Chapter 27 Integrative commentary on *Ecology and Evolution of Poeciliid Fishes*

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THE SPECIES DIVERSITY, accessible biology, well-defined and accessible habitats, short generation time, and ease of laboratory culture make poeciliid fishes extraordinarily good subjects for research in both academic and applied biology. The chapters in this book show that nearly every major problem in biology has been addressed with poeciliids and that they have given major new insights in behavioral ecology, evolutionary biology, and genetics related to sexual reproduction. The chapter topics are so diverse that most readers (including me) will learn something new and interesting from this book. Unlike any other model system, poeciliids, and guppies (*Poecilia reticulata*) in particular, have a well-described and accessible ecology, allowing unusual power in understanding both the function of traits and the causes of their origin and evolutionary maintenance. This is impossible or very difficult in other model systems such as *Caenorhabditis*, *Drosophila*, zebrafish, or mice. The foreword, preface, and chapters extol the virtues of poeciliids, describe much interesting biology, and pose many unanswered questions, so I will not elaborate on them here. Instead, I will make some general remarks on poeciliids and identify some interesting and unanswered questions that are only hinted at in this volume.

The family has high diversity: more than 260 species in 22–28 genera, with 6 genera having 21–43 species each (e.g., see Stockwell & Henkanaththegedara, chapter 12). This means high potential power for using the comparative method to deduce the pattern, if not the causes, of evolution in many suites of traits, as well as the sequences of evolutionary events. In spite of this significant phylogenetic

power, there are no large-scale (100+ species) comparative studies. This is at least partially due to insufficient sampling of species. A repeated theme of almost all the chapters is that too few species in too few genera have been studied to make generalizations about the family or the processes discussed, let alone to undertake serious comparative studies. In fact, most subjects are supported by work from only 3–10 species, or less than 5% of the total diversity. The potential for comparative studies is also hindered by insufficient species sampling; the best phylogenetic tree (Hrbek et al. 2007) includes only 48 species (18% of poeciliid diversity), although these species were well spread among the poeciliid lineages and they probably give us a good skeleton of the phylogenetic relationships within the family. A further complication, which plagues all phylogenetic and comparative work, is the possible presence of cryptic species, as suggested by the recent discovery of 21 new *Phalloceros* species (Stockwell & Henkanaththegedara, chapter 12) and many new *Xiphophorus* species (Schartl et al., chapter 24). Species sampling is a formidable gap in our knowledge and understanding, and obtaining more data on more species for more traits should have top priority because it can so easily lead to really significant new evolutionary (and biological) insights.

An indication of the power of phylogenetics to elucidate evolution can be seen if we step back and consider the Atherinomorphs, which include the Poeciliidae (within the order Cyprinodontiformes). This analysis (Mank & Avise 2006c) shows that viviparity evolved at least four times, once in Beloniformes and three times in Cyprinodontiformes, with only one (partial) reversal—in the poeciliid

Tomeurus. It would be interesting to know the conditions that favored viviparity in these clades and why reversals are so rare, as well as why poeciliids show the one possible reversal. The viviparous clades are more species rich than their oviparous sister clades but show no difference in extinction rates. This implies a tendency for increasingly viviparous species but is contradicted by the fact that only about 25% of Atherinomorph species are viviparous, and even fewer in the Actinopterygii as a whole. Perhaps the genetic, physiological, and morphological limitations of forming viviparous mechanisms are evolutionarily or developmentally difficult, or perhaps internal fertilization, which is also rare in fishes, must evolve first, making their joint evolution less likely (Mank & Avise 2006c). Interestingly, there is no evidence for differences in speciation in marine versus freshwater lineages, although freshwater lineages tend to have higher rates of extinction, as one would expect from the more geologically unstable nature of freshwater compared with marine habitats. If we had more complete data on more poeciliid species, we could ask similar questions: for example, the evolutionary steps to matrotrophy, what habitats favor it, what habitats and conditions favor particular degrees of matrotrophy, and whether certain traits and/or habitats favor speciation, extinction, and persistence.

Our understanding of the generation and maintenance of poeciliid diversity is rudimentary, and there are many unanswered questions. Rosenthal and García de León (**chapter 10**) suggest that the species diversity of poeciliids is low compared with African lake cichlids (500 species) and American *Anolis* lizards (400 species), and they ask why there are not more species. Are poeciliids actually less diverse than other fish, other aquatic groups (such as decapod Crustacea), or even terrestrial groups in the same landmass and same habitats? A different impression comes from a local perspective: poeciliids represent 35% of the Central American fish fauna, and only the cichlids are comparable in diversity there (Hrbek et al. 2007). *Anolis* have similar diversity: in Costa Rica, a Central American country with high habitat diversity, there are only 26 *Anolis* (now known as *Ctenonotus*, *Dacyloa*, and *Noropos*), where they make up 35% of the lizard fauna, and only 13% if we include all squamate reptiles, which are closely related (Savage 2002). According to *FishBase* (www.fishbase.org) there are 158 native freshwater fishes in Costa Rica, of which 13% are endemic. Poeciliids are the second most diverse family, composing 13.3% of the Costa Rican fauna. Cichlids are only slightly more diverse (15.2%), characins are similar with 12.7%, and the next most diverse Eleotridae provide only 7% of the fauna. The Costa Rican poeciliids are not significantly less diverse than cichlids and actually have the highest percentage of endemic species, 4.4%, compared with a little more than the 3.2% for characins, and much

more than the 1.3% for cichlids (there are no endemic eleotrids). There is no evidence for poeciliids having low diversity compared with other fish families in Central America. Poeciliids are much more diverse than other freshwater fish families in the Greater Antilles (when present): they are 38% of the fauna on Cuba and 52% on Hispaniola, but there are no natives on Puerto Rico and the smaller islands (*FishBase*). Cichlids and eleotrids form less than 1% of these faunas, which contain no characins. Endemism is even higher, with 66% of poeciliids endemic on Cuba and 84% on Hispaniola. This is in contrast to *Anolis*, where island and mainland populations are similar in diversity but have diverged with habitats in different ways (Pinto et al. 2008). Studies of poeciliids with the sophistication of the *Anolis* studies would be revealing, and the ability to do both laboratory and field experiments would make such studies even more powerful tools for understanding evolution and biodiversity than is possible with *Anolis*. Also, are some families more likely to speciate in lakes (such as cichlids) and others more likely to do so in river systems (poeciliids, characins, etc.)?

Poeciliids are a much smaller fraction of the South American fish fauna, yet they appear to have originated in South America and colonized Central America at least three times (Hrbek et al. 2007). Is this because they are excluded from most of the South American habitats by high predation except in shallower, more peripheral stream systems, which have fewer predator species? Are they also excluded by competition from the more diverse characins, cichlids, and catfish in South America? The relative effects of predation and competition are unknown, but both are likely to be important (Robinson & Wilson 1994). Putting them in a phylogenetic context and relating them to dispersal and invasion patterns would be even more interesting and should yield general new evolutionary insights. Another possible explanation for lower diversity in South America is that omnivory impedes dietary and other divergence because there is no need to diverge (Rosenthal & García de León, **chapter 10**). This might also explain the lower morphological diversity in Cuba and Hispaniola but is problematic for the diverse Central American poeciliid fauna. Even if omnivory does not impede divergence, perhaps the lower diversity in South America is due to fewer microhabitats as well as the less temporally and spatially stable differences among habitats and microhabitats in the smaller, shallower waters that poeciliids inhabit (as suggested in chapters 7 and 10). The fewer-habitats argument is supported by the lack of significant ecological radiation in the West Indies (no specialists like *Belonesox* or *Alfaro*), where there are much smaller river and lake systems than in Central America. Is species diversity related to the fraction of freshwater habitat area that is in the lowlands, given that fish habitat diversity and areas of each habitat type

increase downstream? What other geographical properties favor diversity? What are the relative effects of habitat diversity, habitat geography, invasion, and evolutionary history? Were there fewer colonizations of the Greater Antilles than of Central America? Poeciliids would be particularly good models for addressing these questions.

Diversity and ubiquity may depend upon which taxa get to a landmass first and which can establish populations more quickly. Did poeciliids reach a higher diversity, endemism, and importance in Central America because their generalist ecology and viviparity allowed them to colonize the reemerging land more rapidly than the richer but more conservative fish clades in South America? Viviparity, matrotrophy, and superfetation may be an advantage in poorer and more fluctuating conditions, which may be characteristic of freshwater habitats on newly emerging landmasses (see chapters 2–4), as well as in extreme environments (Tobler & Plath, chapter 11), facilitating rapid invasion of these habitats. Moreover, viviparity may specifically allow poeciliids to invade newly evolving fish communities (Trexler et al., chapter 9). It is striking that the most divergent and ecologically specialized poeciliid genera, Belonesox (a pikelike predator) and Alfaro (a characinlike mid- and fast-water species feeding on objects that drop in the water), are found in Central America. Is this because their ancestors dispersed there earlier than other families and preempted these two niches? There is much evidence for competition, competitive release, and character displacement in fishes (Robinson & Wilson 1994), and competition could keep later arrivals out of relatively new freshwater habitats. Perhaps the relatively weaker radiation in morphology and ecology in the Greater Antilles is due to significant competition and predation from primarily marine fish families that range only a few miles upstream; most of the freshwater habitats in Caribbean islands are close to the sea, but only a small fraction of Central American freshwater habitats are so close to the sea. Of course, in South America even a smaller fraction of freshwater habitats are close to the sea, and poeciliids are mostly found near the coasts. What is the relationship between time since colonization of a previously empty landmass, colonization ability, and the presence of existing aquatic communities to speciation and to the degree of divergence? These questions also apply to recolonization after natural or human disturbance and to the future effects of climate change.

There are a host of questions about what makes colonization, establishment, persistence, divergence, and speciation more likely. Most of these could be addressed with poeciliids more easily than with other vertebrates. What is the effect of competition within the family or genus after establishment? In Anolis lizards there is some niche conservatism, and divergence in niches appears to occur more easily among distantly related sympatric species (Losos et al.

2003). Does this imply that multiple invasions are needed for strong divergence and specialization? It is suggestive that the two strongly divergent poeciliid genera (Belonesox and Alfaro) are found in Central America, which had several invasions from South America. It would be interesting to know if the smaller divergence in Cuba and Hispaniola is associated with fewer colonization events. Does matrotrophy and/or superfetation allow faster dispersal and faster establishment in new or well-established communities in similar habitats? Does the length of sperm storage, possible sperm nourishment by females, and the degree of polyandry in stored sperm (e.g., Greven, chapter 1; Evans & Pilastro, chapter 18) also affect establishment and initial growth of new populations in invasions of new landmasses as well as reinvasions after local catastrophes or seasonal fluctuations? Do these traits also encourage rapid colonization of new, as well as evolutionarily familiar, habitats and therefore divergence and even speciation among habitats? What are their effects relative to other fishes and decapod crustaceans with similar ecology but lacking these traits?

Do all these poeciliid-specific traits, which also favor higher genetic variation, also favor lower extinction rates? Which traits favor evolutionary persistence if not radiation over the range of degrees of environmental fluctuation and favor reinvasion after fluctuations or environmental change (see also Stockwell & Henkanaththegedara, chapter 12)? If the environment fluctuates so much that recolonization of streams is required each year, does this favor asexuality (Schlupp & Riesch, chapter 5) because asexual populations can colonize faster and expand faster than sexual ones? On the other hand, does asexuality result in poor persistence at intermediate levels of disturbance over geological time because of the loss of the capacity to evolve under slower or less frequent environmental change? Does ecological generalization allow faster dispersal but slower diversification and speciation? Are all these traits needed to invade extreme habitats (Tobler & Plath, chapter 11)?

Given that some poeciliids are invasive after human introductions and that species vary widely in expansion after human-induced colonization, poeciliids would be excellent for explicit studies of what favors colonization, establishment, and interaction with already-present species communities (Stockwell & Henkanaththegedara, chapter 12) and can be used to address experimentally the complex question of the relative importance of numbers of founders, frequency of repeated colonizations of the same place, genetic bottlenecks during colonization, or natural selection during establishment (Keller & Taylor 2008). A combination of population genetic and phylogenetic studies can reveal geographic and numerical patterns of previous colonizations and their effects on evolution (Olivieri 2009), and these ideas can be tested with known human-induced colonization and establishment events. A comparison among

human-induced introductions of various poeciliid species, with various degrees of success, and colonizations of the Greater Antilles and of Central America would be very interesting.

The other side of invasion and colonization is species replacement and introgressive hybridization; this involves the invasion and recomposition of communities and genomes. These phenomena are intertwined with problems in conservation biology (Stockwell & Henkanaththegedara, chapter 12) as well as being fundamental to evolutionary biology (e.g., Lindholm et al. 2005). Poeciliids would be ideal to investigate these phenomena experimentally and in the field. This is especially important in a world of climate change and habitat destruction because habitat changes can change community structure, affect gene flow, and induce hybridization (e.g., Seehausen et al. 1997). Moreover, habitat changes can confuse taxonomy and hence conservation status, making it still more difficult to understand what has happened in the field. A case in point is Endler's livebearer (*Poecilia wingei*); see box 27.1.


Box 27.1 Endler's livebearer (*Poecilia wingei*): interactions between ecology, taxonomy, conservation biology, aquarists, and habitat disturbance

Endler's livebearer (*Poecilia wingei*) is also known as Endler's guppy, the Cumaná guppy, and the Campoma guppy and is a close relative of guppies (Alexander & Breden 2004). It is a good example of multiple problems arising from habitat disturbance and the multiple interactions between ecology, biology, conservation biology, taxonomy, and aquarists. I found these fish with guppies (*Poecilia reticulata*) in the Laguna de Los Patos, at Cumaná, in northeastern Venezuela in 1975 while looking at geographic variation of color patterns in guppies (Alexander & Breden 2004). At the time I thought that they were very different from guppies and gave them to Dr. Donn E. Rosen, of the American Museum of Natural History, to describe. Although he died before having a chance to describe them, he gave some live fish to Dr. Klaus Kallman, who then introduced them to aquarists, who in turn spread them around the world, under the name of "Endler's livebearer." Shortly after discovering them, I found a collection of guppies in the University of Michigan Museum of Zoology collected by Franklyn F. Bond in 1935–1937, also from the Laguna de Los Patos, and mixed in among many guppies in that museum bottle were the same fish I saw in 1975. These should have been the type specimens, but when Poeser described the fish as *P. wingei* (Poeser et al. 2005), he was unable to find the Laguna del Los Patos bottle of "guppies" in the museum. He also did not think that what was in the Laguna de Los Patos was the same fish that he found elsewhere in 2002, and so he used fish from Campoma (further east along the coast) as the type specimens. Given the strong interest by aquarists in these fish, but the striking lack of variation in aquarium fishes, I encouraged many groups of people to go back to my original site and find them again, and this has resulted in an interesting plot of the fraction of guppies in the Laguna de Los Patos as a function of time (box-fig. 27.1).

Several things have happened since F. F. Bond and I visited the site. When I visited, guppies (*P. reticulata*) were more common than *P. wingei*. First, as shown in box-figure 27.1, I sampled in the early stages of the decline of the frequency of *P. reticulata* versus *P. wingei*; the most recent visitors to the lagoon found no guppies at all (particular thanks to Armando Pou, who visited several times).

Second, I was interested in the genetics of color patterns, particularly the bright gold-bronze of this population, so I tried to hybridize them. After trying for more than a year with many pairs of individuals, I obtained three and gave up. In the meantime breeders had managed to hybridize the two entities, and photographs taken about five years after my first collection started to show clear introgression with guppies, and the distinction between the two species in aquaria stocks began to blur. This resulted in heated debates in the aquarium literature and Web sites (including some devoted to these
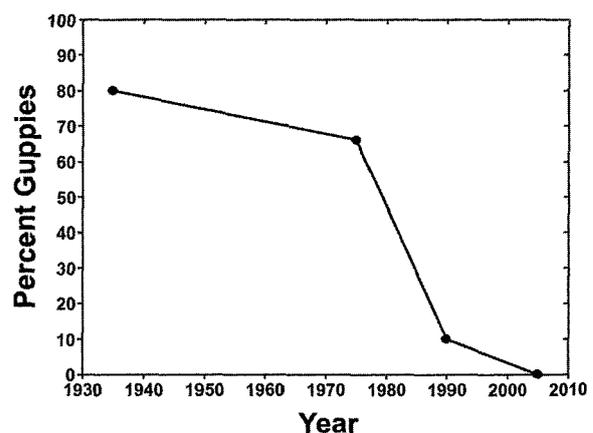
Box Figure 27.1 Decline of guppies (*Poecilia reticulata*) and increase in either *P. wingei* or a hybrid swarm of the two species

There are large numbers of fundamental evolutionary, ecological, and behavioral questions that could be addressed with a much greater knowledge of the phylogeny and ecology of a much higher fraction of the family. There is probably a tight linkage between community ecology, divergence, speciation, and extirpation and extinction, yet this has not been studied in any animal group, and poeciliids would be an ideal group to investigate these joint processes. For example, if poeciliids invade an area with high predation, this might restrict them to peripheral habitats (as in South America) with at least two suites of consequences. Peripheral habitats (small, higher-gradient streams) are less productive, and this selects for generalists rather than specialists, which may lead to less speciation. Peripheral habitats and other habitats with low microhabitat diversity will lead to less natural-selection-induced divergence within and among stream systems and also less speciation, although random divergence might be higher. What happens when poeciliids invade low-predation areas? Would the reverse be true? Does this explain the differ-

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fish) about just what Endler's livebearer was, as some people who had hybrids claimed that these were pure strains, etc. Clearly something happened in the aquarium stocks after 1975.

Third, it appears that something similar happened to the fish in the Laguna de Los Patos. The collectors who went there and brought back fishes found that the two entities hybridized readily in aquaria. It is possible that the declining proportion of guppies meant that the rare-male effect and other effects of asymmetrical abundances of two closely related species resulted in hybridization and introgressive hybridization in the lagoon, and collectors were now sampling a hybrid swarm. This caused even greater controversy among aquarists, but also caused problems in taxonomy. In fact, by the time Poeser visited the lagoon, he thought that *P. wingei* had been introduced there by aquarists and that the population was not suitable for being the type locality. The introgressive hybridization clearly has extended beyond appearances to molecular markers, as the fish vary in their similarity to guppies (Alexander & Breden 2004; Poeser et al. 2005; C. Dreyer & E. M. Willig, pers. comm., 2008). In any case, something interesting happened there in the 1980s.

Fourth, there has been increasing disturbance, fragmentation, and pollution in the Laguna de Los Patos. When I visited in 1975, the city dump was encroaching on one end of the lagoon, but the rest was intact and in reasonably good condition. Collectors who went back in the 1980s and 1990s found that the lagoon had become fragmented by development and that some parts were so polluted that no fish were present and others had many introduced fishes as well as the natives. A look at the lagoon on Google Earth in June 2009 confirmed the massive disturbance and fragmentation; I could not even recognize my original collecting site. It is a pity that the change in ecology, the change in the relative abundance of guppies, and the extent of hybridiza-

tion were not monitored over this period, because this might be a case similar to that of the human-induced hybridization of the cichlids described by Seehausen et al. (1997); as in that system, eutrophication, pollution, and concomitant changes in the visual and chemical environment may have caused or abetted the hybridization. It also stresses the importance of good long-term records (Reznick et al. 1994), which were not taken here given that the process was not initially (before 1980) obvious.

The same process may be at earlier stages in the other populations described and mapped by Poeser (Poeser et al. 2005). *P. wingei* is particularly vulnerable to human disturbance because all known populations are found below 250 meters in elevation, and these lowlands are particularly popular for human development, both urban and agricultural. Such disturbance not only endangers this interesting relative of guppies but also makes it difficult even to know exactly what the species is (compare Alexander & Breden 2004 with Poeser et al. 2005), further thwarting our understanding of the process of divergence (divergence at least to semispecies status), coexistence of closely related species or semispecies, and speciation itself. The situation is further complicated by aquarists and fish breeders, as well as introductions of aquarium fishes back into the wild.

Here we see a cycle of human disturbance possibly causing hybridization and replacement of two species by a hybrid swarm that confuses the species status in the affected population and confuses the taxonomic status of the entire entity, making conservation as well as ecological and evolutionary studies difficult. This problem is not limited to poeciliids. But it is a problem that perhaps could be best addressed experimentally and theoretically with poeciliids and may help us to conserve other species as well as understand conservation problems more deeply.

ence in diversity between Central America (colonization of new land areas) and the West Indies (already occupied by secondary marine-fish families)? What is the relationship between central and peripheral habitats in molding geographic patterns of community structure and speciation? It is ironic that the wonderfully accessible ecology of poeciliids that has allowed many first-class field experiments has not been utilized in ecological experiments addressing such questions as competition, predation, population dynamics, and community structure. Such studies would be valuable for ecology and would further illuminate all the questions asked with poeciliids as study animals.

Ecological speciation is finally being taken seriously (Schluter 2009), and some aspects of this process could be investigated experimentally in poeciliids in conjunction with sensory ecology (Coleman, chapter 7) and behavioral ecology (see chapters 16–21). For example, speciation might require strong divergence first, then sexual isolation. Although *Poecilia mexicana* shows significant morphological, physiological, and behavioral divergence between ordinary stream habitats and both sulfide-rich and cave habitats, there is no genetic incompatibility, and isolation appears to be achieved as a result of mortality of individuals traveling between habitats (Tobler et al. 2008a). Full speciation requires either postmating or premating isolation. It would be interesting to compare the degree of nonsexual and sexual divergence among the entire family in order to see whether divergence precedes or follows sexual isolation, and whether pre- or postmating isolation evolves first. Sexual communication may also be affected by environmental conditions (Endler 1992, 1995; Endler & Basolo 1998; Boughman 2002). For example, predation intensity may affect speciation probability and rates through its effect on sexual signal visibility. If there is higher predation, then males will evolve duller coloration, which may lead to fewer choice criteria and fewer ways to discriminate among males, which would lead to lower speciation rates. Alternatively, higher predation may lead to a change from primarily visual to olfactory and/or lateral-line signaling and female choice. This would either lead to more cryptic species (morphologically similar species) or perhaps have little effect on the speciation rate once the change was achieved. Changes to olfactory-based mate choice might affect olfactory-based foraging and allow the addition of new foods and hence divergence and possibly increased speciation, if other (nonpoeciliid) species did not prevent expansion into new niches. Higher predation may also lead to more cryptic (postcopulatory) female choice as another alternative to visual displays. This might lead to an unchanged speciation rate but much less morphological diversity. More predation may also lead to more sneaky mating and coercion (Magurran, chapter 19), more complex and longer gonopodia

(Langerhans, chapter 21), and various female means of counteracting the male strategies, and this could also increase the speciation rate (see Rosenthal & García de León, chapter 10). Of course, increased predation could also increase the extirpation rate, which would favor divergence among populations, or the extinction rate of new species, which would reduce species diversity. For all these reasons the relationship between predation, species diversity, and speciation rate is complex but could easily be investigated in a phylogenetic context in poeciliids.

Some species have discrete variation in color patterns (polymorphic) in both sexes, others show color pattern polymorphism only in males, others have monomorphic but different sexes (sexually dichromic), and others are monomorphic in both sexes (sexually monomorphic). There are many competing explanations for polymorphisms involving both predation and mate choice (Archer et al. 1987, Endler 1980, 1991; Brooks 2002; Hurtado-Gonzales & Uy 2009), and the reasons for these patterns, and their phylogenetic distributions, need further study. Interestingly, color polymorphism appears to be independent of the degree of sexual dichromatism (Endler 1983), and polymorphic species tend to be the only member of their genus in a single location, parapatric with all congeners, or syntopic with very few other congeners compared with the wide range of sympatry with congeners and other poeciliids in most monomorphic species. This should be investigated in more detail and may also be true for body shape and other visual or chemical cues. If generally true, this would suggest that speciation might be bi-stable, depending upon the degree of polymorphism in the basal part of the lineage. If a basal species is polymorphic, it may be harder to develop species recognition traits than if it were monomorphic (or less polymorphic), leading to a lower speciation rate. A lower speciation rate may lead to fewer syntopic species and hence encourage (or be permissive of) polymorphism, sending the system further in that direction. Alternatively, if a basal species is monomorphic, species recognition is easier, leading to a higher speciation rate and more syntopic species and favoring more monomorphism and monomorphic divergence. This might be difficult to test in a single family because it is tightly bound up with evolutionary history, and so many clades would be needed for a proper test. For example, is this why there are so many polymorphic species in the genus *Poecilia* (*reticulata, wingei, picta, parae*)? Or is this because these species live in peripheral habitats in the otherwise fish species rich South America? Why do *Xiphophorus maculatus* and *X. cortezi* have polymorphism (Fernandez & Morris 2008), whereas other congeners do not? The *Xiphophorus* polymorphisms may be partially linked to balancing selection between sexual selection and oncogenes (Fernandez & Morris 2008; see also Schartl &

Meierjohann, chapter 26), but the more extreme *Poecilia* polymorphisms are much more difficult to understand. In spite of these difficulties, it would be interesting to know if evolution tends to get trapped in monomorphism or polymorphism, with respect to visual, olfactory, sound, or lateral-line traits.

Sperm storage in females may also have an effect on speciation rates. If the sperm storage time is long (Evans & Pilastro, chapter 18), this may mean slower sperm turnover during storage. This may also be the case if more sperm were stored. Both would result in higher gene flow among populations and hence lower divergence and speciation rates. Moreover, the larger effective population sizes resulting from longer or larger sperm storage would also result in fewer random differences between source and both founder and exchanging populations, further inhibiting population divergence and speciation. On the other hand, these traits would result in greater founding effective population sizes, hence more genetic variation and faster expansion and adaptive divergence than in species with shorter and smaller sperm storage, and hence more speciation. This suggests that longer and larger sperm storage would favor more divergence and speciation after invasion of new habitats or landmasses but less divergence of speciation in situ. Shorter and smaller sperm storage may lead to more speciation in situ but also greater extinction. Greater extinction would cause greater species turnover, possibly resulting in competitive release of other species, which might inhibit the newly formed species from establishing and spreading. It would be interesting to test these ideas.

Because poeciliids are so experimentally tractable, they are particularly good for studies of development (**part I** of this volume), physiology, neurobiology, and neuroethology (e.g., Coleman, chapter 7). This means that we may be able to discover trade-offs between different traits that might be important to their ecology and evolution but have not yet been considered. For example, the presence of viviparity, matrotrophy, and superfetation immediately identifies trade-offs in the evolution of life-history traits (e.g., chapters 2–6), but there may be additional trade-offs. Frazier and Roth (2009) found that *Caenorhabditis elegans* nematodes can alter the maternal environment of their embryos adaptively in response to environmental stress (as may be the case for poeciliids), but because the mechanisms of salt tolerance interfere with hypoxia tolerance, mothers adapting for more saline conditions need more oxygen, and their offspring are more hypoxia sensitive. Do these kinds of trade-offs affect poeciliids, not only in maternal-offspring relationships but also more generally in the ability to disperse from freshwater across estuaries and the sea and invade extreme environments? Johnston (2006) reviewed fish muscle development and plasticity of response of muscle

development to both active use and environmental conditions during embryonic and early growth stages. When early development is rapid, the environment can have significant effects on subsequent muscle mass and significantly affect all aspects of fitness. There are also trade-offs between fast-muscle mass, energy and nutrient supply and function in streamflow, predator escape, and courtship, and these are all affected by temperature and oxygen levels during embryo and larval development. Temperature and oxygen levels jointly affect the optimal fiber number. Johnston et al. (2009) found in zebrafish (*Danio rerio*) that there is an optimal temperature that results in more fast-muscle fibers; embryonic temperature affects both the intensity of muscle fiber production as well as the body length at which the transition between new fiber production and fiber growth occurs. Even within a short stretch of stream there is significant spatial variation in oxygen level, temperature, and flow rates, and these vary and covary with stream order.

Microhabitat preferences of populations and species should favor different sets of traits and solutions to all these physiological trade-offs, and the diversity of habitats and ease of experimental study make poeciliids particularly good for studies of physiology, plasticity and evolution. A good start has been made with plasticity in response to resource availability (Grether & Kolluru, chapter 6), but relating this to physiology and development would be particularly fruitful. Moreover, if physiological trade-offs of the kinds reviewed by Johnston (2006) and Grether and Kolluru (chapter 6) are commonplace, we should ask whether female poeciliids choose times and places for optimum development of the muscles of their broods, and whether such microhabitat choice is more important in high-flow environments, or in environments with frequent predator encounters, than in other environments. For example, do females spend more time in relatively deeper water to escape from male harassment (Magurran, chapter 19) or to provide better physiological conditions for offspring, or both? Can these trade-offs be used to predict what sorts of handicaps may be examined by females during mate choice? Moreover, do the muscle-environment trade-offs affect the evolution of size and shape in poeciliids, and do the existing sizes and shapes cause natural selection on the trade-offs themselves? Do poeciliids have physiological trade-offs that prevent them from invading niches and habitats held by other species from families that got there first? What is the general pattern of joint evolution of physiological traits, morphological traits, microhabitat choice, and the trade-offs induced by these factors? Do the patterns of multiple-trait evolution and constraints prevent speciation or encourage it? These questions are unexplored and poeciliids would be an ideal group to study them.

In spite of much research on the evolution of sex (Schartl et al., chapter 24), sex-linked color patterns (Brooks & Postma, chapter 23), and sexual selection (chapters 17–21), relatively little has been done with sexual size dimorphism and its consequences (see Endler 1983; Evans & Pilastro, chapter 18). Males are usually smaller than females (mean 0.7 male/female length), but there is a range of size ratios from 0.4 in *Poecilia scalprides* and *Poeciliopsis gracilis* to about 1.0 in *Poecilia petenensis* (Endler 1983). What ecological and behavioral factors are associated with these differences, and are they also associated with differences in gonopodium size and shape? What is the phylogenetic pattern of size dimorphism and how does it relate to changing mating systems, sneaky copulation, social-network structure, predation, and stream velocity? Is there sexual dimorphism in nonsexual traits such as those affecting life history, swimming, and foraging? In *Anolis* lizards Butler and Losos (2002) found that both males and females of many species repeatedly evolve morphology that matches their microhabitats, but that the sexes diverge in shape more than can be explained by sexual selection alone. Shape influences many different ecological factors, so these differences may have profound implications. It would be interesting to follow this up in poeciliids. Combinations of size dimorphism, gonopodium and other morphology, mating system, and morphology may covary in interesting ways that might be predicted from first principles and could be used to understand simultaneous evolution of multiple traits.

Poeciliids are one of the few taxonomic groups where a network of cause-and-effect relationships in natural selection on multiple traits has been worked out, for example, the multiple effects of predation risk on a range of color, life-history, and other traits (Endler 1995). In spite of wonderful work on the function of various poeciliid traits (reported throughout this volume) there is little work integrating function and selection on multiple traits with entirely different functions. One way to integrate genetically unrelated traits is sensory ecology (Coleman, chapter 7), because the interplay between signals, receivers, and habitats is inescapable. Sensory drive is a particularly promising approach to the integration of function, selection, and evolution of unrelated traits (Endler 1992; Endler & Basolo 1998). Sensory drive involves a hypothesized cycle of selective interactions between senses, signals, and preferences (Endler 1992) and includes known processes such as sensory exploitation and preexisting bias (review in Endler & Basolo 1998). Sensory drive has the following cycle of cause-and-effect relationships. New habitats or changing environments result in new sensory conditions that affect the efficacy of signal generation, transmission, reception, and perception (Endler 1993b) and therefore affect the ability to detect and discriminate among potential mating

traits. This leads to the evolution of sexual traits with better properties in the new conditions. Mate preferences evolve in parallel by a correlated response to sexual-trait selection (review in Andersson 1994) but will also be driven directly by changed sensory conditions; traits perceived in new ways affect existing preferences and favor new traits and preferences. If signaling traits work best in certain environments, this favors choice of microhabitats with the beneficial sensory conditions. Specific sensory conditions favor sensory systems that work best in those conditions, leading to evolution of the senses and brain, with further evolutionary effects on preferences and chosen traits. If changed prey visibility or new prey species require different sensory processing, sensory evolution may affect mating preferences via sensory properties that evolved in the context of prey detection and discrimination (Rodd et al. 2002), biasing the direction of sexual-trait and preference evolution (Endler 1992). Studying sensory drive is valuable for understanding the evolution of multiple suites of traits and also has important implications for the origin of population divergence and the origin and maintenance of species because senses, choice, and traits are used in species recognition (Boughman 2002; Maan et al. 2006; Terai et al. 2006).

Each component of sensory drive has been demonstrated in guppies (*P. reticulata*): male color patterns evolve increased visual contrast under sexual selection over many generations (Endler 1980). Visual contrast changes with ambient light and depends upon eye properties (Endler 1991; Smith et al. 2002; White et al. 2003). Some (long-wavelength-sensitive) visual pigments are genetically polymorphic (Archer et al. 1987; Archer & Lythgoe 1990; Hoffmann et al. 2007; Weadick & Chang 2007), allowing color perception to evolve as well as inducing variable female perception and hence choices even if females use the same criteria (Archer et al. 1987; Endler 1991). Courtship timing (associated with specific light environments) results in higher male visual contrast than would be achieved at other times (Endler 1987, 1991). Female choice changes with visual backgrounds (Endler 1983) and with ambient-light spectra (Long & Houde 1989; Gamble et al. 2003). Female preferences are predictable from male visual contrast (Endler & Houde 1995). Female preferences may also be related to food choice (Rodd et al. 2002). Female choice is geographically correlated with male color patterns (Endler & Houde 1995). Artificial selection for color patterns results in changes in female preferences (Breden & Hornaday 1994; Houde 1994). Artificial selection for spectral sensitivity results in changes in the visual system (Endler et al. 2001). Many of these components have also been found in other taxa, but it is unusual to have all in a single experimentally tractable species. This means that

sensory drive is likely to be important in guppies and provides a means of predicting the direction of evolution of male signals, perception, female preferences, and microhabitat choice—traits that are usually studied separately. This and other integrative approaches could easily be applied to other poeciliids and yield significant new insights about the evolution of multiple suites of genetically unrelated but functionally related traits.

Poeciliids provide extraordinary potential for studying the function, ecology, and evolution of traits and integrated organisms and relating them to environmental conditions. They have already shown their worth in helping us understand the balance between sexual selection and predation, how sexual selection works, how and why life-history traits and color patterns evolve, and other evolutionary mechanisms. Their greatest potential is still hardly touched, in the coevolution within and among suites of genetically unrelated traits and this coevolution relative to environmental parameters, the assembly of communities after invasion of new areas (both natural and man-made), the evolution of physiological traits (including both classical environmental physiology and sensory physiology), the evolution of behavior, and the function and evolution of both neuroethological and behavioral mechanisms. I really look forward to the third book on poeciliids, when many of these areas will have been explored.

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