult as the numbers of “forms” counted vary. As most gynogens are thought to have had multiple origins and coexist in multiple, genetically identifiable lineages, it is very difficult to decide which should be counted as a distinct entity. Excellent lists of gynogens and other parthenogenetic metazoans are provided in Beukeboom & Vrijenhoek 1998, Suomalainen et al. 1987, and Vrijenhoek et al. 1989. It appears that gynogenesis has evolved multiple times independently in several taxonomic groups. In one genus, *Poeciliopsis*, both gynogenesis and hybridogenesis have been described (Schultz 1967). Gynogens and parthenogens are likely to be overlooked by classical methods used to catalogue biodiversity. This is highlighted by the recent description of a cryptic clonal lineage of loach, *Misgurnus anguillicaudatus* (Morishima et al. 2002), which was detected using flow cytometry. Nonetheless, it is curious that so few gynogenetic taxa have been described.
Gynogenesis is absent in some major groups of vertebrates, like mammals. It is thought that genomic imprinting, an epigenetic process responsible for differences between homologous chromosomes depending on parental origin (Georgiades et al. 2001), plays a role in the absence of gynogenesis in mammals.

Hybrid Origin

Most gynogenetic vertebrates are of hybrid origin (Beukeboom & Vrijenhoek 1998, Vrijenhoek et al. 1989). One important consequence of a hybrid origin is that such species start out with extremely high heterozygosity and are therefore often called “frozen F1.” Molecular tools offer a powerful approach to identify hybrid origins (Alves et al. 1997, Dawley et al. 1987, Schartl et al. 1995b, Turner et al. 1990).

The Amazon molly (Poecilia formosa), a livebearing fish, seems to represent a case of a single hybrid origin (D. Möller, J. Parzefall & I. Schlupp, in preparation). Hubbs & Hubbs (1932) suggested that Amazon mollies have a hybrid origin. They proposed P. sphenops and P. latipinna to be the parental species. Later it became clear that P. mexicana was the maternal ancestor, but at the time, what is now known as P. mexicana was not recognized as a separate species. The Amazon molly was originally described by the French ichthyologist Girard in 1859 (Girard 1859), but it was not until 1932 that Laura and Carl Hubbs recognized that Amazons are unisexual (Hubbs & Hubbs 1932). Supporting molecular evidence for the hybrid origin was provided using genetic methods (Avise et al. 1991, Schartl et al. 1995b, Turner 1982). Multiple origins are known, e.g., for Ambystoma salamanders (Bogart 1989, Hedges et al. 1992), and triploid Poeciliopsis (Quattro et al. 1992, Vrijenhoek 1993).

For gynogens of hybrid origin it is usually assumed that they acquire all characteristic features of gynogenesis at once. Two scenarios for the evolution of gynogenesis with hybrid origin seem possible:

1) Single step. Here multiple evolutionary changes occur simultaneously. This includes disruption of meiosis, discarding the second sex, and several other features. Although this seems to be the most widely accepted scenario, it is not clear how exactly this complex change happens. However, if this hypothesis is correct, it may explain why the de novo formation of gynogens seems so rare: If only one of the multiple changes fails to function, the successful formation of a unisexual fails. Apparently the conditions under which the Amazon molly arose are not repeatable. Numerous attempts to create unisexual F1’s using various populations of the putative parental species invariably led to sexually reproducing F1 (Dries 2003, Schartl et al. 1991, Schlupp et al. 1992). Such F1 hybrids have been repeatedly used in research (Dries 2003, Schartl et al. 1991, Schlupp et al. 1992) but comparisons with true Amazon mollies should be made with caution, because the sexual lineages used to produce the F1 have had an independent evolution over many generations. The repeated successful formation of hybridogenetic fishes (Poeciliopsis;
Schultz 1973; Vrijenhoek 1993, 1994) and triploid planthoppers of the genus \textit{Muelleriana} (Drosopoulos 1978) are in agreement with this hypothesis, as no intermediate stages were reported.

2) \textit{Multiple steps.} A sexual \(F_1\) might be formed first, potentially with a strongly biased sex ratio according to Haldane’s rule. Subsequently an additional evolutionary step may lead to loss of sexuality and selection might then favor the gynogen.

\textbf{Nonhybrid Origin}

Several invertebrate gynogens are probably not of hybrid origin. In these cases, an elevation of ploidy, through autopolyploidization, apparently led to mostly triploid forms. The only vertebrate that seems to be of nonhybrid origin is \textit{Carassius auratus gibelio}. A recent report noted sexual reproduction within the gynogenetic species (Zhou et al. 2000), and it is presently difficult to estimate whether this is a recent evolutionary event or an overlooked old phenomenon.

\textbf{Age of Gynogens}

Gynogens are conventionally seen as evolutionarily short lived. Age estimates of up to 100,000 years have been published for some of the gynogenetic vertebrates (Avise et al. 1991, Hedges et al. 1992, Schartl et al. 1995b, Spolsky et al. 1992). These estimates are often based on the molecular clock and have large confidence intervals. This was referred to by Dries (2003), who argued that Amazon mollies, for which several age estimates ranging between 10,000 and 100,000 years have been published (Avise et al. 1991, Schartl et al. 1995b), might be as young as the lower confidence limit (8900 years). Dries (2003) correctly pointed out that in this case not enough time may have elapsed for evolutionary changes. One might also argue, however, that Amazon mollies are as old as the upper confidence limit (600,000 years), which should have been sufficient time for evolution. Nonetheless, the roughly 100,000 years that have been mentioned for individual lineages of \textit{Ambystoma} (Spolsky et al. 1992) and \textit{P. formosa} (Schartl et al. 1995b) are old under models of mutational meltdown based on the accumulation of deleterious mutations (Gabriel & Bürger 2000, Gabriel et al. 1993). Their ages pale, however, compared to those of the so-called “asexual scandals” (Judson & Normark 1996), especially bdelloid rotifers (Poinar & Ricci 1992) and ostracods (Judson & Normark 1996; Maynard Smith 1978, 1992), which are several millions of years old.

\textbf{CONSEQUENCES OF SPERM DEPENDENCY}

Sperm dependency has two main consequences: (a) it provides a mechanism for the introgression of paternal DNA into the clonal genome of gynogens, and (b) the gynogens cannot ecologically out-compete their hosts. Their physiological sperm
dependency leads to behavioral and ecological interactions with males and females of a host species.

**Genetic Consequences of Sperm Dependency**

The need for sperm to trigger embryogenesis results in an intimate association of egg and sperm. One result of this is the occasional introgression of paternal DNA into the clonal genome of gynogens. Paternal DNA may be incorporated as a heritable component into the genome. This has been documented in salamanders (*Ambystoma laterale* complex; Bogart 1989, Bogart & Licht 1986, Bogart et al. 1989). In Amazon mollies, two genetic interactions between asexuals and sexu- als have been described, formation of triploids and introgression of subgenomic amounts of DNA.

**TRIPLOIDY** The inclusion of the complete sperm genome leads to triploid lineages (Schultz & Kallman 1968; Lamatsch et al. 2000a,b; Nanda et al. 1995). Fertile triploids have been reported from natural populations (Lamatsch et al. 2000a,b, but laboratory-produced triploids were sterile (Nanda et al. 1995, Schultz & Kallman 1968). Ploidy levels higher than 3N have been described for *Ambystoma*, where it can reach 5N. In *Ambystoma*, there is an inverse relationship between ploidy and fitness (Lowcock et al. 1991). In Amazon mollies, triploids are thought to be restricted to the Rio Purification drainage in Mexico (Balsano et al. 1989), and it is unclear why triploids do not have a wider geographical distribution. A recent study suggested that triploidy arose only once within the Amazon mollies (Lampert et al. 2005), whereas it arose multiple times independently in the *Poeciliopsis* complex (Mateos & Vrijenhoek 2005). The overall morphology, including size, does not allow the identification of triploid Amazons in the field, suggesting they might be more widespread than currently appreciated.

In many complexes, a present sperm donor species has been involved in the hybridization that lead to the gynogenetic hybrid. Consequently, the additional genome is provided by a species that has already contributed to the hybrid. In triploid Amazon mollies, the parental species have been *P. latipinna* and *P. mexicana*, and in the triploids typically a *P. mexicana* genome has been added (Balsano et al. 1989). Triploids with an added *P. latipinna* genome are extremely rare (Balsano et al. 1989). This allows study not only of the effects of elevated ploidy, but also of the interactions of an ancient genome with a recently recombined one.

In other species, triploids have an added genome from a species not involved in the hybridization. Especially in *Ambystoma*, the situation is very complex and paternal chromosome sets have been added from several species (Hedges et al. 1992). Behavior of triploid Amazon mollies, fitness consequences, and the coexistence remain to be studied, but good data on distribution and ecology are available from intensive field studies (Balsano et al. 1989). In triploid Amazon mollies, laboratory-born males have been reported to produce sperm, although spermatogenesis was abnormal. Breeding these males produces no offspring with sexual
females, but males were capable of triggering embryogenesis in Amazon mollies (Lamatsch et al. 2000a,b).

MICROCHROMOSOMES A second mechanism for adding paternal genetic material is the inclusion of only a small part of the sperm genome. Microchromosomes are very small, centromere bearing parts of a paternal chromosome. Their addition to a clonal genome leads to aneuploid lineages. In Amazon mollies, stable, microchromosome-bearing lineages (Schartl et al. 1995a, 1997) have been described both from the laboratory and the field. Triploid lineages can also bear microchromosomes. Given the size of the microchromosome, only limited amounts of new genetic material will be added this way. Whether this has important evolutionary consequences is still unclear, but clearly possible: In a laboratory-produced lineage of Amazon mollies bearing microchromosomes originating from “Black Mollies” (an all-black strain, which is a hybrid of several species of *Poecilia*), some individuals develop melanoma, which is unknown in Amazon mollies otherwise, because they lack the cell type (macromelanophores) for this cancer (Schartl et al. 1997). The gene coding for the tumor is located on the microchromosome.

Both mechanisms of stable introgression give us insights into the mechanism of egg activation. It appears that the sperm nucleus enters the egg cell and that the paternal chromosomes are being destroyed. If this process is halted before the entire chromosome is digested, it results in a microchromosome.

Stability of Mating Complexes

Asexual females have an intrinsic advantage over sexual females: They do not have to produce male offspring. Assuming equal reproductive output (which is true for *P. mexicana* and *P. formosa*: I. Schlupp & A. Taebel-Hellwig, in preparation), theoretically the number of gynogens in a population should grow much faster as compared to the sexuals. At the same time, the sex ratio of all females (combining gynogens and sexuals) to males becomes increasingly female biased. If no mechanisms counter this, eventually the sexuals in the population go extinct. As a direct consequence, the gynogens will also go extinct. Two mechanisms have been suggested to explain stability in complexes of gynogens and sexuals: behavioral regulation and ecological differences.

ECOLOGICAL DIFFERENCES Stable coexistence can be expected if gynogens and sexuals use different ecological niches. Gynogens of hybrid origin differ genetically from both parental species, which predicts differences in niche usage (Vrijenhoek 1994). However, the physiological dependence on sperm forces the gynogens into close ecological proximity of the sexuals. The conditions for stable coexistence of sexuals and gynogens have been reviewed by Vrijenhoek (1994). His *Frozen Niche Variation* model (Vrijenhoek 1979) is very well supported. It argues that clones of multiple origin may use resources underutilized by the sexual parental species. Case & Taper (1986) argued that the broader niche width of the
sexuals is important for stable coexistence. They also argued that the intrinsic advantage of the asexuals is not always twofold. A related argument was presented by Doncaster et al. (2000). In a model studying the hybridogenetic frog (R. esculenta) (Hellriegel & Reyer 2000), a combination of factors was found to allow for stable coexistence: female mating preferences, female fecundity, larval performance, and dispersal were important. Hakoyama & Iwasa (2004) argued that parasites might also significantly contribute to stability.

On a small scale, instability and extinction might go undetected, but a recent study (Heubel 2004) suggested that this dynamic might actually be present in nature. Heubel (2004) found that frequencies of gynogens in six mixed populations of P. formosa and P. latipinna increased over the reproductive season, apparently according to different population growth rates of the two types of females. However, environmental instability caused by the winter, floods, draughts, or other environmental perturbations prevent the system to reach climax (mosaic-cycle hypothesis) (Hutchinson 1961), which in this particular system would be the extinction of the sexuals. It would also lead to the extinction of the gynogens. Other mechanisms for stability are also likely. There could be a significant reduction of the gynogen’s fitness at any stage of their life history, but to date, few studies are available. In a field study of the population biology of Amazon and Sailfin mollies (Heubel 2004), equal reproductive output (I. Schlupp & A. Taebel-Hellwig, in preparation), absence of differences in parasite loads (Tobler & Schlupp 2005), and no difference in the degree of filial cannibalism (C. Hubbs & I. Schlupp, in preparation) indicate a remarkable ecological similarity of the females.

Earlier models argued that niche separation is not required to explain stable coexistence (Moore 1975, Moore & McKay 1971, Stenseth et al. 1985) and highlighted the importance of behavioral decisions, especially male choice and male sperm allocation.

**Behavioral Regulation** Behavioral mechanisms may be critical in regulating the coexistence of gynogens and their sexual hosts. Gynogenetic females have to obtain access to sperm, but males do not gain from matings with gynogens. Consequently, good candidates for stabilizing mechanisms include male behavior, especially male choice. Theoretically it would be easiest for gynogens to obtain sperm from males that release sperm for external fertilization. However, several gynogenetic species have internal fertilization. Females require intimate contact with males to obtain sperm. The Amazon molly uses the two species that were involved in the hybridization, P. latipinna and P. mexicana (Schlupp et al. 2002). A third host species, P. latipunctata, has recently been described (Niemietz et al. 2002). In this case, the third host may have made secondary contact with the Amazon molly only recently.

Internal fertilization is a severe constraint for the females—something other unisexuals with external fertilization do not face (like, e.g., the Crucian carp, Carassius) (Hakoyama & Iguchi 2002). From the male’s perspective, these matings are wasted because they have no fitness-relevant offspring with gynogens.
This should promote strong discrimination resulting in the extinction of the gynogen. Obviously males do mate with gynogens, raising the question, How can this be explained? A connected question is whether gynogens show adaptations countering male discrimination (Dries 2003, Schlupp et al. 1991). An example for such adaptations and the underlying evolutionary “arms-race” might be sexual mimicry. This was described in the hybridogenetic fish *Poeciliopsis* (Lima et al. 1996), where asexual females mimic the color pattern around the genital opening found in their sexual competitors.

So far three hypotheses have been offered to explain heterospecific matings.

1) Males may make mistakes and/or use a “best of a bad job” strategy (Kawecki 1988). They might be unable to distinguish between the two types of females or have only weak preferences. However, numerous studies have reported male discrimination in the sperm donors of the Amazon mollies (Dries 2003, Schlupp et al. 1998), as well as in other species like bark beetles (*Ips*) (Loyning & Kirkendall 1996). In addition, one study showed reproductive character displacement in male *P. latipinna* (Gabor & Ryan 2001). Males from sympatric populations were better able to distinguish between gynogenetic and sexual females.

Interestingly, a small number of studies were unable to find male preferences, either in general (Balsano et al. 1981, Balsano et al. 1985, Heubel 2004, Woodhead 1985) or under certain circumstances (Schlupp et al. 1991). The latter study provided an explanation for the lack of preference: Females that were receptive were more attractive to males, independent of species. Male preferences may be influenced by the females’ sexual cycle (Parzefall 1973): Females are receptive only for a few days during each monthly cycle. Therefore, only a small proportion of the females of a population are fertile at any given time. Males are probably under selection not to forsake any potential matings (Schlupp & Ryan 1997). Alternatively, mate choice under certain environmental conditions might become so costly—especially time-consuming—that males will do better by indiscriminately mating with every female. Heubel & Schlupp (2005) identified natural turbidity as potential “visual noise” limiting male mating behavior.

The methods used to study female preferences and male mate choice (Jennions & Petrie 1997) differ, and it is unclear whether this interacts with the results reported. In several studies, full interaction of all participating individuals was allowed (e.g., Gabor & Ryan 2001, Ryan et al. 1996, Schlupp et al. 1991). This approach provides a relatively high degree of biological realism, as it mimics the natural interactions leading to actual insemination. In these studies, male choice is usually scored using male copulation attempts as proxy for actual sperm transfer. The disadvantage is that the outcome of such interactions only partly reflects male mating preferences, partly female choice, and (depending on the design) partly female-female interactions. A recent study indicated that
not all copulation attempts do result in sperm transfer (Schlupp & Plath 2005).

Another approach to measuring male preferences is to separate the choosing male from the stimulus females. Using such a setup will limit the amount of information available to the choosing male. The female stimuli may be presented live (Niemeitz et al. 2002) or as video-playback (Körner et al. 1999, Landmann et al. 1999), as well as simultaneously or sequentially (K.U. Heubel & I. Schlupp, manuscript submitted). A study conducted by K.U. Heubel & I. Schlupp (manuscript submitted) raised the possibility that seasonality might be an important component in male choice: Males were choosier during the peak of the reproductive season.

Nonetheless, in the majority of studies, males were found to prefer conspecific females, although not under all circumstances. So far, male mating behavior was mainly studied at the behavioral level, without examining the possibility of differential sperm transfer. A recent study (Aspbury & Gabor 2004) showed that males of one of the host species (P. latipinna) of the Amazon molly prime more sperm after being visually exposed to a conspecific female as compared to a P. formosa female. This demonstrated that males can adjust their investment in sperm, but did not determine if males actually transfer less or no sperm in matings with the Amazon molly. This was addressed in a recent study (Schlupp & Plath 2005), which found that behavioral preferences match the sperm transferred to females. Amazon mollies received less sexual behavior and also less sperm.

2) Male choice may be frequency- or density-dependent: The basic idea is that males should decline matings with the most common female phenotype, thereby selectively favoring the rare females. Males, however, should not selectively mate with gynogens when frequencies of sexuals are high. Several studies addressed this problem (Moore & McKay 1971, Stenseth et al. 1985).

3) Males may gain from mating with the gynogens: This hypothesis has been proposed by Schlupp et al. (1994). In several species, females do not always exercise independent mate choice, but may be influenced by observing the mating decisions of other females (reviewed by Brooks 1998, Westneat et al. 2000). Schlupp et al. (1994) showed that females of P. latipinna (Sailfin mollies) copied the mating preference of Amazon mollies, thereby providing an indirect benefit for males. Subsequently, K.U. Heubel & I. Schlupp (manuscript in preparation) showed that female P. mexicana (Atlantic mollies) also copy the mate choice of Amazon mollies and that Amazon mollies copy each other. Essentially, all females from sympatry copy each other, including the sexual females (K.U. Heubel & I. Schlupp, manuscript in preparation; Witte & Ryan 1998, 2002). It is noteworthy that Witte & Ryan (2002) demonstrated that mate copying also takes place in the field. For mate copying to work, males must visibly interact with Amazons, but it does not require actual sperm transfer. It can also be
argued that male mating behavior is a signal of male presence. It is not clear why sexual females imitate the gynogens. This is in agreement, however, with the overall ecological similarity of the two types of females.

**FEMALE–FEMALE INTERACTIONS** A more indirect consequence of sperm dependency is that gynogens also have to interact with sexual females. This goes beyond typical intraspecific interactions. Amazon mollies, e.g., and sexual *P. latipinna* can distinguish each other (Schlupp & Ryan 1996). They prefer to associate with conspecifics, but trade off this preference for a larger group. This preference for larger groups facilitates the formation of mixed shoals (Schlupp & Ryan 1996), which set the stage for all interspecific interactions. Females may also compete over resources. In this context, aggression between sexuals and gynogens has been described (Foran & Ryan 1994, Schlupp et al. 1991), with the gynogens being more aggressive than the sexuals.

**EVOLUTIONARY POTENTIAL OF GYNOGENS**

**Microevolution**

So far, studies comparing the behavior of gynogens and their sexual hosts have found very few differences. The female preference for large males, e.g., in Amazon mollies (Marler & Ryan 1997), did not differ from the same preference exhibited by the sexual females. The host males and the gynogens may be locked into a coevolutionary cycle with adaptations and counter-adaptations that are difficult to detect. Interesting exceptions are two studies on visual preferences in Amazon mollies. When given a choice between a host male (*P. latipinna*) with or without a novel ornament, Amazon mollies and Sailfin mollies differed. Amazon mollies showed no preference for the novel trait, but the sexual females did. In a second case, sexual *P. mexicana* preferred a novel trait, but the Amazon mollies did not (Schlupp et al. 1999). In another study, also using the Amazon molly, the gynogens rejected images of males with signs of a parasitic infection, but sexual females (*P. latipinna* and *P. mexicana*) did not show any preference (Tobler & Schlupp 2005). It is not certain, however, that differences between gynogens and sexuals indicate evolution of the Amazons, because alternately the sexual species might have evolved. Equally, differences between gynogens and F₁ hybrids cannot establish evolution of gynogens (Dries 2003, Schlupp et al. 1992).

**Macroevolution**

Macroevolutionary events, like speciation or adaptive radiation, are not known from gynogens. In the *Poeciliopsis* system, the formation of a sexual species from a hemiclonal lineage has been reported (Vrijenhoek 1993).

One problem associated with assessing the evolutionary potential of gynogens is that many events are very likely to go undetected: suppose a triploid gynogen, with two genomes of parental species *A*, *A*⁺ and one of parental species *B*,
randomly loses one genome. If the lost genome is the rare one ($B$), the resulting genotype ($AA^+$) is probably not distinguishable from the true sexual and furthermore probably less fit owing to the accumulated deleterious mutations.

**Cryptic Sex?**

Mutations may be the main source of genetic diversity in gynogens, but they are clearly not the only source. Mutations alone would allow for a considerable evolutionary potential if mutation rates were high enough and population sizes were large. It is unclear how frequent the de novo addition of genetic material is and what the evolutionary consequences are. In Amazon mollies, triploids found in the Rio Purification seem to have a single origin. It has been proposed that adding genetic material to a clonal genome can influence the rate of genetic decay and prolong the gynogen’s evolutionary lifespan (Schartl et al. 1995a). Although there is not enough evidence on this subject yet, it is interesting to speculate if this qualifies as a form of rare, cryptic sex and whether less sex is as good as recombination of the whole genome every generation (Green & Noakes 1995). Of course, gynogens would still be dependent on a sexual species.

**Red Queen**

The Red Queen Hypothesis states that an immediate advantage of sexual reproduction lies in the production of genetically diverse offspring that provide a “moving target” for parasites. Common genotypes will quickly be targeted by parasites and experience reduced fitness. This predicts coevolutionary cycles of hosts and parasites in sexual species. It also predicts higher rates of infection of asexuals, when asexuals and sexuals have comparable exposure to parasites (Vrijenhoek 1994). This has been tested using Crucian carp (*Carassius auratus*): Here, diploid sexuals had fewer parasites than triploid gynogens (Hakoyama et al. 2001), which may play an important role in the stability of this complex (Hakoyama & Iwasa 2004). In Amazon mollies, comparing several parasites, Tobler & Schlupp (2005) did not find consistent differences between the gynogens and the syntopic sexual species, *P. latipinna*.

**OPEN QUESTIONS**

Sperm dependency is the defining feature of gynogens and a major puzzle in evolutionary biology. Organisms that apparently combine disadvantages of both sexuality and asexuality are a challenge to theory. A number of open questions are still associated with this.

1) Two major patterns of the taxonomical distribution of asexuals lack a convincing explanation. Gynogenesis and sperm dependency occur in some
fishes and amphibians, whereas all parthenogenetic reptiles do not require sperm. Within taxa that occasionally give rise to asexuals, like teleosts, large groups show no signs of asexuals, although hybrids are common (Dowling & Secor 1997). In East African cichlids, hybridization is hypothesized to form new species (Seehausen 2004), but no unisexuals have been detected. Relevant questions about the conditions for the de novo generation of asexual hybrids can be addressed experimentally. Is it a certain genetic distance that allows for the formation of asexuals? It is likely that many asexuals go undetected, especially sperm-dependant species, because they are observed and collected in the field together with males. Only careful behavioral and genetic studies can identify them as gynogens.

A related set of questions has to do with the first generations after the de novo formation. What selection pressures shape the new species? In the Poeciliopsis group, gynogenesis and hybridogenesis coexist, but it is unclear how this situation has evolved.

2) A better understanding of the consequences of sperm dependency is needed: It is still not clear what the costs and benefits associated with sperm dependency are. In many species, males provide direct benefits to females (Andersson 1994). In gynogens indirect benefits cannot play a role, because the males are in a different gene pool, but direct benefits might in theory ameliorate the cost of mating for asexual females (Neiman 2004).

Gynogenesis must be maintained against both the already present sexuals and against a potentially arising sperm-independent mutant. In other words, why does the occasional truly parthenogenetic mutant not spread in the population? If the cost of gynogenesis relative to parthenogenesis is low, the advantage of a newly arisen parthenogenetic mutant may be insignificant. It is important to note that gynogens and other parthenogens have already committed a major investment in female traits like morphology, so that the added cost of engaging in matings may be relatively small. Interestingly, in some parthenogenetic species, sexual behavior is still present. The best documented cases are female–female pseudocopulations in parthenogenetic Cnemidophorus lizards that enhance reproductive output in the asexuals (Crews & Fitzgerald 1980, Crews et al. 1986).

Many of these questions can be resolved by long-term field studies of ecology and life-history, such as studies published by Balsano et al. (1989), Heubel (2004), and Hubbs (1964), combined with mathematical models of population dynamics.

3) Behavior is context dependent. There are at least two categories of environmental variables that interact with behavior: (a) social context, i.e., other individuals nearby, and (b) abiotic conditions. Recent studies have established the idea of communication networks (McGregor & Peake 2000). This conceptual framework considers individual behavior in the presence of audiences. In many animals, signaling and sexual behavior takes place...
in close proximity of other individuals of the same species. These individuals may use information conveyed in interactions to their own advantage. This can be illustrated with mate copying (see above). In a mixed group of Amazon mollies and Sailfin mollies, the two types of females can be either the audience or the actor, leading to a large number of possible interactions. All of these can occur in rapid sequence. In nature these interactions may additionally be influenced by other behaviors, such as predator avoidance, male–male interactions (Schlupp & Ryan 1997), and female–female interactions (Foran & Ryan 1994), leading to very complex social interaction networks (Matos & Schlupp 2005). An example for an environmental variable influencing behavior is turbidity: Male choice is hampered under turbid conditions (K.U. Heubel & I. Schlupp, 2005). Especially male choice, which can be critical for the stability of gynogenetic mating systems, should be studied using a communication network approach.

Once a gynogenetic lineage has evolved it may remain gynogenetic or evolve a different mode of reproduction. The lineage may evolve into sperm-independent parthenogens (not observed), or hybridogens (not observed, although the transition from hybridogenesis to gynogenesis, or vice versa, has been reported in the hybridogenetic Poeciliopsis) (Vrijenhoek 1994), or finally into a sexual species. Evolution of an asexual into a sexual species is likely to go undetected, but has been reported for Poeciliopsis (Vrijenhoek 1989, 1993). Given the relatively young phylogenetic age of most gynogens, the genes coding for male functions are likely to be intact. In the Amazon molly, it was possible to induce male phenotypes by administering androgens (Schartl et al. 1991, Schlupp et al. 1992, Turner & Steeves 1989). Furthermore, spontaneous masculinization does occur. Lamatsch et al. (2000a,b) reported that males spontaneously occurred in a triploid lineage. These males had functional sperm and sired offspring with Amazon molly females, but not with sexual females.

4) Our knowledge of the exact mechanisms of fertilization and interactions of sperm and egg is still limited (Jun & Yigui 1991). In most species conclusive experiments showing that sperm is actually the trigger are lacking. As in parthenogenetic lizards (Cnemidophorus), copulatory stimuli might play an important role. Another problem in this context has to do with the acquisition of host species. Are all host species equally efficient? In most cases of gynogens of hybrid origin one of the parental species is a sperm donor. Additional hosts have been acquired in Amazon mollies (Niemetz et al. 2002) and Ambystoma (Bogart 1989). It is unknown how these relationships evolve, especially in gynogens of nonhybrid origin.

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