Poeciliid Research

Clonal-sexual contrasts in livebearing fishes: evolutionary, ecological and behavioral insights from *Poecilia* and *Poeciliopsis* complexes

[1]Claudiu Gavriloaie, [2]Aurel Maxim, [2]Daniela Bordea, [2]Bianca Moldovan, [3]Maria Popescu, [2]Ioan Brașovean

[1] Bioflux SRL, Cluj-Napoca, Romania; [2] Department of Environmental Engineering and Protection, Faculty of Agriculture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania; [3] Equine Clinic, Faculty of Veterinary Medicine, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania. Corresponding author: A. Maxim, aurel.maxim@usamvcluj.ro

Abstract. Livebearing fishes of the family Poeciliidae provide one of the most powerful comparative frameworks for evaluating the evolutionary consequences of clonal versus sexual reproduction. In complexes centered on the unisexual Amazon molly, *Poecilia formosa*, and hybridogenetic lineages of *Poeciliopsis monacha–Poeciliopsis lucida*, all-female clones coexist with closely related bisexual species, enabling direct contrasts in genetic architecture, ecological performance and adaptive potential. Gynogenetic and hybridogenetic systems preserve highly heterozygous hybrid genomes and confer short-term demographic advantages through exclusive daughter production, yet they depend on sperm from sympatric sexual hosts. Sexual congeners, by contrast, incur the cost of males but generate continuous recombination, extensive within-population genetic variance and diversified sexual traits shaped by mate choice and conflict. Empirical studies demonstrate that clonal assemblages can achieve high densities in heterogeneous habitats through niche partitioning among distinct “frozen” genotypes, while sexual populations retain superior capacity for long-term adaptation under sustained environmental change and coevolving biotic pressures. Behavioral dynamics, including rare-female advantage and fluctuating male discrimination, further mediate the stability of mixed sexual–clonal systems. Together, *Poecilia* and *Poeciliopsis* complexes illustrate that clonal and sexual strategies represent alternative solutions optimized for different temporal and ecological horizons: rapid colonization and demographic efficiency versus evolutionary flexibility and diversification.

Key Words: clonal reproduction, evolutionary potential, geographical parthenogenesis, gynogenesis, heterozygosity, hybridogenesis, niche partitioning, Poeciliidae, reproductive conflict, sexual selection.

Introduction. Livebearing fishes of the family Poeciliidae provide an exceptional natural experiment for contrasting the reproductive strategies of all-female, clonal lineages with those of sexually reproducing relatives (Schlupp et al 1991; Petrescu-Mag 2007a, b; Petrescu-Mag 2008; Petrescu-Mag & Bourne 2008; Petrescu-Mag 2009; Jeon et al 2016; Van Kruistum et al 2020; Furness et al 2021). Within this group, unisexual gynogenetic and hybridogenetic complexes coexist with bisexual species in shared habitats, allowing direct comparison of short-term demographic advantages of clonal reproduction with the long-term evolutionary potential conferred by sex and recombination (Schultz 1969, 1971; Vrijenhoek et al 1977; Vrijenhoek 1979). This review focuses on all-female *Poecilia* and *Poeciliopsis* complexes as model systems to examine how monosexual clones and sexually reproducing populations differ in genetic variability, ecological performance and capacity to respond to abiotic and biotic environmental change, including predation and competition.

The purpose of this mini-review is to synthesize genetic, ecological and behavioral evidence from *Poecilia* and *Poeciliopsis* systems in order to clarify how clonal and sexual reproductive strategies differ in short-term demographic performance and long-term evolutionary potential.

Mechanisms of clonal versus sexual reproduction in poeciliids. All-female lineages in *Poecilia* and *Poeciliopsis* arise via interspecific hybridization and then reproduce asexually while remaining dependent on sperm from sympatric sexual species. In *Poecilia formosa*, the Amazon molly, unisexual females produce diploid apomictic eggs (Georgescu et al 2020; Boaru & Petrescu-Mag 2024); sperm from *P. latipinna* or *P. mexicana* is required to trigger embryogenesis but paternal genomes are effectively excluded, so offspring are clonal copies of the mother (Schultz 1971; Avise et al 1991). This gynogenetic system produces monosexual populations of females, doubling the per-mating output of daughters relative to sexual species, which must invest half of reproductive effort in sons (Schultz 1971).

In *Poeciliopsis*, unisexual lineages include both gynogenetic triploids and hybridogenetic diploids (Georgescu et al 2020). In hybridogenetic forms such as *Poeciliopsis monacha–lucida*, oogenesis is preceded by the selective elimination of the paternal genome so that only the maternal genome (from *P. monacha*) is transmitted; subsequent fertilization by a sexual male restores the hybrid genotype in each generation (Schultz 1969; Cimino 1972; Vrijenhoek et al 1977). The result is clonal transmission of one parental genome, with continual "refreshment" of the other from sexual hosts, blurring the boundary between sexual and clonal strategies. In contrast, sympatric bisexual *Poecilia* and *Poeciliopsis* species reproduce by ordinary sexual meiosis and syngamy, generating genetically diverse broods and continuous recombination among loci (Schultz 1969; Evans et al 2011; Reznick et al 2021).

Genetic diversity, **heterozygosity and evolutionary potential**. The core trade-off between clonal and sexual strategies concerns genetic diversity. Classical theory predicts that obligate clonality freezes genotypes, limiting adaptive potential but preserving well-adapted combinations, whereas sex reshuffles alleles each generation, producing both maladapted and highly adaptive combinations in novel environments (Van Der Kooi et al 2017; Jaron et al 2020). Poeciliid systems provide empirical support for both sides of this trade-off.

Electrophoretic and DNA studies show that many unisexual poeciliids are strikingly heterozygous at the time of origin because they represent F1 hybrids between divergent sexual species (Schultz 1969, 1971; Cimino 1972). In *P. formosa*, allozyme variation is low among clones, but each clone is nearly fixed for heterozygous combinations that bridge *P. latipinna* and *P. mexicana* alleles, producing high genome-wide heterozygosity that likely contributes to physiological robustness and broad environmental tolerance (Schultz 1971; Avise et al 1991). Similarly, hybridogenetic *Poeciliopsis* unisexuals maintain fixed combinations of parental genomes that capture niche-relevant adaptations from each progenitor (Schultz 1969; Vrijenhoek et al 1977; Vrijenhoek 1979).

Comparisons of sexually and clonally reproducing *Poeciliopsis* populations using electrophoretic markers revealed that sexual populations maintain high within-population variation and can generate novel genotypes each generation, whereas clonal complexes consist of multiple, discrete clones, each internally uniform but differing from one another (Vrijenhoek et al 1977; Vrijenhoek 1979). Vrijenhoek (1979) argued that clonal reproduction "freezes" portions of the niche-width variation present in the ancestrally sexual gene pool, creating a mosaic of specialized genotypes that can coexist if they partition heterogeneous environments. Over macroevolutionary timescales, however, studies in other parthenogenetic animals indicate that loss of sex is associated with erosion of heterozygosity and reduced efficacy of positive selection, supporting the view that sexual reproduction facilitates rapid adaptation to changing conditions (Jaron et al 2020).

Ecological performance and niche use of clonal poeciliids. Despite their genetic uniformity within clones, all-female poeciliids can be ecologically successful, particularly in spatially structured or marginal habitats. In *Poeciliopsis*, natural populations often contain numerous sympatric clones alongside their sexual ancestors. Multiclonal assemblages reach significantly higher densities than either monoclonal or purely sexual populations, presumably because different clones specialize on slightly different microhabitats or resources, collectively exploiting environmental heterogeneity (Vrijenhoek 1979). Clonal reproduction here acts as an efficient mechanism to capture and preserve locally advantageous genotypic combinations, allowing each clone to function as a "frozen niche variant" within the broader habitat mosaic (Schultz 1971; Vrijenhoek 1979).

Similar patterns emerge in *P. formosa*. Its hybrid origin and high heterozygosity are associated with robust colonizing ability and rapid geographic expansion, consistent with the idea that a single successful genotype can spread efficiently when mates of the appropriate host species are available (Schultz 1971; Avise et al 1991). In such contexts, the demographic advantage of producing only females and the lack of a need for conspecific males confer strong short-term benefits, particularly in newly available or fluctuating environments where mate limitation would constrain sexual reproduction, a pattern echoed more generally in cases of geographical parthenogenesis (Van Der Kooi et al 2017; Kearney 2005; Hörandl 2023).

However, clonal poeciliids are constrained by their sperm dependence. All-female lineages must remain sympatric with at least one sexual host species and compete for sperm, space and resources. The theoretical advantage of producing twice as many daughters is offset by the risk of overexploiting the sperm supply; if clones become too abundant and outcompete their sexual hosts, they risk driving their own reproductive support to local extinction (Schultz 1971). This ecological interdependence sharply contrasts with sexually reproducing poeciliids, whose persistence does not depend on heterospecific sperm donors.

Sexual selection, **conflict and the richness of sexual strategies in poeciliids**. Sexually reproducing poeciliids exhibit remarkable diversity in reproductive modes and sexual traits. Females range from lecithotrophic species, provisioning eggs before fertilization, to highly matrotrophic species, where most resources are delivered after fertilization via placental analogues (Reznick et al 2021). This shift in provisioning timing profoundly alters sexual conflict and sexual selection dynamics. In lecithotrophic species, strong pre-copulatory female choice favors conspicuous male ornaments and courtship displays, whereas in matrotrophic species, selection shifts toward post-copulatory mechanisms such as cryptic female choice and sperm competition, driving the evolution of specialized gonopodia and ejaculates (Reznick et al 2021; Oroian & Kovacs 2022).

This sexual diversification has macroevolutionary consequences. Comparative analyses across Poeciliidae indicate that the evolution of maternal provisioning itself does not directly accelerate speciation, but male traits associated with sexual selection correlate with higher speciation rates, suggesting that divergence in mating signals and preferences is a major engine of diversification in this family (Păsărin & Petrescu-Mag 2011; Reznick et al 2021). Sexual systems thus generate not only within-population genetic variability, but also a rich tapestry of behavioral and morphological traits that promote reproductive isolation and adaptive radiation into new ecological niches. Such opportunities for innovation and lineage splitting are largely absent in strictly clonal, all-female systems.

Biotic interactions: **male choice**, **rare**-**female advantage and predator**-**prey dynamics**. In mixed sexual-clonal poeciliid assemblages, reproductive success of clones depends critically on male behavior. Males of sexual species generally prefer conspecific females over unisexuals, constraining clonal expansion (Petrescu-Mag et al 2020). However, behavioral studies in *Poeciliopsis lucida* interacting with unisexual *Poeciliopsis* clones have revealed a "rare-female advantage": males more readily court unfamiliar clonal types than common ones, and learning to discriminate against one clone does not fully generalize to others (Keegan-Rogers & Schultz 1988). As a result, rare or novel clones enjoy higher insemination and pregnancy rates than common clones, promoting coexistence among multiple clonal lineages and with their sexual hosts (Keegan-Rogers & Schultz 1988).

In *Poecilia* complexes containing *P. formosa*, skewed sex ratios and asynchronous female receptivity create conditions where male mating behavior becomes effectively indiscriminate during mating frenzies, ensuring that both sexual and unisexual females receive inseminations (Balsano et al 1985). Such "behavioral noise" in mate choice acts as a stabilizing mechanism that maintains all-female lineages despite male preferences. These dynamics illustrate how the reproductive strategy of clones is tightly linked to the behavior of their sexual partners, in contrast to sexual species where both sexes are subject to reciprocal mate choice and sexual conflict (Balsano et al 1985; Keegan-Rogers & Schultz 1988; Reznick et al 2021; Petrescu-Mag 2023).

Predation and other biotic pressures can interact with reproductive mode (Papuc et al 2025; Petrescu-Mag & Păsărin 2025). Theory predicts that sexual populations, with their high genotypic variance, are better able to generate predator-resistant phenotypes and respond to coevolving parasites and predators (the Red Queen hypothesis), whereas clones may be vulnerable to specialized enemy adaptation (Kearney 2005; Van Der Kooi et al 2017; Jaron et al 2020). Although direct experimental tests in poeciliids are limited, the persistence of multiple, ecologically differentiated clones within the same drainage systems suggests that clonal diversity, hybrid vigor and behavioral avoidance strategies can mitigate some of these risks, at least over intermediate timescales (Schultz 1971; Vrijenhoek et al 1977; Vrijenhoek 1979; Avise et al 1991).

Responses to environmental variation and range dynamics. Environmental heterogeneity and change, whether abiotic or biotic, pose a stringent test for any reproductive strategy. Sexual poeciliids, by generating recombinant genotypes each generation, are predicted to adapt more readily to novel or rapidly changing conditions, while clonal lineages may excel in stable or predictably fluctuating environments where an already well-adapted genotype can be propagated unchanged (Van Der Kooi et al 2017; Jaron et al 2020; Hörandl 2023). Evidence from poeciliids and other partially clonal taxa supports a nuanced view.

In *Poeciliopsis*, clonal diversity within rivers appears to be maintained by habitat heterogeneity: different clones achieve higher fitness in different microhabitats, and migration among pools and arroyos continually reshuffles their spatial distribution (Vrijenhoek 1979). Multiclonal populations thus can track fine-scale environmental variation without recombination, by shifting the relative frequencies of pre-existing clones. In contrast, sexual populations adapt by changes in allele frequencies within a single, recombining gene pool, potentially allowing continuous fine-tuning but at the cost of breaking up coadapted gene complexes (Vrijenhoek et al 1977; Vrijenhoek 1979).

On broader spatial scales, unisexual poeciliids illustrate a pattern analogous to geographical parthenogenesis described in plants and invertebrates: clones often occupy marginal or recently disturbed habitats, benefiting from uniparental reproductive assurance and high colonizing ability, while sexual relatives dominate core ranges where biotic interactions and long-term adaptive demands are stronger (Avise et al 1991; Kearney 2005; Van Der Kooi et al 2017; Hörandl 2023). The rapid northward expansion and wide distribution of *P. formosa* from a likely recent hybrid origin fit this model, underscoring the capacity of a single successful clonal genotype to exploit new environments, at least over evolutionary short to moderate timescales (Schultz 1971; Avise et al 1991).

Advantages and limits of clonal and sexual strategies in poeciliids. Poeciliid fishes reveal that the reproductive strategy of all-female clonal lineages is characterized by immediate demographic advantages, efficient colonization and the capacity to preserve highly heterozygous, hybrid genotypes that can perform well across diverse habitats (Schultz 1969, 1971; Cimino 1972; Vrijenhoek 1979; Avise et al 1991). Clonal reproduction "locks in" successful combinations of alleles and doubles the production of reproductive females, but at the cost of reduced generation of novel variation and strong dependence on heterospecific sperm donors and male behavior (Schultz 1971; Vrijenhoek 1979; Balsano et al 1985; Keegan-Rogers & Schultz 1988).

Sexual poeciliids, in contrast, pay the cost of producing males and continually shuffling genomes, yet they gain access to vast combinatorial genetic variability, powerful responses to abiotic and biotic environmental fluctuations, and rich arenas for sexual selection and speciation (Schultz 1969; Vrijenhoek et al 1977; Evans et al 2011; Reznick et al 2021). Their reproductive mode fosters diversification in morphology, behavior and life history, enabling adaptation to extreme environments and promoting long-term evolutionary persistence.

Taken together, *Poecilia* and *Poeciliopsis* complexes illustrate that monosexual clonal and sexual strategies are not simply better or worse, but adapted to different temporal and ecological horizons: clones excel in short-term numerical and colonization success, especially where mates are scarce or habitats are newly available, whereas sexual populations hold the advantage in the face of sustained environmental change, coevolving enemies and the open-ended opportunities for innovation and diversification that recombination affords.

Conclusions. Comparative evidence from poeciliid fishes demonstrates that clonal and sexual reproduction are not hierarchically superior or inferior strategies, but context-dependent evolutionary solutions. All-female clonal lineages capitalize on hybrid vigor, fixed heterozygosity and exclusive daughter production to achieve rapid population growth and efficient colonization, particularly in spatially heterogeneous or newly available habitats. Their success is reinforced by mechanisms such as multiclonal niche partitioning and behavioral dynamics that maintain access to sperm donors. However, clonality constrains the generation of novel genetic combinations and ties persistence to the continued presence of sexual host species.

Sexual poeciliids, although burdened by the demographic cost of males, sustain high standing genetic variation and ongoing recombination, enabling adaptive responses to abiotic fluctuations, predator–parasite coevolution and shifting ecological interactions. Sexual selection further promotes morphological, behavioral and life-history diversification, contributing to speciation and macroevolutionary persistence.

Ultimately, *Poecilia* and *Poeciliopsis* complexes reveal that clonal systems excel over short ecological timescales and in colonization contexts, whereas sexual systems retain advantages under long-term environmental instability and in the generation of evolutionary novelty.

Conflict of interest. The authors declare that there is no conflict of interest.

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Authors:
Claudiu Gavriloaie, SC Bioflux SRL Cluj-Napoca, 54 Ceahlau Street, 400488 Cluj-Napoca, Romania, e-mail: claudiugavriloaie@gmail.com
Aurel Maxim, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Agriculture, Department of Environmental Engineering and Protection, 3-5 Calea Mănăştur Street, 400372 Cluj-Napoca, Romania, e-mail: aurel.maxim@usamvcluj.ro
Daniela Bordea, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Agriculture, Department of Environmental Engineering and Protection, 3-5 Calea Mănăştur Street, 400372 Cluj-Napoca, Romania, e-mail: bordeadana@yahoo.com
Bianca Moldovan, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Agriculture, Department of Environmental Engineering and Protection, 3-5 Calea Mănăştur Street, 400372 Cluj-Napoca, Romania, e-mail: bianca.bordeanu@usamvcluj.ro
Maria Popescu, Equine Clinic, Faculty of Veterinary Medicine, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, 3-5 Mănăștur Street, 400372 Cluj-Napoca, Romania, e-mail: maria.popescu@usamvcluj.ro
Ioan Brașovean, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Faculty of Agriculture, Department of Environmental Engineering and Protection, 3-5 Calea Mănăştur Street, 400372 Cluj-Napoca, Romania, e-mail: ioan.brasovean@usamvcluj.ro

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