

4 SPECIES IN THE EYE OF THE BEHOLDER

*Lake, oh fresh lake of rivulets in-land sea . . .
In riches is Africa, Malawi's reigns of all lakes*
—Paul Mwenelupembe, 2013

If your memory stretches back to incandescent bulbs, you will know how different a room looks and feels with the warm, somewhat-red tones of incandescent lighting relative to more sterile “cool white” fluorescent lights. You may also have noticed that the colors of paint and furniture can seem different depending on the light source. Our brains compensate somewhat for this, but these effects are still detectable and at times quite strong. This is because the color of an object is a result of both the wavelengths of light hitting it and which wavelengths are most likely to bounce off it (and in which directions, though we will not explore that point for now) versus being absorbed. Thus, in terms of the environment’s role, an animal’s color is quite different from the sounds it makes. We produce sounds, but only reflect the light that conveys color. It is a bit like the difference between a motorboat, which propels itself, and a sailboat, which has to work with the wind.

As with artificial lighting, environmental light in nature varies with the light source as well as the weather and time of day. Habitat too has an effect; forests, for example, have green-tinted light in their interiors. We perceive such differences because our eyes contain cones that are sensitive to long (red cone), intermediate (green cone), or short (blue cone) wavelengths of light. When one or two cones are stimulated more and the other(s) less, we perceive color rather than white, black, or shades of gray. But not everyone's perception is the same. For instance, those with red-green color blindness are typically missing either a functional red or green cone and can completely miss colors and patterns that are obvious to everyone else—something it is wise to take into account when choosing colors for a graphic or illustration. Much variation in color vision is based in genes that encode the different opsin proteins that are characteristic of each cone type.

Underwater, ambient lighting differs more from place to place than it does in terrestrial environments. This is because water generally absorbs much more light than does air, and different wavelengths are often absorbed unequally, affecting the light spectrum. These effects can vary depending on how much sediment and other materials are in the water.

Ole Seehausen recognized early on that variation in underwater light environments could have major implications for speciation and species persistence in groups for which color is important in communication and reproduction. In an influential 1997 study, he and two colleagues presented a novel data set that provided evidence of such effects. Their focus was three groups of rock-dwelling cichlid fish from Lake Victoria. Males of closely related species in each group typically have different

coloration, with one species mainly blue, and the other mainly red or yellow; these colors are a good match to the peak sensitivities of cones in the eyes of the fish. Distinct color patterns are also present within some species, especially for males, once again usually blue individuals versus others with differing amounts of red or yellow. Conveniently for Seehausen's study, these fish inhabit rocky bottoms associated with islands that are frequently separated from each other by long stretches of sand or mud that are inhospitable to the fish. Thus, the populations and fish communities on each rocky area are substantially independent, making them well suited to analyses comparing the characteristics of different populations.

For fish from thirteen rocky islands in southern Lake Victoria, Seehausen and his colleagues documented an unexpectedly strong relationship between male color, the number of species present from these three groups of cichlids, and the turbidity of the water. Where the water was more turbid, or cloudy, and the light hitting the fish comprised a reduced range of wavelengths, there were fewer distinct male color patterns present and males more often exhibited duller hues. It seems there is little point having intense blue color—reflecting light from the short wavelength end of the spectrum, the blue portion—if there is no such light in the environment. The same would go for the long wavelength red light at the opposite end of the spectrum. Further, there were fewer species of each group at the islands with a narrower range of light (figure 4.1).

Seehausen and his colleagues suggest that the reduction in the number of species at narrowly illuminated sites results from a breakdown in mating isolation. In a light environment that reduces the ability of females to perceive color differences

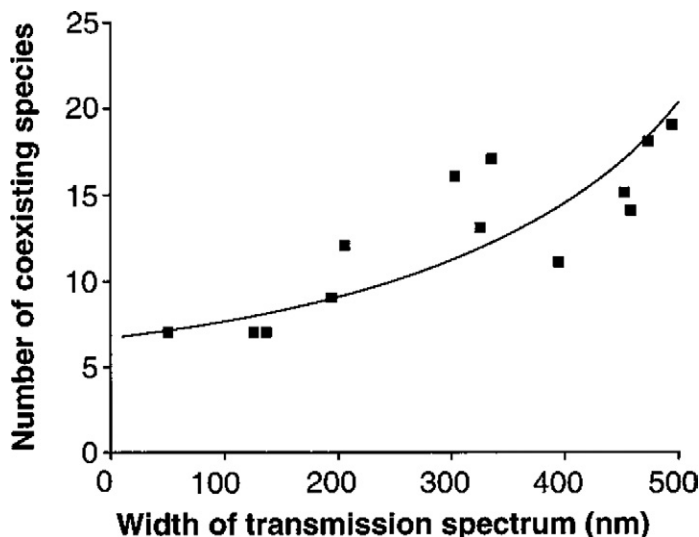


Figure 4.1

Relationship between the width of the underwater light spectrum at Lake Victoria rocky islands and the number of species present. *Source:* Reprinted with minor modifications with permission from AAAS, from Seehausen et al., “Cichlid Fish Diversity Threatened by Eutrophication That Curbs Sexual Selection,” *Science* (1997).

between species, it becomes harder to identify their own males—a difficulty that increases further as male color patterns evolve to be less distinct. Mismatings result, and because intrinsic incompatibilities are largely absent in this young radiation, two well-differentiated species can quickly become a single, somewhat variable one, or one species can be essentially absorbed into another. Seehausen’s group has obtained additional support for this interpretation in laboratory experiments in which the light spectrum is manipulated.

This is a significant conservation issue because human activity causes much of the turbidity that affects what fish can see. Historical data indicate that the cutting down of forests and changes in farming practices have been causing Victoria's water to become murkier since at least the 1920s. When we think of extinctions caused by human activity, we usually think of over-exploitation, like what happened to the passenger pigeon, or catastrophic consumption by introduced predators, such as the effect of feral cats and foxes on Australian marsupials. Habitat destruction also comes quickly to mind, as for the enormous numbers of tropical forest species now extinct, or nearly so, following the conversion of forests to palm plantations and pastures. But with turbidity, human-initiated environmental changes often lead different species to merge rather than one or both disappearing in the familiar way—yet biodiversity is just as surely lost as through better known processes. These effects are not confined to fish or even vision. Whether through increased underwater turbidity, elevated noise in cities, or explosions in the deep sea from weapons tests, disruptions of animals' sensory environments by human activities are increasingly acknowledged to be a significant conservation problem.

COMPETING FOR MATES: SEXUAL SELECTION

The findings from Lake Victoria highlight the importance of competition for mates in the evolution and persistence of species, and emphasize how the environment can mediate such competition. Selection of this sort, known as sexual selection, is the solution that Darwin identified to a difficult challenge

to his theory of evolution by natural selection: the puzzling existence of conspicuous traits—like the absurdly large tails of peacocks or vibrant colors of some fish—that seem unlikely to help animals survive better or be better parents. Frequently the opposite appears more likely: a brilliantly colored tail longer than one's body should attract the attention of predators and make it harder to escape from them—and such costs have now been documented in studies with a wide range of animals. In addition, extravagant, expensive traits may disadvantage an animal trying to catch prey or provide for its offspring. All else being equal, conspicuous and costly traits would seem destined for quick elimination by natural selection, which made their ubiquity in nature a long-standing puzzle.

Darwin hypothesized that although potentially costly in terms of survival, ornaments could be advantageous in the pursuit of matings. So even if a long tail makes predation more likely, if females reject males lacking these cumbersome appendages, the males contributing their genes to the next generation will be the ones with long tails—and their sons will also have such tails. Thus, sexual selection, in which males with conspicuous, exaggerated traits get more matings, could compensate for natural selection against such ornaments and lead to their evolution.

Comparative analyses suggest that sexual selection has contributed, alongside divergent natural selection, to adaptive radiations of cichlids. Catherine Wagner and colleagues' analyses, reviewed in chapter 2, also reveal that color differences between the sexes are positively associated with diversification. These differences function as a proxy for the strength of sexual selection in some comparative studies and are thought to

indicate strong sexual selection on males. Patterns suggestive of sexual selection's influence are weaker in Matt McGee and colleagues' larger survey.

There is also a good deal of evidence from African Great Lakes' cichlids that not only does the overall hue of a male's coloration—that is, whether it is red or blue—influence his success at obtaining matings but the intensity of his color is important too, at least in suitable lighting. Mike Pauers, then at the Milwaukee campus of the University of Wisconsin, conducted one of the first studies documenting such effects. I helped Mike with some of this work and got to know him along the way. He studied the Lake Malawi species *Labeotropheus fuelleborni* (since renamed *Labeotropheus chlorosiglos*), which has a complex color pattern including an orange belly and sky-blue back. Mike showed that females prefer males whose orange and blue patches are intensely colored rather than washed out. His results also suggest that females prefer males with greater dissimilarity between their various color patches—as if the more striking contrast between a vivid orange and intense blue, compared to the contrast between a dull orange-brown and faded blue, was attractive in and of itself. It is reminiscent of how people sometimes choose articles of clothing, selecting a skirt or tie to contrast strongly with the blouse or jacket next to it, for a more eye-catching overall effect.

Pauers's fascination with sensory biology and the aesthetics of animal social preferences likely has roots in his second career, based in nightclubs and recording studios rather than laboratories and classrooms. Mike is an accomplished saxophone player, recording and performing with a jazz ensemble as well as joining in with touring acts in need of a skilled saxophonist. This is

not as unusual as it might seem, as I have often seen artistic and scientific creativity side by side in colleagues, and their families. There seems to be great overlap in the wellsprings of creativity, regardless of the form in which it is expressed.

I have so far focused on sexual selection on males, and that is the norm in evolutionary studies because males more often display extravagant ornaments and perform strangely complex, conspicuous displays. The most widely accepted hypothesis to explain this pattern is based on investment: simply put, sperm are small and cheap whereas eggs are big and expensive. Consequently, in the marketplace of mating, there usually should be an excess of sperm available and males ready to mate, while eggs will take longer and more resources to generate. Other factors also influence the costs and benefits of mating for each sex along with the direction of sexual selection, but investment is central.

Since sexual selection concerns mating success and patterns, it makes good sense that it could play a role in speciation. It was not until late in the twentieth century that this possibility started to attract sustained attention from researchers, but the scientific community had been aware of the issue for considerably longer. One of the most important ideas about how sexual selection could accelerate the evolution of reproductive barriers came from the famous statistician and mathematical biologist R. A. Fisher. In the first decades of the twentieth century, Fisher hypothesized a mechanism by which the rate of evolution by sexual selection could be rapid indeed and proceed to almost shocking extremes.

Fisher, however, was more than a talented theoretician. He was also a eugenicist, and a case study in how science in the

twenty-first century is struggling with the challenge of giving appropriate credit for scientific contributions while rejecting destructive or unethical ideas and behaviors. Eugenic thinking has led to forced sterilization and worse, and because of Fisher's support for eugenics, his name is being removed from awards, buildings, and so on. It is a difficult legacy, but one which is crucial to acknowledge.

THE RUNAWAY HYPOTHESIS OF SEXUAL SELECTION

Fisher pointed out that the strength or even presence of a female preference for, say, males with long tails will generally vary among individuals, and such variation will usually have a genetic basis. Some females might carry an allele that causes them to mate only with long-tailed males, while others might have alleles and preferences for short-tailed males or be ambivalent about tail length. Tail length, or whatever conspicuous ornament is the target of the preference, should be genetically variable as well. With both traits genetically variable, it follows that when a long-tail-preferring female produces offspring, they will possess alleles for both the preference, inherited from their choosy mother, and long tails, inherited from the long-tailed male their mother chose to mate with, their father. Daughters of this union will choose long-tailed partners, as their mother did, and sons will express their dad's long tail (though each sex will carry alleles for both traits). As time goes on, a population-wide pattern should emerge for individuals with alleles for long tails in males to also carry alleles causing a *preference* for such tails.

Where this gets really interesting is if long-tailed males are favored in the population overall, which could cause the pace of change to accelerate. This might occur if the preference for long tails is a little more common than that for short tails, or maybe long-tailed males are carrying other beneficial alleles, sometimes known as “good genes.” In any case, if the long tail allele is favored, it will get a little more common each generation—and since males with long tails usually carry an allele for the long tail-preference, the frequency of the preference will get pulled upward. With the preference getting more common, the benefit of having a long tail keeps increasing too! Thus, long-tail success begets a stronger preference begets still more long tails, and so on. This self-reinforcing process is sometimes described as *runaway* sexual selection. It can result in not only rapid but also somewhat arbitrary changes in both male ornaments and female preferences.

The female preferences and male traits that evolve to extremes through the runaway process may not be the same in different populations. Chance typically plays some role in evolution, whether through which mutation happens to appear first or other random processes that become especially significant when populations are small—and the runaway process has immense potential to amplify such random differences. The important insight here is that if the potential for sexual selection is high, even briefly separated populations can quickly evolve different preferences and ornaments and come to reject each other as mating partners. Some modeling suggests that such processes can even propel a single population to divide into two daughter species without any physical barriers.

With the development of some of the first thorough mathematical models of runaway sexual selection in the 1980s, enthusiasm was so great that some suggested the runaway process should be the default explanation (the *null hypothesis* is the five-dollar term scientists usually use) for extravagant male courtship traits and female preferences for them. Speciation by runaway sexual selection was also championed as a possible explanation for the mind-boggling rates of speciation that were starting to be confirmed through molecular studies of some ancient lake radiations. Genetic patterns consistent with the runaway process, though possibly not unique to it, have indeed been observed in natural populations including freshwater fish and in laboratory evolution studies. But further models have called into question whether this process will play as big a role in divergence as was supposed, and almost forty years after runaway models first began to appear, there are no examples of speciation in nature that we can point to as clearly the result of such sexual selection. Ruling out competing explanations for the evolution of female preferences is always difficult, so it is important to acknowledge that the absence of evidence in this case may not be definitive evidence of absence. In addition, runaway-like processes may complement and augment ecological divergence, thereby contributing to speciation without being the sole driver; indeed, sexual selection is generally thought to be most likely to contribute to speciation when acting in concert with natural selection. A different approach to the evolution of mating preferences and male display traits has, however, lately supplanted runaway as a research focus, especially in the context of speciation.

SENSORY DRIVE

As we have seen, Seehausen and his colleagues provided persuasive evidence, starting in the late 1990s, that water turbidity can influence cichlid mating patterns and the expression of mating preferences. When water clarity deteriorates enough, speciation can even reverse itself, and two well-defined species can collapse into a swarm of ill-defined hybrids. But there is more going on. In the 1980s and 1990s, shortly after the study of sexual selection began its resurgence, the role of sensory systems in sexual selection started to receive more attention. One of the leaders in this body of work was (and remains) John Endler, a scientist who hails originally from Canada and has worked extensively on guppies and bower birds, among other groups. I first met John while a graduate student, and was impressed (as I still am) with the breadth of his knowledge and interests as well as how he was able to link the details of natural history and physiology with mathematical models of genetic processes, generating unexpected insights along the way. When John was at the University of California at Santa Barbara, I once spent a happy Saturday afternoon with him while visiting to get help with an instrument calibration. We drank tea and watched hummingbirds court from the balcony of his house, which was set on a hillside and surrounded by trees. His enthusiasm for closely observing the behavior of these birds was contagious, and I have no doubt that such habits of careful observation in natural settings helped lead him to the highly synthetic sensory drive hypothesis that emerged from work by himself and several other scientists.

Sensory drive is, in essence, the hypothesis that environmental factors play a central role in the evolution of both mating

preferences and ornaments. In the case of mating preferences, this will typically occur when sensory systems are molded by natural selection to function effectively in an organism's particular sensory environment. The strongest selection is expected to be for finding food and other activities directly related to survival, with effects on mate preferences often a by-product. Ornaments that have evolved to attract mates should be influenced by both the sensory biases of receivers and the direct effects of the environment on which types of ornament are most conspicuous. In the case of visual signals, these effects can arise through the spectra of light that illuminate ornaments as well as through the backgrounds against which courting males are seen and extent to which ornaments contrast with those backgrounds (figure 4.2).

Working in Sulawesi's Lake Matano, Suzanne Gray, along with several collaborators including myself, found evidence for the importance of contrast with the background in a comparison of different populations of a fish, *Telmatherina sarasinorum*, in which five different male color patterns are present. She first evaluated *Telmatherina* vision using a closely related species and characterizing the types of cones present in their eyes and their sensitivities. She then used those data to evaluate the conspicuousness of each type of male in each of the two environments in which they courted and spawned, using careful measurements of the light reflected from the bodies of the males in addition to measuring the background light spectrum. She included ultraviolet light as well as wavelengths visible to our species, since these fish, like many animals, can see in ultraviolet light. In one environment, spawning took place on roots hanging in relatively open water with a mainly bluish

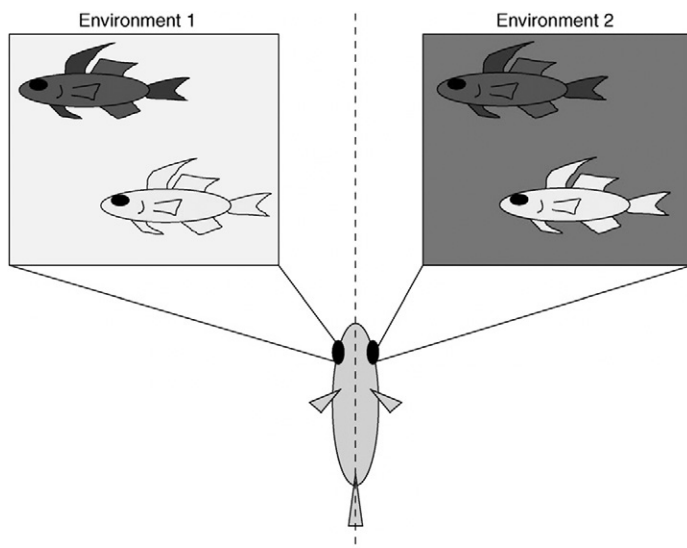


Figure 4.2

Conspicuousness can vary with color and background. Here lightness versus darkness is illustrated, but examples discussed in this chapter mainly concern hue, such as for blue- versus yellow-colored fish. *Source:* Reprinted with minor modifications with permission from Elsevier, from Gray and McKinnon, "Linking Color Polymorphism Maintenance and Speciation," *Trends in Ecology and Evolution* (2007).

background. In the other, fish spawned in shallow water where they saw each other mainly against the typically yellow-brown rocks. Blue and yellow males had the most extreme difference in coloration among the five color types. Suzanne found that blue males were most conspicuous to females, and had the highest mating success, in the shallow-water habitat where they were most abundant and also appeared most conspicuous to the human eye. Yellow males were more conspicuous and most successful in the root-spawning site, with its blue-green open

water background, where they were also most abundant. We don't know yet if color vision varies between the environments, but this possibility has been investigated in Lake Victoria cichlids in the context of speciation.

Pundamilia nyererei, in which males are usually red, and *Pundamilia pundamilia*, in which males are usually blue, are two closely related species that were introduced earlier. Work has continued on this species complex, and provided insights into not only how environmental change can cause species to merge but also how environmental variation can contribute to the maintenance and formation of species through sensory drive. These two species often overlap in where they are found, but there are subtle differences as well, with *P. pundamilia* usually occurring in shallower water than *P. nyererei*. In locations with intermediate turbidity, Victoria's waters tend to filter short wavelength, blue light quickly with depth, resulting in *P. pundamilia* being found in a more broad-spectrum light environment and *P. nyererei* occurring in a habitat in which light is red shifted. This is thought to be the reason that the visual tuning of the two species also varies consistently with depth, as has been shown repeatedly along the descending slopes of different islands.

The opsin proteins found in the long wavelength, red-sensitive cones of *P. nyererei* have a genetic difference from those of *P. pundamilia* that causes their peak sensitivity to be a little further toward the red end of the spectrum, likely enabling *P. nyererei* to make better use of the limited light in their environment, much of which is red. This could help them, for example, in finding prey. Seehausen and his colleagues hypothesize that this difference also contributes to selection for red coloration in

P. nyererei males; not only do red males ensure they are reflecting light and making themselves visible in their local environment but they also ensure they are reflecting wavelengths of light readily detected by females. Of course, they may not contrast well with the background in terms of hue, but with modest ambient lighting there may be little option. Not all links in this hypothesized scenario are fully confirmed yet. Still, evidence of one key connection, linking survival to the light environment and thus natural selection, has now been obtained.

Martine Maan of the University of Groningen in the Netherlands led a study of how rearing in different light environments affects lab-bred *P. pundamilia*-like and *P. nyererei*-like (they are referred to as “like” because these fish came from Python Island and are the result of “parallel hybrid speciation”; henceforth I will omit the “like”) as well as hybrids between them. Measuring survival was not initially a goal of the study; in their published paper describing the work, the authors note that “the results reported here emerged serendipitously from counts that were conducted for administrative purposes only.” I am sure many scientists reading this feel envious of an important finding arising entirely as a by-product of another study and leading to a major publication. Many of our seemingly best-designed and most laborious experiments do not yield such consequential outcomes.

The key result was that the juvenile *P. pundamilia* survived better in a blue-shifted light environment, akin to that of the shallow waters they typically inhabit, whereas the *P. nyererei* suffered fewer deaths in more red-shifted light similar to what is present in the slightly deeper waters of Lake Victoria, where

they are usually found. The differences were surprisingly large: almost 40 percent after a year. Hybrids of the two species were roughly intermediate, as would be expected. Hybrid survival did not differ between light treatments and from the “pure” forms in either light environment, although the trend was for them to generally do a little worse than *P. pundamilia* under blue light or *P. nyererei* under red light. There are at least two plausible reasons for the survival differences observed, though additional data would be needed to resolve which, if either, applies. First, fish may not be as good at detecting and capturing food in an ill-suited light environment. This could result in reduced growth, social disadvantages, and ultimately an early death. Alternatively, inappropriate light environments may cause stress and contribute to aggression and conflict. The essential outcome in terms of sensory drive and speciation is that sensory divergence that can influence mating preferences is shown to be favored by natural selection entirely outside the context of mating, facilitating the formation and maintenance of species. Such divergence could operate in isolation, but seems more likely to complement other forms of ecological divergence between environments.

LEARNING AND DEVELOPMENT

Biologists have often treated mating preferences and numerous other traits as if they were strictly genetically determined—as if, say, one allele means a female always chooses the red male while a different allele means she always chooses the blue male. It makes sense to start with simple assumptions like these, see

how much insight they can provide, and then layer complexity on top. In the case of mate preferences, there is a good deal of layering that we can do. In particular, we know that experience and the environment in which an organism develops can modify sensory systems, color patterns, and social behavior, and such effects are now being studied and incorporated into our understanding of how species are formed.

Several studies have built on the Lake Victoria *Pundamilia* system. They were mainly conducted in Maan's laboratory in Groningen by a former research student of mine, Shane Wright. I sometimes tell Shane's story to my undergraduate students at East Carolina University, many of whom come from struggling small towns and cities in our economically stressed region and are the first in their families to attend university; Shane is a model for some. He too comes from a small city, in his case in western Virginia. He worked terrifically hard, funding his education himself, and made excellent use of the opportunities that came his way, including a spell in my laboratory working on stickleback fish. He went on to join the Maan laboratory for his PhD, conducting fieldwork in Tanzania and laboratory work in the Netherlands—all of it a long way from small-town Virginia. I visited him in Groningen while he was there and was reminded that he is one of the most positive people I have known.

Shane's investigations of how a fish's early light environment shapes its mate preference, vision, and color patterns made use of individuals from the rearing experiment described above in which fish were raised in different light regimes. When Shane and his colleagues tested the mating preferences of the surviving adults, they found that the early environment of the

fish had had a significant effect. Fish raised in the shallow-water, broad-spectrum light regime in which *P. pundamilia* normally reside showed a stronger preference for blue *P. pundamilia* males than did fish raised in the red-tinged environment typical of *P. nyererei*; the latter individuals tended to respond more to the red *P. nyererei* males. In contrast, the rearing environment had little effect on how male color developed. *P. nyererei* males consistently turned out red while *P. pundamilia* males were consistently blue as breeding adults. Both, though, developed a little more green on their bodies in the red-shifted habitat.

One interpretation of the preference results is that an early light environment should have a similar effect to that of selection acting on vision and cause fish to prefer males native to the environment in which they were raised; this could contribute to speciation. But in the paper presenting these findings, Shane and his coauthors also point out that the opposite effect on speciation is possible, though perhaps less likely. Should a female end up in the “wrong” light habitat early in life, developmental effects will cause her to be more likely to choose males of that habitat rather than those of her own population—inhibiting speciation.

In additional analyses of the genes associated with color vision, there was no straightforward relationship between a female’s opsin expression and her mate preference. The opsin genotypes (genotype refers to the variants of genes present at one or more genes) of the red cones, however, for which there was unexpectedly extensive mixing of different combinations of *P. pundamilia* and *P. nyererei* genes, proved more important. Under wide-spectrum light, females with exclusively *P.*

nyererei-like red cones preferred red males whereas females with only *P. pundamilia*-like red cones preferred blue males; females with one cone gene of each type showed no preference. Yet in red-tinged light, there were no clear differences in preference. The upshot of these experiments is that the light under which fish are reared affects mating preferences in the same direction—with deeper-water fish preferring red males and shallow-water fish preferring blue males—as the effects of the red cones characteristic of each depth.

During the rearing of the fish used in these studies, special care was taken to minimize interactions between the recently hatched young cichlids and their mothers. This is because the mother cichlid often cares for her offspring for several weeks, carrying them in her mouth, and then guards them even after they are free swimming—and parent-offspring interactions are well-known to influence mating preferences. Birds have been found to “imprint” on their parents and the songs they hear such that their choice of mates as adults reflects their experience during early life. Machteld Verzijden, then at Leiden University in the Netherlands, wondered if such effects might also be present in these cichlid fish and if they could play a role in the explosive speciation rates in the African Great Lakes.

To test this possibility, she switched fertilized eggs between mothers. Two to five days after spawning, she gently induced new *Pundamilia* mothers to spit out their recently fertilized eggs. She then moved the eggs between mothers—sometimes mothers of the same species, as a control, and sometimes those of different species. Mothers were left with the eggs and fry for four weeks, and then the fry were raised to maturity. The mature

females were tested with a red male *P. nyererei* and blue male *P. pundamilia* using an experimental design that took advantage of the male-female size difference. Males were kept apart using grid dividers that the smaller females could cross but the males could not, ensuring females had a full opportunity to choose and males could not directly interfere with one another.

The results showed an unexpectedly strong effect of which type of mother had reared the females. Those reared by mothers of their own species preferred males of their own species. But females reared by females of the other species preferred those males! Thus, a *P. nyererei* female who had been mouth brooded and guarded by a female of her own species, but not her mother, preferred a red male of her own species over a blue male of *P. pundamilia*. But a *P. nyererei* female who had been mouth brooded and guarded by a *P. pundamilia* female rejected the courtship of males of her own species and responded positively to the courtship of *P. pundamilia* males. The key issue was the species of the female who had cared for her, not who her genetic parents were. The fish could interact fully, so it is possible that the preference was based on chemical cues, but other studies suggest these are not important in *Pundamilia*. Visual cues are a possibility because females, although generally similar between species, weakly express some aspects of the color patterns that distinguish males. In any case, what is unequivocal is that a female's choice of mate is influenced by the mother who rears her, and in a way that could accelerate speciation as populations diverge. It has long been thought that sexual selection can complement or even reinforce divergent natural selection's role in the speciation process if mating with members of one's

own species is favored to avoid producing hybrids with poor prospects. These experiments suggest that imprinting may lead to an analogous outcome.

CONFLICT

We have seen how female preferences and male traits can coevolve to yield good “fits” within populations, and how early developmental effects and imprinting can complement such coevolution. Yet most of us have had our share of disputes with our family members (whether by birth or marriage) and friends. We know from experience that social interactions often involve conflict as well as cooperation, including the interactions involved in mating and reproduction. It is becoming clear that conflict is a major part of animal courtship as well, with potential consequences for speciation and diversification.

An example of sexual conflict is seen in Gray’s work, on which I was a collaborator, on the fish *Telmatherina sarasinorum* in Lake Matano, Sulawesi. This species feeds mainly on the eggs of other *Telmatherina* as they are spawning, especially *Telmatherina antoniae*, but this feeding habit can lead to conflict in reproduction. When a female goes to spawn with a male, frequently other males rush in to try to fertilize the eggs too. The first conflict arises if the female is not interested in having the other males fertilize her eggs—but it gets worse.

Males sometimes turn around immediately after spawning and try to eat the eggs of the female they just mated with (figure 4.3). This rarely happens if there is only one male involved in the spawning. But as more males are involved, the probability of such cannibalism goes up rapidly.

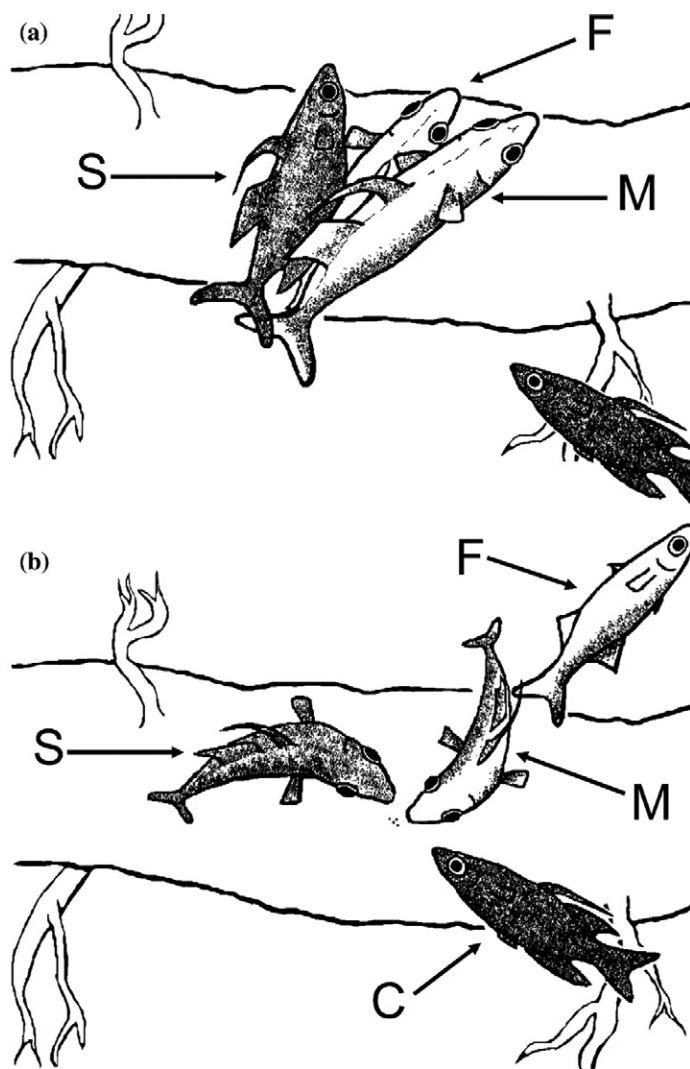


Figure 4.3

Spawning of *Telmatherina sarasinorum* sailfin silversides (a) followed by (b) males attempting to cannibalize eggs. F = female; M = paired male; S = sneaker male; and C = nonmating cannibal male. *Source:* Reprinted with minor modifications with permission from Springer Nature, from Gray and McKinnon, "A Comparative Description of Mating Behaviour in the Endemic *Telmatherinid* Fishes of Sulawesi's Malili Lakes," *Environmental Biology of Fishes* (2006).

When two or more additional males join in the spawning, the original male tries to cannibalize the eggs over 80 percent of the time. Before collecting any data, we hypothesized that this would happen because the likelihood that the male is the father should go down as more males are involved. There are just more sperm in the water around the eggs, and although Suzanne did not collect data on paternity for her study, it is well-known from other animal species that paternity is easily diluted as more sperm compete for fertilizations. In addition, if the other males are going to eat the eggs anyway, it probably pays for a male to try to get his share; if he can't become a father, at least he won't go hungry. Suzanne also collected data supporting the latter interpretation. Even with no sneakers, males were more likely to try to eat the eggs of the female with whom they just spawned when other males rushed in to feast. It was satisfying, if a little macabre, to see our predictions borne out. The paper was titled "Cuckoldry Incites Cannibalism."

A more subtle form of conflict can occur within individual genes when different forms of a gene, different alleles, are favored in different sexes. We already explored an example of such conflict, or sexual antagonism as it is formally known, when discussing the rapidly evolving sex determination systems of cichlids. It is becoming clear that the coexistence of different sex-determining systems even within cichlid species and populations is a quite ordinary state of affairs, and cichlid sex determination can rapidly evolve along different pathways in different populations. For instance, different genes can determine sex, or a gene for maleness can be dominant in one population (and femaleness recessive) and a gene for femaleness can be dominant in a different population (and maleness recessive).

As I write, at least twenty-two different sex determination systems have been identified in East African cichlid fishes, spread across eighteen of their twenty-three chromosomes. Potentially, such differences can cause incompatibilities between males and females of different populations and result in offspring of reduced fitness, thereby contributing to the evolution of reproductive isolation between the populations and ultimately speciation.

When crosses between young species have been conducted, the predicted incompatibilities have been observed. Sina Rometsch, Julián Torres-Dowdall, and Axel Meyer of the University of Konstanz compiled all available data on such crosses for cichlids. They confirmed that sex ratio distortions (unexpectedly high proportions of males, or of females) were common between even closely related forms and their frequency increased rapidly with the evolutionary distance between species—much more quickly than other incompatibilities, such as the reduced survival of hybrid offspring. Additional data and analyses will be needed to assess whether the surprising diversity of cichlid sex determination systems and the ensuing problems with some hybrids have helped cause the elevated speciation rates often seen in these fish—or alternatively, are themselves a by-product of explosive adaptive radiation.

* * *

Some traits are difficult to explain solely in terms of their survival advantage. For such traits, an advantage in mating is frequently the explanation and thus the process of sexual selection. Like natural selection, sexual selection may play an important role in speciation, and the direction and strength of sexual

selection will also be influenced by an organism's ecology. Comparative evidence suggests that sexual selection has contributed to ancient lake adaptive radiations. Sexual selection necessarily involves a social component in which both learning and conflict may be important, with consequences for speciation. How natural and sexual selection interact to generate biodiversity is one of the most exciting areas of research in ancient lakes.

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