

# 8

## Variation and Selection in Swordtails

Michael J. Ryan and Gil G. Rosenthal

A View from the Field: 10 March 1999,  
Río Choy near Tamim, Mexico

We are at the birthplace of the Río Choy, in the foothills of the Sierra Madre of eastern Mexico. Water surges from deep underground, through the cave where we stand watching it cascade down a little waterfall. The water flows into a sunny blue pool flanked by ruins from the 1920s, when this *nacimiento* was a weekend resort. Myron Gordon, the eminent geneticist and ichthyologist, no doubt descended the long concrete staircase to the water, to peer at northern swordtails *Xiphophorus nigrensis*, courting in the shallows. He was followed by other geneticists, Klaus Kallman and Don Morizot, in the decades to follow.

Today the stairway's bottom half is a heap of rebar on the rocks, the diving board has collapsed, and they have melted down the great bronze plaque of mediocre poetry that was this place's centerpiece. The rock faces cast deep shade all day, and soft winds blow down the mountain and through dark stands of bamboo. On the surface, the *nacimiento* is a melancholy place.

Dive underwater and this changes. The section of staircase that has fallen underwater is now encrusted with a generous brown carpet of algae and tiny animals. A group of a dozen female *X. nigrensis* graze along this surface, taking little nibbles here and there. Among them is a large male, a brilliant blue on this sunny afternoon, who approaches a certain female and begins to court her. His dorsal fin fully raised, he executes a series of five rapid turns before her eyes. The lower rays of his caudal fin are extended into a long sword, black to us but probably bright to her. Unimpressed in any case, she returns to her feeding. The male, most likely seeking more promising ground, ventures into open water toward the next patch, trying to avoid the sharp teeth of the many Mexican tetras (*Asynanax mexicanus*) in his path. Sure enough, a large tetra nips off most of his long sword. He reaches his destination diminished but alive, ready to court again. He performs a brief display, similar to his courtship dance, to an intermediate-sized male, smaller than himself, followed by a brief chase. The intermediate male flees.

Our female, meanwhile, continues feeding. She is almost ready to mate, and would prefer to do so with a large male, a male who has waited five long months to mature into a robust, ornamented dancer. Instead, a bright yellow male, smaller than herself, surprises her as she grazes, forcibly in-

seminating her with no preliminaries whatsoever. Thirty days later, she gives birth to about two dozen young, who seek refuge and food among fine algal filaments. All of her sons will mature in only three months; like their father, they will be small and bright yellow throughout their adult lives. And like their father, once mature they will try to force themselves on females, abandoning any pretext of the seduction or cajoling characteristic of the large courting males.

We're at the birthplace of the Río Choy, the birthplace of *Xiphophorus nigrensis*, which lives nowhere else in the world but here. To see these things, we need only slip down the waterfall and out of the cave, into the light. Yet to truly understand these phenomena, we must admit that Plato had it right; we remain here, forced to discern pattern from the shadows of experiment and observation. They're pleasant little sirens, these bright fish, and the silhouettes they throw off yield moments of real revelation and insight into the wider workings of nature; but never, in their infinite variety, do they tolerate complacency. Each experiment, each new population we find in a forgotten ravine, yields its own share of surprises. Some of these surprises follow.

### Size Variation and the *P* Gene

The watchword for our studies of swordtails is *variation*—what does it mean, and how is it maintained? In nature, there is a striking disparity in size and style among these male swordtails. At one extreme are brilliantly blue, deep-bodied animals sporting large dorsal fins and swords, and engaging in the rapid figure eight that constitutes the courtship display. On the other extreme are small, slender, somewhat drably colored males lacking the elaborate fins and complex courtship of their larger counterparts. In fact, these smaller males have abandoned courtship altogether; they force themselves on females for sex rather than courting them.

Prior to the sociobiology revolution, reproductive behavior was viewed in the context of species specificity. The New Synthesis in evolutionary biology in the mid-twentieth century wrestled with the problem of the "species," and ethologists made critical contributions to this endeavor by documenting the species-specificity of both male courtship and female response to such behavior (Mayr 1982). Variation in reproductive behavior among males, as we see in the swordtails, was not given serious consideration. But sociobiology brought with it an emphasis on selection on individual variation within a population, and alternative mating systems presented a focal point for examining how such drastic behavioral variation can be maintained (Wilson 1975).

Alternative processes can account for qualitative variation in male mating behavior. Variation can result from phenotypic behavioral plasticity. For ex-

ample, it can have an ontogenetic basis—younger males exhibit noncourting mating strategies until they achieve larger size (e.g., bullfrogs; Howard 1978). Others are merely "making the best of a bad situation" (Dawkins 1980). Environmentally induced variation has dealt them a poor hand; they lack the strength, fortitude, attractiveness, or charm to compete successfully for females. There are certainly a plethora of other environmental and gene-by-environment interactions that bias an animal's phenotypes, including but not restricted to alternative mating strategies (West-Eberhard 1989).

It is also possible that alternative mating behaviors can be strongly or even primarily influenced by genetic variation. If there is heritable genetic variation for courting versus noncourting strategies, both forms could be maintained in the population under certain conditions of spatial and temporal fluctuation in the intensity of selection. Perhaps a more likely process would be the maintenance of alternative mating behaviors in genetic equilibrium; that is, all strategies would have equal lifetime reproductive success. There are only a few mating systems in which alternative mating strategies appear to be in genetic equilibrium: swordtails, ruffs (Lank et al. 1995), and stomatopods (Shuster & Wade 1991). There were none when we were first enticed into the blue waters of the Río Choy.

A challenge to understanding the genetic basis of behavior of animals in the wild is having a system that is amenable to both quantitative or molecular genetic and behavioral studies in the lab, or having a system in which the genetic variation underlying the behavior is simple and readily identifiable in the wild. Few mating systems have these qualities; there are systems that are wonderful for laboratory genetic analysis of behavior, such as aggregative behavior in *C. elegans* (DeBono & Bargmann 1998) and mating behavior in fruit flies (Hall 1994). But these systems are not usually characterized by variation in mating strategy. The genetic variation underlying alternative mating strategies in the wild is rarely known. Swordtails, however, offer a clear exception.

The swordtails and platyfish, genus *Xiphophorus*, are members of the live-bearing family Poeciliidae. It is not clear if swordtails and platys are each monophyletic, but monophyly seems certain for both the genus as a whole and the northern swordtails (Rauchenberger et al. 1990; Borowsky et al. 1995; Morris et al. 2001; cf. Meyer et al. 1994). Species in this group are distributed throughout the Río Pánuco Basin in northeastern Mexico, in the foothills and areas just east of the Sierra Madre Oriental (Fig. 8.1). The consensus of a variety of phylogenetic analyses is that the group consists of nine species; these species are in three clades of three species each. The species we have studied most extensively are in the pygmy swordtail species group: *X. nigrensis*, *X. multilineatus*, *X. pygmaeus*.

Klaus Kallman and his colleagues have been studying the genetics of phenotypic variation in *Xiphophorus* for the past three decades (reviewed in Kallman 1989). These animals sport a variety of traits, such as color and

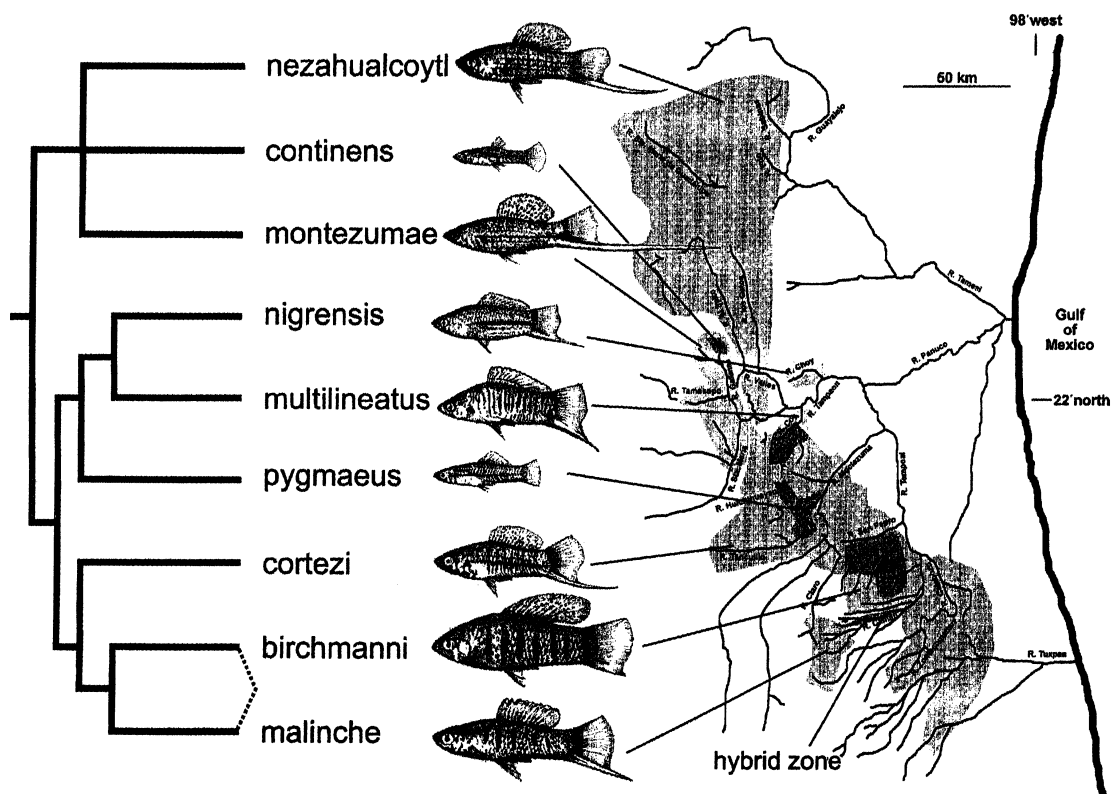


Figure 8.1. The Río Pánuco Basin swordtails. Phylogenetic hypothesis after Rauchenberger et al. (1990), Borowsky et al. (1995), and Morris et al. (2001). The tritomy in the *montezumae* group reflects the placement of *X. montezumae* and *X. nezahualcoytl* as sister species in Rauchenberger et al.'s (1990) hypothesis, and of *X. montezumae* and *X. continens* in the later phylogenies. Map and ranges after Rauchenberger et al. (1990), with range extensions based on recent collections by GGR. Darker areas indicate sympatry between two species; "hybrid zone" refers to *X. birchmanni* x *X. malinche*. Line drawings by Christopher Elmore.

melanophore patterns, whose genetics have been well-characterized. Many of these traits are exhibited as if they are under simple allelic control; the variation is often linked to the Y chromosome. One of the more astounding forms of variation is in body size. In poeciliid fish, male growth decreases drastically upon reaching sexual maturity. In *Xiphophorus nigrensis*, one of the species that has received most of our attention, the standard length (SL; snout to hypural plate, a basic measure of size in fish) of mature males can vary from 18 to 38 millimeters, as measured from the snout of the fish to the base of its tail. Size breeds true through the father. Large males produce large sons while small fathers produce small sons. The size of the mother has no detectable influence on how large their sons grow. Kallman's analysis reveals three size genotypes in *X. nigrensis*: small (> 26 mm SL), intermediate (26 to 31 mm), and large (< 31 mm). There is only slight overlap between the size classes, and the narrow-sense heritability for size in lab-bred animals is greater than 90 percent (Ryan & Wagner 1987; Kallman 1989; Dries et al. 2001).

The gene responsible for size variation in these fish is the pituitary (*P*) gene. It achieves its effect by activating the hypothalamic-pituitary-gonadal axis, resulting in the circulation of androgens in males which initiates sexual maturity and drastically halts growth. The earlier androgens are circulated, the sooner, and smaller, the males mature. In *X. nigrensis* there are three *P* alleles, *s*, *l*, and *L*. The *P* gene on the X chromosome appears fixed for *s*; females mature early but continue to grow, as do most poeciliid females.

#### Advantages of the Swordtail System

As of the mid-1980s, the studies of Kallman and colleagues seemed not to have penetrated the literature in behavioral ecology, even though the maintenance of *P* gene variation was synonymous with the critical issue of the maintenance of behavioral variation. Kallman's work not only provided a motivation for our studies of behavioral ecology, but also elucidated an elegant genetic system whose logistics provide a number of advantages.

The *P* gene, as well as several pigment and melanophore patterns, is Y-linked and shows high heritability. Combined with the fact that females are live-bearers, this readily allows paternity analysis to estimate changes across generations in the frequencies of alleles underlying the traits. For these Y-linked traits, assessing the phenotype provides the male genotype. This can be estimated directly from field collections or surveys. Females can be collected and returned to the lab, and the genotype of their sons can then be quantified. Few systems allow one to document changes in allele frequencies of traits under sexual selection.

Swordtails tend to live in cool, clear, slowly moving streams in mountain foothills. They quickly habituate to a human observer, and underwater obser-

vation of their behavior offers no special challenges. Most of their behavior is restricted to within a meter or so of the surface, permitting easy observation by snorkelers. Males do not defend permanent territories but maintain individual distances while feeding on small invertebrates in plants and algae on rocks. Females move through these areas, where they are courted and mated by males.

Swordtail behavior can be studied in more detail in the lab. The males readily court and fight with one another in captivity, and females exhibit mating preferences in free-ranging tests or when males are confined behind glass partitions. A major advance in our studies occurred when it was shown that female swordtails, *X. helleri*, respond to video playbacks of courting males (Rosenthal et al. 1996). Subsequent studies have used frame-by-frame (Rosenthal & Evans 1998) and synthetic animations (see below), which allow almost unlimited degrees of freedom in varying stimuli. The study of visual signaling has lagged behind that of acoustic signaling, largely due to the relative ease with which acoustic parameters can be quantified and manipulated. The importance of these advances in stimulus presentation should not be underestimated.

Finally, knowledge of the phylogenetic relationships within northern swordtails provides the basis for comparative studies. The detailed phylogenetic analysis of the northern swordtails by Rauchenberger et al. (1990) was recently challenged by an analysis of Meyer et al. (1994) of the entire genus *Xiphophorus*. Recent studies by Borowsky et al. (1995) and Morris et al. (2001) largely support the original phylogenetic hypothesis advanced by Rauchenberger et al. (1990; Fig. 8.1).

We are not able to summarize the large number of studies we have conducted on sexual selection in swordtails. Instead, we will concentrate on two earlier series of studies that provide the foundation for much of our subsequent and future work in this system.

### Genetic Equilibrium and Alternative Mating Strategies

We first asked how the *P* gene polymorphism is maintained in wild populations of *X. nigrensis*. Populations are polymorphic for three *P* genotypes that result in distinct size classes. We conducted paternity analysis for females collected from a population in which we estimated the frequency of male size classes and, by extension, *P* genotypes (Ryan et al. 1990). Across generations, there was a significant decrease in the *P* alleles for small size relative to the *P* alleles for intermediate and large sizes, while the relative reproductive success of the intermediate and large males did not differ. The reproductive success of small males was only 44 percent that of intermediate and large males. This raised two obvious questions: What is the nature of selec-

tion acting against small males, and how are small males maintained in the population?

As noted above, males of different sizes vary in their mating behavior (Ryan & Causey 1989). Males below 26 millimeters rely almost exclusively on chasing after females in quick darting motions and rarely exhibit the courtship behavior shown by larger males (Fig. 8.2). Female mate choice studies using live males show a preference for intermediate and large males over small males but no preference between males of intermediate and large size (Ryan et al. 1990). These results mirror the differences in reproductive success seen in the wild. They do not, however, elucidate the relative contribution of body size and behavior to male attractiveness.

Male-male interactions also favor larger body size. In the field, larger males had greater access to females than did smaller males (Morris et al. 1992). Larger males also excluded smaller males from their territories more often than smaller males excluded larger males. In the laboratory, larger males blocked access to females more often than did smaller males. Large size usually provided an advantage in male-male competition regardless of the size classes of the males. In the female choice studies, however, the effect of male size was more categorical: females preferred males in the larger and intermediate size class to small males, but did not discriminate between males in the intermediate and large size classes.

Selection generated by female choice and male competition favors larger males over small males and, by extension, acts against the *s* allele at the Y-linked *P* locus. Size variation is under a strong genetic influence in this species; the alternative mating strategies are not conditional. There are several processes that could maintain genetic variation, including spatially or temporally varying selection. But one must remember that the differences in size at maturity among the size classes results from differences in time to maturity. Males of different sizes grow at similar rates but reach maturity at different times. Conveniently, males cease depositing otolith rings when they stop growing (Morris & Ryan 1990). Counts of otolith rings from males in the field showed that small, intermediate, and large males matured in the wild at average ages of 78, 90, and 124 days, respectively. Although small males have lower instantaneous reproductive success than larger males, that is, they are less likely to mate on any given day, they enter the reproductive lottery sooner. The costs to smaller males derived from sexual selection might be offset by advantages of time to sexual maturity. As the daily mortality rate in a population increases, the advantage to maturing earlier should increase as well.

Given our data on the relative reproductive success and time to maturity of small versus larger males, we calculated the daily mortality rate necessary to yield equal fitnesses among the genotypes (Ryan et al. 1992). That rate is 0.028/day. Despite considerable effort, we were not able to measure mortality rates in the field. But we used a more circuitous route to ascertain the

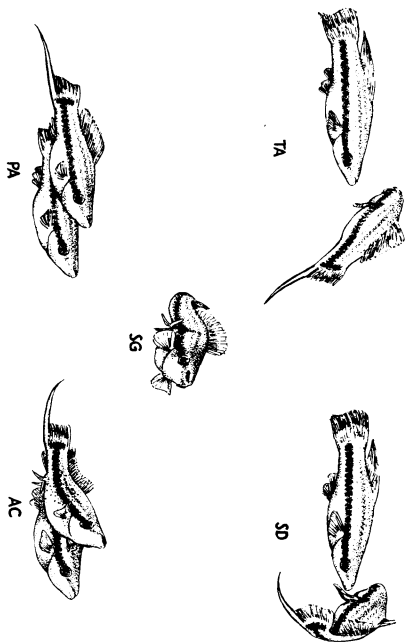


Figure 8.2. Mating behavior of *Xiphophorus nigrensis*: transverse approach (TA), sexual display (SD), sigmoid display (SG), parallel approach (PA) and attempted copulation (AC).

validity of our mortality estimate. We expect population size to be constant over an ecologically relevant time span, thus the rate of population increase,  $r$ , should be zero. We combined data on the female fecundity schedule, which includes age at sexual maturity, brood size, and interbrood interval (Morris & Ryan 1992), with our estimate of daily mortality to calculate  $r$ . If our estimate were much lower than the true mortality rate, the population should drastically increase in population size:  $r$  would be strongly positive. If our estimate of  $r$  were too high, the population would go extinct:  $r$  would be strongly negative. Using our empirical data on the female fecundity schedule and our estimate of daily mortality of 0.028/day we calculated an  $r$  of 0.00. This suggests that the daily mortality rate needed to maintain the  $P$  genotypes in equilibrium is the same mortality rate needed to maintain the population at a constant size.

Our model supports the hypothesis that  $P$  genes are maintained in genetic equilibrium in *X. nigrensis*. But caution needs to be exercised. The 95 percent confidence intervals around the mortality rate generated from a bootstrap statistic are relatively large, 0.006 to 0.06/day. Furthermore, our analysis assumes that mortality does not vary among the genotypes or between the sexes. We can envision scenarios that would favor the survivorship of each genotype and sex. For example, large courting males might suffer greater mortality because of their conspicuousness, but smaller males might be more vulnerable because they are within the gape limit of more predators. Nevertheless, this simple model supports the contention that the variation in body size and the  $P$  alleles that underlie this variation can exist in the wild because they result in very different types of males with very similar Darwinian fitness.

### When Size Doesn't Vary, Does It Matter?

South of the Río Choy, another *nacimienta* births another river, the Río Huichihuyán. It is a tributary of the Río Axtila, whose drainage is home to *X. pygmaeus*. The specific name refers to the unusually small size of males (Hubbs & Gordon 1943); males look and behave much like  $s$  males in *X. nigrensis*, with slender, swordless bodies and lacking courtship (Kallman 1989). Interspecific crosses suggest that *X. pygmaeus* are in fact fixed for the  $s$  allele. Parsimony analysis suggests that alleles for larger size classes were secondarily lost in *X. pygmaeus* (Morris & Ryan 1995). The major predators of swordtails, Mexican tetras *Astyanax mexicanus*, are far more abundant in *X. pygmaeus* habitat than elsewhere; predation pressure could have driven the  $s$  allele to fixation in an ancestor of *X. pygmaeus*.

Although the large, courting phenotype was lost in *X. pygmaeus*, females retained the ancestral preference for these sexually dimorphic males. Experiments by Ryan and Wagner (1987) showed that female *X. pygmaeus* preferred large, courting *X. nigrensis* males over conspecifics.

From the mid-1930s to 1982, ichthyologists and hobbyists made extensive collections throughout the range of *X. pygmaeus*. All of the males in museum collections were below 29 millimeters SL, and most were diminutive, below 24 millimeters SL. In 1988, we visited the *nacimienta* of the Río Huichihuyán, which no one had sampled before, and were surprised to find large males—some twice the size of the *X. pygmaeus* males previously known. A year later, we found these behemoths downstream, at the town of Huichihuyán. This site had been well-surveyed over the previous fifty years, and not a single large male had been found. Additional collections at several localities suggested a recent spread of large body size (Morris & Ryan 1995).

These large males were not like the larger males in other northern swordtails: like their smaller counterparts, they were slender-bodied, with short dorsal fins and lacking swords. We never observed them courting, either in the wild or in the laboratory. Behaviorally and morphologically, they were simply "blown-up" versions of small males. We were able to rule out a  $P$  gene system for the inheritance of this phenotype: large males produced only small sons, both in intraspecific crosses and in crosses to *X. nigrensis* (Morris & Ryan 1995; Dries et al. 2001). We have tried for over ten years to recover the large male phenotype in the laboratory, both in aquaria and in large outdoor ponds. So far, we have yet to produce a single captive-born large male *X. pygmaeus*. The genetic and environmental mechanisms producing this phenotype remain mysterious.

Females from la Y-Griega Vieja—a hamlet downstream from Huichihuyán, where large males are rare—have retained the ancestral preference for large males, preferring both large, courting *X. nigrensis* and the large *X.*

*pygmaeus* from upstream over their own small males. Yet at the upstream sites, where high frequencies of large males have been found, females fail to prefer the larger males. This loss of preference appears to be stable over time: females tested in 1988 and in 1993 showed identical patterns. These females also failed to prefer courting *X. nigrensis* over size-matched, noncourting conspecifics, suggesting that both the preference for large size and that for courtship had been secondarily lost (Morris et al. 1995).

Why have females from populations with large males lost the preference? The obvious suggestion is that there is a cost associated with mating with large males (Morris et al. 1995; Holland & Rice 1998). Yet large males produce normal, small male offspring in the laboratory. Females mated to large and to small males produce equal numbers of fry, and there is no detectable difference in the viability or fertility of offspring (Dries et al. 2001). While it is of course impossible to exclude the possibility that our methods are insensitive to small fitness differences in the offspring of large and small males, the lack of any *detectable* fitness cost of mating with large males makes it unlikely that loss of preference would have swept through the Huichihuyán population in at most sixteen years, or about forty-eight *X. pygmaeus* generations.

Recent data suggests that heterospecifics may play a role in the loss of size preference (Rosenthal & Ryan, in review). *X. pygmaeus* are sympatric throughout their range with *X. cortezi*, which share many characteristics with larger morphs of *X. nigrensis*. Male *X. cortezi* are on average much larger than male *X. pygmaeus*, ranging between 24 and 55 millimeters (Kallman 1989; personal observation), have deep bodies and swords, and perform courtship displays (Franck 1970). There is no evidence to suggest that the large *X. pygmaeus* males arose from a hybridization event with *X. cortezi*, but these and other swordtails can be readily crossed in the laboratory. Both *X. pygmaeus* and *X. cortezi* inhabit thickly vegetated, shallow areas (approximately one meter in depth) of slow to moderate current. There is broad overlap in their use of space, and individuals of the two species are frequently observed within a few centimeters of one another—close enough for a mating opportunity. Could the loss of preference for large size in *X. pygmaeus* be associated with avoidance of *X. cortezi*?

We asked females to choose between *X. cortezi* and size-matched *X. nigrensis* males. Since *X. nigrensis* are in the sister group to *X. pygmaeus*, we controlled for phylogenetic distance by also comparing responses to *X. cortezi* versus size-matched *X. malinche*, sister to *X. cortezi* (Fig. 8.1). Responses paralleled preferences for body size: females from the *nacimientito* showed strong preferences for both *X. malinche* and *X. nigrensis* over the sympatric *X. cortezi*, while females from Y-Griega failed to show a preference in either case. This pattern appeared to be due to correlated responses in individual females: when we tested the same *X. nigrensis* male against a male *X. pygmaeus* and a male *X. cortezi*, the females that showed the stron-

gest preference for *X. nigrensis* against *X. pygmaeus* showed the weakest for *X. nigrensis* over *X. cortezi*, and vice-versa. There is thus a negative correlation between species recognition—avoidance of heterospecifics—and a mating preference for large size. The loss of large size preference in *X. pygmaeus* females may thus be a correlated consequence of selection against mating with a closely related swordtail (Rosenthal & Ryan, in review).

This still leaves the mystery of the large males—how they are generated, and if there are any fitness consequences to mating with them. These large males are now appearing only sporadically in collections at the *nacimientito* and at Huichihuyán, so we may soon lose our chance to understand this phenomenon.

### Natural Selection on Sexually Dimorphic Traits

No account of the behavioral ecology of *Xiphophorus* would be complete without mention of the trait that gave the genus its name. Males in most swordtail species have the lower rays of the caudal fin extended into a conspicuous “sword” bearing high-contrast pigment patterns. The sword starts growing around the age of sexual maturity. Female *X. helleri* prefer to mate with males with longer swords (Basolo 1990). This preference is shared by females in species that diverged from swordtails prior to the appearance of the ornament (Basolo 1995), suggesting that swords arose in response to a preexisting bias on the part of females. This bias appears to reflect a more general preference for large body size: a swordless male enlarged to the same total length as a sworded male is equally effective at eliciting preference (Rosenthal & Evans 1998). Swords are metabolically inexpensive to produce, and males allocate proportionately more energy to swords when on a restricted diet (Basolo 1998). Given that swords are cheap to produce and that they exploit a shared ancestral mating preference, one should expect them to be ubiquitous throughout the swordtails.

Yet sword length varies considerably across our nine study species, ranging from the hypertrophied sword of *X. montezumae*, which exceeds the length of the rest of the body, to its close relative *X. coninens*, which lacks the sword altogether (Fig. 8.1). Across populations of *X. multilineatus*, there is a threefold difference in mean sword length. Within populations of *X. multilineatus* and *X. nigrensis*, swords are highly polymorphic; one large male may have an elongate ornament, another none at all. What are the factors responsible for maintaining this variation?

Predation pressure is an obvious candidate. Signals that are more conspicuous to potential mates are often more conspicuous to predators as well (Endler 1980; Zuk & Kolluru 1998). Based on gut content analyses and total abundance, the major visual predator of swordtails is the Mexican tetra, *Astatyx mexicanus*, a widely distributed, omnivorous, toothy relation of the

piranha (Rosenthal et al. in press). These and other small characid fish are infamous throughout Latin America as *pica-culo*, or ass-nippers, for their attacks on swimmers. They also nip the posteriors of swordtails; we commonly find otherwise healthy males with the sword or other portions of the caudal fin bitten off.

The visual preferences of *A. mexicanus* parallel those of female swordtails. Like females, they go preferentially to the large and intermediate morphs over small males, and yet fail to show a preference for large males over intermediate males. *A. mexicanus* prefer male *X. multilineatus* with long swords over males with artificially shortened swords. This preference appears to be ancient, rather than the result of coevolution with the prey; tetras from localities far outside the range of swordtails show the same preference (Rosenthal et al. in press).

Swordtails have responded to predation in two ways. With the exception of *X. malinche*, which lives in *Astyanax*-free waters, the swords of the Río Pánuco *Xiphophorus* have a strong component in the ultraviolet. The lenses of female swordtail eyes transmit ultraviolet light, while the lenses of *Astyanax* eyes, like ours, filter it out. Swords that appear black or clear to predators, both characid and scientist, may thus exhibit a private, high-contrast ultraviolet band to females (M. Cummings, G. Rosenthal, & M. Ryan, unpublished data).

Selection has also favored an overall reduction of sexually dimorphic traits in high-predation areas. Recall that body size is highly correlated with age at maturity: if males mature earlier, they are smaller throughout their lives. A basic prediction of life history theory is that predation pressure should drive down age at first reproduction (Stearns 1992; see also Ryan et al. 1992). Mean male body size is negatively correlated with predator density across swordtail populations; this may be due to the predators' visual preference for large males, but it may also simply reflect increased predation on juveniles (G. Rosenthal, M. Stephens, & M. Ryan, unpublished data).

Sword length is also negatively correlated with *A. mexicanus* density. Yet sword length is correlated with body size, and when we expressed sword length as a function of body size the relationship with predation disappeared. The allometry of sword length on body size—the slope of the relationship within each population—actually showed a *positive* relationship with predation! Swords were proportionately larger as a function of body size in high-predation regimes. This suggests to us that swords may represent yet another alternative mating tactic: they are inexpensive to produce and grow after sexual maturity, and they elicit the same female preference as an equivalent increment in body size. In high-predation regimes, it may thus benefit males to mature early and start growing a sword. Yet swords are themselves attractive to predators, and are easy to lose. Variation in sword length may thus reflect a compromise between accommodating lethal predation, by maturing

early, and sublethal predation, by minimizing sword expression (G. Rosenthal, M. Stephens, & M. Ryan, unpublished data).

### Summary and Future Prospects

We were initially drawn to swordtails by the simple genetic mechanisms underlying variation in suites of conspicuous traits. Yet correlated traits cry out for dissection: What are the factors maintaining the correlation? Are all traits equally important from the point of view of female preference, or are females choosing males based on only a subset of these traits? We have begun to address these questions by playing back synthetic animations to females. We begin by using population parameters—the mean and standard deviation of a slew of behavioral and morphological measures—to construct three-dimensional models of large, courting males and small, noncourting males. We can then vary these parameters independently of one another and ask the females which ones are relevant. Is a large, courting male with a sword as effective against a small male when shrunk down to the same total length as that small male? Can a small, slender, swordless male be made attractive if he courts at a rate one standard deviation above the mean for large males? This approach will allow us to understand the precise nature of the female preferences maintaining the *P* gene polymorphism in species like *X. nigrensis*. Moreover, it will allow us to elucidate the loss of preference for large size in *X. pygmaeus*. Have preferences for other traits, like body shape and courtship, been reduced along with the preference for large size? Are preferences for *X. cortezi*-like traits more reduced than others?

Using synthetic animations to break down correlated phenotypes is a powerful approach, yet it would be ideal if these correlated trait complexes could be dissected in nature—if there were wild populations with males recombinant for suites of sexually dimorphic traits. Yet despite the fact that swordtails hybridize readily in the laboratory, until now there have been no well-documented cases of hybridization in nature. In 1997, we stumbled on natural hybrids between *X. birchmanni* and *X. malinche* in the Río Calnali, in the state of Hidalgo. The two parental species are at opposite extremes of the signaling spectrum—*X. birchmanni* is vertically dimorphic, with a nuchal hump, a sail-like dorsal fin, a deep body, no sword, and parallel vertical bars, while *X. malinche* is a typical swordtail with a long sword, a more modest dorsal fin, a slender body, and irregular blotches on the flank. Most individuals in the hybrid zone are recombinant for these traits. We can now ask questions about female preferences for particular trait combinations found in nature, a task facilitated by the geographic structure of the hybrid zone, which shows an upstream-to-downstream gradient from *malinche* traits to *birchmanni* traits. Curiously, the sword, for which females show an ancestral

preference, disappears earlier than other *malinche* traits, including allozyme markers. Perhaps novel trait combinations are more attractive to females than this ornament (Rosenthal et al., unpublished data).

#### A View from the Field: 15 March 1999 above Calnali, Mexico

On this Saint Patrick's Day the steep relief and green hills are reminiscent of Ireland, but we have just hiked up to the ridge which separates the Río Calnali from the next valley, which you cannot reach by road. We get our first glimpse of the Río Pochula far below, a thin ribbon gleaming in the noonday sun. People in Calnali say there are deep pools with bright little fish—*poxtas de colores*. This may be a second, replicate contact zone between *X. birchmanni* and *X. malinche*. Will we see rampant hybridization like we do behind us, with the same distribution of traits? Will we climb all the way down the mountain only to find a stream that is swordtail-free? Or will these small treasures of the Sierra Madre once again surprise us with something totally unexpected? There's no alternative but to go and look—and no chance we'll make it back by nightfall.

#### Acknowledgments

We are extremely grateful to Klaus Kallman and Don Morizot for introduction to the system; B. Causey, D. Hews, and W. Wagner for collaborating on early studies; M. Morris for her critical work on this system that is reviewed here; M. Cummings, T. Flores Martinez, F. García de León, and M. Stephens for collaboration; and to everyone who has provided invaluable assistance in the laboratory and in the field. We are indebted to Christopher Elmore for the line drawings in Figure 8.1. We appreciate the financial support from the National Science Foundation, the National Geographic Society, Dr. Lorraine Stengl, and the Department of Zoology, University of Texas at Austin. L. Gilbert, J. Crutchfield, and A. Alexander of the Brackenridge Field Laboratory, University of Texas at Austin, have provided facilities for stock maintenance and numerous experiments. We appreciate logistical support provided by the Laboratory of Zoology at the Technological Institute of Ciudad Victoria, Mexico. We are grateful to D. Hendrickson of the Texas Memorial Museum, Héctor Espinosa of the Mexican National Museum of Ichthyology, and A. Narvaez and the United States Embassy in Mexico for assistance with collecting permits. We thank the Mexican National Institute of Fisheries, National Institute of Ecology, and Foreign Ministry for allowing these studies. Finally, the people of the Huasteca region deserve special thanks for their warm hospitality and for their commitment to the rivers and streams they steward.

#### References

- Basolo AL, 1990. Female preference for male sword length in the green swordtail (Pisces: Poeciliidae). *Anim Behav* 40:332–338.
- Basolo AL, 1995. Phylogenetic evidence for the role of a preexisting bias in sexual selection. *Proc Roy Soc Lond B* 259:307–311.
- Basolo AL, 1998. Shift in investment between sexually-selected traits: tarnishing of the silver spoon. *Anim Behav* 55:665–671.
- Borowsky RL, McClelland M, Cheng R, Welsh J, 1995. Arbitrarily primed DNA fingerprinting for phylogenetic reconstruction in vertebrates: the *Xiphophorus* model. *Mol Biol Evol* 12:1022–1032.
- Dawkins R, 1980. Good strategy or evolutionarily stable strategy? In: *Sociobiology: beyond nature/nurture?* (Barlow GW, Silverberg J, eds). Boulder, CO: Westview Press.
- DeBono M, Bargmann CI, 1998. Natural variation in a neuropeptide Y receptor homolog modifies social behavior and food response in *C. elegans*. *Cell* 94:679–689.
- Dries L, Morris M, Ryan M, 2001. Why are some pygmy swordtails large? *Copeia* 2001:355–364.
- Ender JA, 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 31:76–91.
- Ender JA, 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environ Biol Fishes* 9:173–190.
- Franck VD, 1970. Verhaltensgenetische Untersuchungen an Artbastarden der Gattung *Xiphophorus* (Pisces). *Z Tierpsychol* 27:1–34.
- Hall JC, 1994. The mating of a fly. *Science* 264:1702–1714.
- Holland B, Rice WR, 1998. Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* 52:1–7.
- Howard RD, 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution* 32:850–871.
- Hubbs CL, Gordon M, 1943. Studies of cyprinodont fishes. XIX. *Xiphophorus pygmaeus*, new species from Mexico. *Copeia* 1943:31–33.
- Kallman KD, 1989. Genetic control of size at maturity in *Xiphophorus*. In: *Ecology and evolution of livebearing fishes* (Poeciliidae) (Meffe GK, Snelson FF, eds). Englewood Cliffs, NJ: Prentice-Hall; 163–185.
- Lank DB, Smith CM, Hanote O, Burke T, Cooke F, 1995. Genetic polymorphism for alternative mating behavior in lekking male ruff *Philomachus pugnax*. *Nature* 378:59–62.
- Mayr E, 1992. *The growth of biological thought*. Cambridge, MA: Harvard University Press.
- Meyer A, Morrissey J, Scharl M, 1994. Recurrent origin of a sexually selected trait in *Xiphophorus* fishes inferred from a molecular phylogeny. *Nature* 368:539–542.
- Morris MR, Barra P, Ryan MI, 1992. Male-male competition and access to females in the swordtail *Xiphophorus nigrensis*. *Copeia* 1992:980–986.
- Morris MR, De Queiroz K, Calhoun SW, Morizot DC, 2001:65–81. Phylogenetic relationships among the northern swordtails (*Xiphophorus*) as inferred from allozyme data. *Copeia* 2001:65–81.



- Morris MR, Ryan MJ, 1990. Age at sexual maturity of male *Xiphophorus nigrensis* in nature. *Copeia* 1990:747–751.
- Morris MR, Ryan MJ, 1995. Large body size in the pygmy swordtail *Xiphophorus pygmaeus*. *Biol J Linn Soc* 54:383–395.
- Morris MR, Wagner WE, Ryan MJ, 1996. A negative correlation between trait and mate preference in *Xiphophorus pygmaeus*. *Anim Behav* 52:1193–1203.
- Rauchenberger M, Kallman KD, Morizot DC, 1990. Monophyly and geography of the Rio Panuco Basin swordtails (Genus *Xiphophorus*) with descriptions of four new species. *American Museum Novitates* 2975:41.
- Rosenthal GG, Evans CS, 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proc Natl Acad Sci USA* 95:4431–4436.
- Rosenthal GG, Evans CS, Miller WL, 1996. Female preference for a dynamic trait in the green swordtail, *Xiphophorus helleri*. *Anim Behav* 51:811–820.
- Rosenthal GG, Flores Martinez TY, Garcia de Leon FI, Ryan MJ, in press. Shared preferences by predators and females for male ornaments in swordtails. *Amer Nat.*
- Rosenthal GG, Ryan MJ, in review. A negative association between species recognition and conspecific mating preferences in the swordtail *Xiphophorus pygmaeus*.
- Ryan MJ, Causey BA, 1989. "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus* (Pisces: Poeciliidae). *Behav Ecol Sociobiol* 24:341–348.
- Ryan MJ, Hews DK, Wagner WE, 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. *Behav Ecol Sociobiol* 26:231–237.
- Ryan MJ, Pease CM, Morris MR, 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses. *Amer Natur* 139:21–31.
- Ryan MJ, Wagner WE, 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific males. *Science* 236:595–597.
- Shuster SK, Wade MJ, 1991. Equal mating success among male reproductive strategies in a marine isopod. *Nature* 350:608–610.
- Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.
- West-Eberhard MJ, 1989. Phenotypic plasticity and the origins of diversity. *Ann Rev Ecol Syst* 20:249–278.
- Wilson EO, 1975. *Sociobiology*. Cambridge, MA: Harvard University Press.
- Zuk M, Kolluru G, 1998. Exploitation of sexual signals by predators and parasitoids. *Q Rev Biol* 73:415–438.

# 9

## Learning from Lizards

Judy Stamps

From an early age, I was convinced that we share our planet with "aliens," creatures who speak their own languages and who view the world from perspectives quite different than our own. Many children probably begin life this way, but are later trained to view animals as inferior beings (and hence unworthy of serious attention) or provided such a surfeit of pets that they eventually outgrow their early interest in animals, and focus instead on members of their own species. Neither of these things happened to me: my parents respected and encouraged my interest in animals while never quite understanding it, and due to several factors, I never met enough animals when I was growing up. One reason is that my natal habitat (San Francisco) is low with respect to biodiversity, another was that as a child I had allergies to a long list of substances, including fur and feathers. As a result, the only pets allowed in the house were lizards and fish, and observations of homeotherms were restricted to the occasional urban birds that alighted in the backyard, or birds and mammals glimpsed during vacations and field trips.

In the days before Jane Goodall and other behavioral behaviorists were presented on TV as role models, it was not apparent to anyone in my family that one could make a living observing animals, and there were many occasions when I was caught staring fixedly at fish in my aquarium, and was told to stop wasting time and start doing my homework. This state of affairs lasted until I reached college at the University of California at Berkeley, and discovered a course called "animal behavior." The professor, Dr. George Barlow, not only revealed that many interesting intellectual puzzles could be addressed, if not solved, by watching animals, but also let drop in one of his lectures an offhand comment that "lizards might be good experimental subjects for studying stereotyped motor patterns," based on earlier work by Carpenter and his colleagues on the headbob patterns many lizards use in communication. Based on my limited experience with pet *Anolis carolinensis* lizards, and filled with a confidence and naive characteristic of sophomores, I showed up at his next office hours and announced that I would like to do such a project. To his eternal credit, he did not laugh and send me away to get more experience, but accepted me as a student. Dr. Barlow played a pivotal role in my career, first as an undergraduate, and later as a graduate student. Knowledgeable in both classical ethology and the more recent innovations in behavioral ecology and sociobiology that were all the rage in the early 1970s, Dr. Barlow trained his students to simultaneously approach behavioral questions from a proximate and an ultimate perspective, and repeatedly emphasized the importance of choosing study animals that could be easily observed and manipulated in both the laboratory and the field.