

Pigments, Patterns, and Fish Behavior

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Abstract

Color patterns in fish are often multicomponent signals, composed of pigment-based and structural color patches that can be used to communicate within species, in both inter- and intrasexual interactions, and between species. In this review, we discuss some of the roles played by pigment-based elements of color pattern. We begin by discussing general forms of coloration, classifying them by appearance (e.g., cryptic vs. conspicuous) and apparent function (e.g., conspicuous coloration and mating displays, stripes and cooperation, and bars and aggression). We then briefly discuss the roles pigments play in the perception of these color patterns via their presence in the eye. In the last section, we look at the relative importance of carotenoid versus melanic coloration in situations where honest signals to potential rivals and potential mates might be required. In this survey, we have highlighted some recent research, especially studies that consider both the physiological and behavioral processes underlying the evolution and expression of pigment-based color patterns in fish. The nature of pigmented color patterns depends not just on the dynamics of pattern development and physiological regulation, but also on the behavioral roles played by these patterns, both now and in the past. As such, advances in particular fields of study on pigment patterns (physiology, developmental biology, behavioral ecology, evolutionary biology, etc.) will increasingly depend on insights from other fields.

Introduction

COLOR PATCHES IN FISH, reptiles, and amphibians are multilayer, multicomponent signals.¹ The basic unit of color in these taxa is the dermal chromatophore, which is generally composed of three cell layers: the xanthophore (contains carotenoid and pteridine pigments), the iridophore (reflects color structurally), and the melanophore (contains melanin). Pigments are compounds that absorb particular wavelengths of light and can contribute to the color of biological patches. Two classes of pigments that are commonly studied in fish are carotenoids (usually yellows, orange, and red) and melanin (browns, blacks, and grays); they are deposited in the integument. Short wavelength (blue and violet) and silvery coloration in vertebrates are almost always structurally based, the result of selective light scatter owing to variable refraction within the integument, and only one blue pigment has been described in fish (reviewed in Bagnara *et al.*²). This type of structural coloration, which occurs in the iridophores, is undoubtedly an important component of animal color patterns but will not be discussed further except in cases where it interacts with pigment-based colors.

From a behavioral perspective, pigment-based color patterns are particularly interesting for several reasons. Pigments (or their precursors) cannot be synthesized and must be ob-

tained from the diet. In many cases, the amount of pigment expressed is dependent on an individual's foraging success and physiological efficiency (discussed by Grether *et al.*^{3,4}); the level of coloration an individual expresses can therefore indicate their quality as a potential mate or competitor, or of their escape potential in the eyes of predators. In addition to this variation in expression based on diet, pigments can be expressed differentially depending on ontogeny (juveniles can possess color patterns that are very different from adult conspecifics), seasonally, and even ephemerally.

Pigment-based color patterns can change through direct regulation of pigment-containing cells, or indirectly through adjustment of the light interacting with the pigment through regulation of iridophores. By changing the structure of the iridophore, the paradise whiptail (*Pentapodus paradiseus*) can change which wavelengths of light are reflected back through the xanthophore, turning from blue to red in a fraction of a second.⁵ A more common mechanism of color change in fish involves changes in the intensity and/or area of black, brown, or gray melanic colors through melanocyte-stimulating hormone (MSH)-induced stimulation of melanin granule dispersion in the melanocytes⁶ (Fig. 1); the size and shape of melanin-based pattern elements can be changed in seconds, with the diameter of completely dispersed and completely aggregated cells often differing by several fold (e.g., see

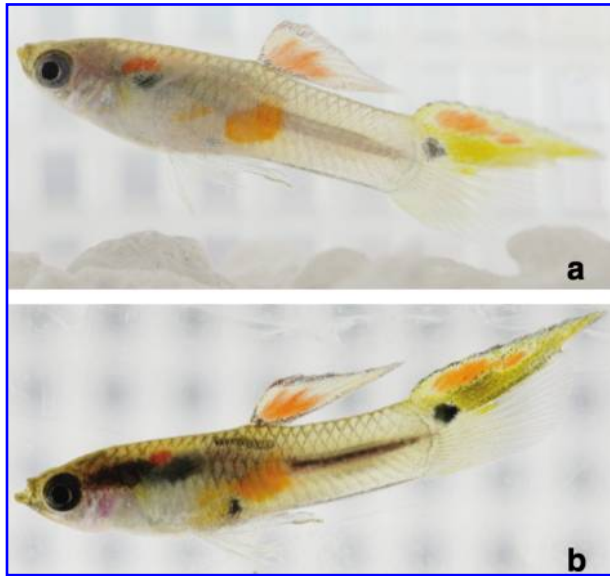


FIG. 1. Temporal variation in expression of melanin spots in a male guppy (*Poecilia reticulata*): one individual in two different treatments. (a) Reduced expression during simulated predator attack. (b) Maximal expression of the same male in anesthetic treatment. (Photos by A. Price, fish courtesy of A. Houde.)

Hawkes⁷). The behavior of pigment-containing cells is controlled by both the nervous and endocrine systems, with more rapid changes typically reflecting neural control.⁸ This flexibility in the expression of color patterns means that coloration can go beyond signaling static properties such as species identity, sex, or developmental stage, but can also indicate an individual's current quality and motivational state (assuming honest signaling).

In this review, we focus on two classes of pigment-based color patterns. We will discuss carotenoid (yellow, orange, and red pigments) and melanin-based coloration because their behavioral functions have been well studied in many fish taxa. We will not discuss pteridine, another pigment commonly found in the xanthophore, as it not well studied from a behavioral perspective (however, see Grether *et al.*⁹). The development of color patterns and the synthesis and deposition of associated pigments in fish are the product of complicated physiological processes. These physiological processes and the color pattern-related behaviors discussed here should inform those interested in the ways in which physiology mediates environmental and social influences on behavior. Examples have been drawn from several well-studied model systems, including guppies, swordtails, mollies, cichlids, gobies, and zebrafish, as well from some note-worthy examples from less well-studied species.

Classes of Coloration

Inconspicuous coloration: background matching

Fish color patterns are shaped by a variety of selective pressures imposed by their predators and prey, their competitors, and their prospective mates. Some of these interactions favor reduced conspicuousness, or crypsis, while others promote the opposite. Plasticity in pigment-based color pat-

terns, or in associated display behaviors, appears to be a common solution to balancing opposing pressures. While the following sections will catalog many striking examples of elaborate color patterns, it is important to note that most fish species have fairly inconspicuous coloration that matches the background in their natural habitat.^{10,11} Field studies involving spectrophotometric measurements of both the color pattern and background, and physiological measurements of the viewing species' visual capabilities are necessary to determine if a color pattern is indeed inconspicuous (or cryptic), because what appears obvious to the human eye may not actually be conspicuous in the natural habitat.¹¹

Crypsis can be achieved by modifying color patterns, behavior, or both. For example, by adjusting the timing of courtship (in response to changes in the spectral qualities of ambient light and because of differences in the visual capabilities of guppies and their predators), guppies are able to reduce conspicuousness to predators and enhance conspicuousness to potential mates.^{12,13} In a number of species, evidence is accumulating that some color elements are specifically tuned to conspecifics' visual capabilities but away from colors that are conspicuous to predators (private signaling).^{14–16}

The underwater light environment is dynamic, both temporally and spatially, and the visual capacities of fish vary dramatically; some species are tetrachromatic and possess the ability to see ultraviolet or far-red light, while others are partially or completely color blind compared to humans.¹⁷ Marshall and Vorobyev's¹⁸ study of colorful coral reef fish provides a striking example. Noting that many coral reef fish are dichromats, they concluded that "at long wavelengths (yellow, orange, and red), the reef is probably less colorful to many fishes than it appears to us" and that "colors of reef fishes are almost always for camouflage."

Field observations of the kelp bass (*Paralabrax clathratus*) suggest that the distinctive calico body pattern possessed by most individuals outside of the breeding season is actually cryptic in the natural habitat.¹⁹ Color patterns can also be modified to enhance or reduce conspicuousness. Individual bass were able to alter their coloration depending on whether they were found in dense kelp or in open water. Similarly, surfperch perform their courtship behavior in specific positions to enhance or reduce the contrast with their environment.²⁰

An organism is said to employ background matching if its color pattern resembles a random sample of the background.¹⁴ For example, in an elegant experimental evolution study carried out on guppies (*Poecilia reticulata*) in artificial streams, Endler²¹ found that predators selected for color patterns with spots that roughly matched the size of the gravel substrate. In this example, the background to be matched was the visually complex stream bottom, but in other species the uniform coloration of the water column can serve as the background as well. Many fish are darker dorsally than ventrally, a pattern termed countershading, and this pattern may serve to reduce conspicuousness against bright downwelling light when viewed from below, and against darker upwelling light when viewed from above.²² Two species that swim upside down, the catfish (*Synodontis nigroventris*) and the cichlid (*Tyrannochromis macrostoma*), have reversed countershading,^{23,24} and studies on reverse-countershading development in these species may provide an interesting complement to the study of dorsoventral patterning in model systems like zebrafish.

Conspicuous patches of color

Conspicuous patches of coloration, especially red and orange, are widespread among fishes and have been the focus of intense scientific study. This is probably because, at least in part, these colors are so obvious to the human eye. In spite of difficulties associated with ensuring ecologically appropriate viewing conditions and consideration of viewer physiology, progress has been made in deciphering the roles color patterns play in many fish species, in the context of both intrasexual communication, that is, mate recognition and mate choice,²⁵ and in aposematic predator-prey communication.⁸

In this section, we will discuss the conspicuous, colorful patches often considered in studies of mate choice. There is a long history of study of conspicuous, sexually selected color patterns by both developmental geneticists and behavioral ecologists, and as such this field represents a fertile ground for collaborative research. We have divided colorful patches into three categories (reviewed in Kodric-Brown²⁵): (i) permanent patches, present year round and fixed in area and intensity; (ii) seasonal patches, often nuptial, generally present during the breeding season for signaling receptivity or sexual maturity; and (iii) ephemeral patches that are flexibly expressed, can be changed in seconds, and are under neuro-hormonal control.

Permanent color patches. Conspicuous coloration tends to be permanent in species that have a prolonged breeding season (e.g., many tropical fish) or that hold territories year-round (reviewed in Kodric-Brown²⁵). Two of the best-studied systems for looking at the role of coloration in mate choice are guppies (*P. reticulata*) and cichlids of the Great Rift lakes of Africa. Many species of cichlid have permanent color patterns thought to be involved in both competition for, and choice of, mates.^{26,27} In the African cichlids, permanent color patterns, which differ between (i) morphs within species, (ii) hybridizing incipient species pairs, and (iii) nonhybridizing species pairs, appear to be important in the different stages of speciation represented by these comparisons (reviewed in Carleton *et al.*²⁸).

Guppies have become a model system for studies of the interacting effects of natural and sexual selection on conspicuous patches of color (reviewed by Houde²⁹ and Magurran³⁰). Male guppies have complex, extremely polymorphic color patterns consisting mostly of orange and black pigments combined with some structural color patches. Female guppies generally show a preference for orange, carotenoid-based color patches. Studies suggest that females can obtain both direct and indirect benefits from choosing a mate with larger, more chromatic, orange patches, because these carotenoid-based spots can reflect an individual's foraging ability and parasite load (carotenoids must be acquired in the diet, and individuals with more parasites tend to have duller orange coloration); however, other models of sexual selection, including sensory bias³¹ and the Fisherian mechanism, may have also contributed to the evolution of female guppy preference for carotenoid-based spots.²⁹

Seasonal coloration. Seasonal, or nuptial, coloration occurs in many species with restricted breeding seasons (reviewed in Kodric-Brown²⁵). For example, many salmonids turn from silver to bright red as they move carotenoids from

their flesh, accumulated during development, to their skin as they mature.³² In salmon at least, the mobilization and transport of carotenoids to the skin is gradual and involves several physiological pathways.^{33,34} In kelp bass (*P. clathratus*), only sexually mature individuals develop bright coloration during the breeding season.¹⁹ In pupfish (*Cyprinodon pecosensis*), only males who successfully establish breeding territories develop bright nuptial coloration.²⁵ Mating behavior and seasonal coloration have been extensively studied in threespine sticklebacks, where males in many populations develop red throats that attract mates and deter competitors³⁵ (reviewed in Rowland³⁶). However, in areas where the water is tea-colored, male sticklebacks with black throats, which are conspicuous against the natural background, are favored by females.³⁷⁻³⁹

Ephemeral color patches. Because of their very nature, ephemeral color patches, which can be turned on and off in seconds, are particularly hard to study. Many of the components of fish color patterns that can be altered instantaneously via neuro-hormonal mechanisms are melanin based,^{6,25} and will therefore be discussed in the following section. However, there are some examples of nonmelanic coloration that can change rapidly. For example, the longspine snipefish (*Macrorhamphosus scolopax*) becomes bright red over the caudal half of its body during courtship (see Kodric-Brown²⁵ for other examples). It is possible that these rapid changes in color come about by changes in the structural layer of reflective cells (the iridophore) that can alter which wavelengths are reflected back through the yellow/orange/red layer of pigment, which lies on top.¹

Conspicuous patches of black

Bars and aggression. Bars are linear patches of color that run dorso-ventrally.⁴⁰ Across a range of species, bars are associated with intraspecific aggression, melanin based, and ephemerally flexible (e.g., *Xiphophorus*⁴¹; various poeciliids [*Xiphophorus*, *Heterandria*, and *Phallichthys*]⁴²; in sailfin mollies [*Poecilia latipinna*]⁴³; and in a cichlid [*Asronotus ocellatus*]⁴⁴). A comparative study by Moretz and Morris⁴² suggests a tight relationship between expression of bars and responsiveness to them; male swordtails vary inter- and intraspecifically in whether they are able to display bars, and, in some cases, males that do not have bars do not seem to interpret bars as an aggressive signal (Fig. 2). In male brook sticklebacks (*Culaea inconstans*), the size of the vertical black bar across each eye peaks at the same time as the male's aggressive nest guarding behavior.⁴⁵ In a species with sex role reversal, the pipefish (*Syngnathus typhle*), where the males brood eggs in a pouch, females can turn on a striped pattern that runs dorso-ventrally.⁴⁶ This pattern is used in female-female competition for matings, and is also preferred by males.

In a phylogenetic study of one of the most species-rich vertebrate families (cichlids, Cichlidae), Seehausen *et al.*⁴⁷ asked which behaviors and natural histories were associated with particular color pattern elements. The appearance of bars in the cichlid phylogeny is associated with the occupation of structural habitats (rather than open water), where individuals are more likely to be territorial and where resources are clumped in space and time, all of which suggest that intraspecific competition for resources and mates is intense (Fig. 3).

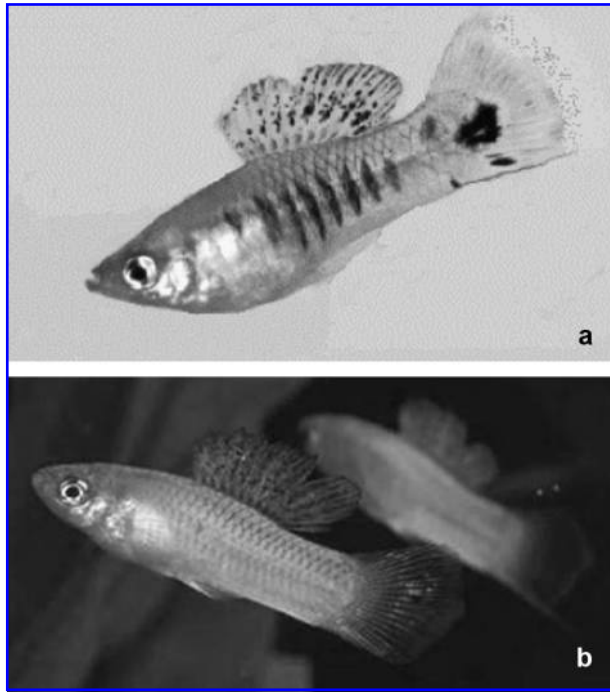


FIG. 2. Intraspecific variation in expression of vertical bars in the delicate swordtail (*Xiphophorus cortezi*). (a) Vertical bar pattern associated with aggression in *cortezi*. (b) Barless *cortezi* do not seem to interpret bars as an aggressive signal. (Photos by K. de Queiroz.)

An association between melanic coloration and aggression has been noted not only in fish (in *Gambusia*⁴⁸; in oscar cichlids⁴⁴; and in tilapia, *Aequidens* cichlids) but also among other vertebrates. Ducrest *et al.*⁴⁹ suggest that this relationship exists due to pleiotropy, as the physiological bases of aggression and melanin-based coloration are linked through the melanocortin system. Pleiotropy could explain both (i) the tightness of the association between melanic coloration and aggressive behavior in these fish species and (ii) the widespread nature of this association across disparate taxa. This proposed pleiotropic relationship suggests the need for comparative work on distantly related species, where associations between physiology, coloration, and behavior can be examined as part of the study of the function of melanin-based patterns; such work will reveal whether the link between melanic coloration and aggressive behavior has been conserved throughout evolution or whether it is the product of convergence.

Stripes and cooperation. Shoaling: Stripes are linear color patches that are oriented cranio-caudally.⁴⁰ In their comparative study of cichlids, Seehausen *et al.*⁴⁷ found that species that inhabit open water and engage in cooperative shoaling behavior tended to have longitudinal stripes (Fig. 3). Other species that show highly developed shoaling behavior have stripes as well (e.g., zebrafish, rainbow fish [Fig. 4]; striped catfish, snappers [*Lutjanus kasmira*]).⁵⁰ There are several hypotheses about how stripes might function in shoaling behavior. Stripes may disrupt an organism's characteristic outline, making it unrecognizable (e.g., Armbruster and Page),⁵¹ or, when viewed against the background of other striped individuals, stripes may make it difficult for a pred-

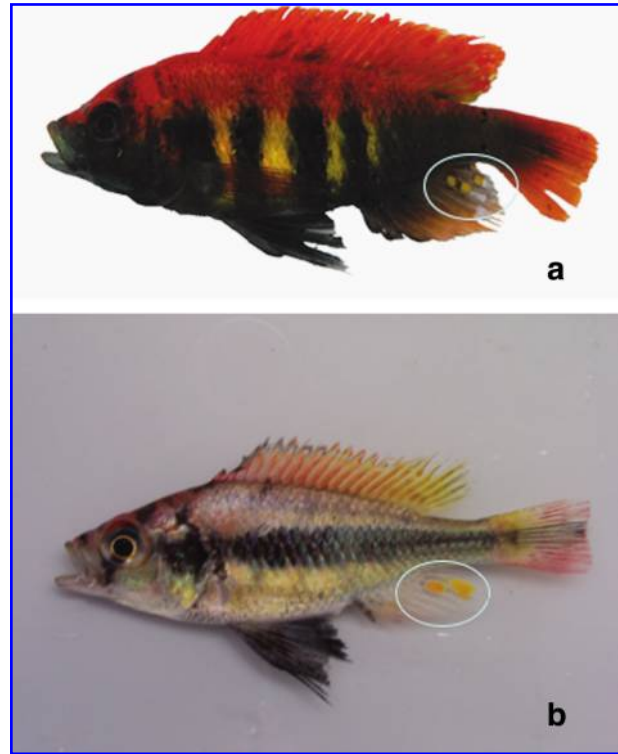


FIG. 3. Vertical bar and horizontal stripe patterns on closely related cichlids of the adaptive radiation in Lake Victoria. Note false eggspots on anal fins of both species. (a) *Pundamilia nyererei*: vertical bars are associated with highly territorial life in structured littoral habitats. (b) *Enterochromis cf. paropioides*: midlateral stripe pattern associated with life in the open water. (Photos by O. Seehausen/University of Bern & Eawag.)

ator to focus on a specific target (the confusion effect).⁵² Endler²¹ posed the idea that, during movement, color patterns are perceived differently than when stationary; for example, during movement, stripes are averaged and appear as a different color than when stationary. Brodie⁵³ suggested that striped individuals moving in a straight line create an optical illusion that foils optically oriented predators because it is difficult to judge the speed of an individual when stripes run the same direction as that in which the individual is moving.

Stripes in many shoaling species are black and white (e.g., zebrafish), but stripes of other colors, such as orange and red in rainbow fish, can play an important role when they are deposited between black stripes.⁵⁰ Dark stripes may help an individual to identify appropriate school mates, either within or among species, as the oddity effect can lead to increased predation on fish associated with mismatched individuals.^{54,55} This is the case within striped and unstriped species and strains of *Danio*, where individuals chose to associate with individuals^{56,57} or computer images⁵⁵ that most resembled their own phenotype or the phenotype of individuals they were reared with. Indeed, this preferential shoaling was strongest in the striped morphs in these studies. Denton and Rowe⁵⁸ suggested that stripes help coordinate shoaling behavior because the way stripes are perceived changes with body orientation.



FIG. 4. Longitudinal stripes are often associated with highly developed shoaling behavior as in the western Australia Rainbowfish (*Melanotaenia australis*) and the zebrafish (*Danio rerio*). (Photo by J. Kelley.)

Cleaning behavior and stripes: Several studies have suggested a role for stripes in another cooperative interaction: cleaning behavior. Incorrect identification of a potential cleaning partner could have negative consequences; that is, the client fish would remain uncleaned (and potentially parasitized), or the cleaner fish could be preyed upon. Studies have shown an association between a striped body pattern and obligate cleaning behavior both within the Labridae⁵⁹ (wrasses) and among obligate-cleaner species in general.⁶⁰ Arnal⁵⁹ found no relationship between body size or shape and cleaning behavior within wrasses, but did find a correlation with the presence of a dark (black, brown, or gray) lateral stripe. The hypothesis is that this stripe functions (i) as a beacon allowing cleaners to be recognized from long distances and/or (ii) that a lateral stripe is generally indicative, within and among species of fish, of reduced aggressiveness.^{47,59} A good case in point is the facultative mimic, the blue-striped fangblenny (*Plagiotremus rhinorhynchus*), which can rapidly adjust its color pattern.⁶¹ By mimicking the black with blue stripe color pattern of a cleaner fish (*Labroides dimidatus*), the fangblenny is able to sneak bites of scales and tissue from unguarded client fish, but at other times it mimics the olive or brown color patterns of shoaling species, presumably obtaining the benefits of safety in numbers. These studies show that, in several groups of fish, species with stripes tend to shoal or be involved in cleaning or other mutualistic interactions. This suggests that lateral stripes may indeed have a general appeasing effect in both inter- and intraspecific interactions.

Conspicuous Coloration: Mimicry

Protective mimicry

When bright coloration serves to deter predation by signaling the unpalatable/toxic nature of a species, this coloration can be displayed constantly. It has been suggested that this type of signaling is especially common among reef fish, including the families Blenniidae (including venomous blennies), Muraenidae (including moray eels with toxic mucous), and Scorpaenidae (including scorpionfish with venomous spines).⁶² Interestingly, several researchers have suggested that colorful signals can become modified to serve both as a warning to predators and as a display to attract mates or deter competitors, because conspicuousness can be important in all of these contexts.¹⁰ Batesian mimicry, where a species adopts

the characteristics of an unpalatable or poisonous species, is one form of protective mimicry and has been documented in several fish species. All of the dangerous aposematic fish mentioned above are models for nontoxic species that mimic them.⁶² There are many cases, especially among tropical reef fish, where a mimic presents the general body shape and bright coloration of the model species.

In some cases, aposematic species can live and forage cryptically, but present a conspicuous display when under threat of predation.¹⁰ In this kind of situation, the mimic must only present a copy of the display, rather than mimic all aspects of the model's morphology. Two Mediterranean fish families (Trachinidae and Uranoscopidae) possess poisonous spines and a striking black spot on the first dorsal fin.⁶³ While foraging, inconspicuously buried in the substrate, members of these species can display this distinctive marking in the presence of danger. Palatable members of the sole family (Solididae) will raise a modified pectoral fin with a similar black spot to avoid attack. This is an example of a signal that is honest in some cases (truly poisonous Trachinidae and Uranoscopidae) and dishonest in others (palatable Solididae). A comparison of the species in these systems could determine whether the physiological basis of the model and mimic traits differs.

Competitive mimicry

While protective mimicry is well understood for a diverse array of vertebrate and invertebrate taxa, a new classification for mimetic interactions has recently been suggested: competitive mimicry. In this type of mimicry, a signal aids in access to, or defense of, a resource (e.g., food or mates).⁶⁴ As with protective mimicry, this is usually based on body shape and/or coloration. In an example of interspecific competitive mimicry, juvenile surgeonfish (*Acanthurus pyroferus*) resemble angelfish (*Centropyge vrolikii*), and this presumably allows them to forage with impunity in damselfish (*Plectoroglyphododon lacrymatus*) territories; damselfish tolerate angelfish, but repel adult surgeonfish.⁶⁵ Intraspecific competitive mimicry is involved, commonly, in alternative male reproductive strategies; in many of the species employing such strategies, sneaker males will resemble either conspecific juveniles or females. For example, bluegill sunfish (*Lepomis macrochirus*) satellite males mimic the morphology and coloration of females and look very different from territorial males, which are larger with red ventral coloration and a conspicuous black spot on their operculum (Fig. 5).⁶⁶

Eyespots, egg spots, and sensory bias

Eyespots are circular markings on the body of an animal that contrast with the surrounding area; in fish they are often black (reviewed in Stevens⁶⁷). Some of the best evidence for the role of eyespots in predator-prey interactions comes from studies of lepidopterans (moths and butterflies). As in some of these insects, eyespots apparently function by mimicking a species that would repel a predator (e.g., large, owl-like eyespots on some butterfly wings); for example, the comet fish (*Calloplelesioptis altivelis*) has a large eyespot that purportedly mimics the eye of the dangerous moray eel. The crab-eyed goby (*Signigobius biocellatus*) uses dorsal fin spots to startle potential predators, rather than to deflect their attacks.⁶⁴ However, in many species, it is thought that fish are

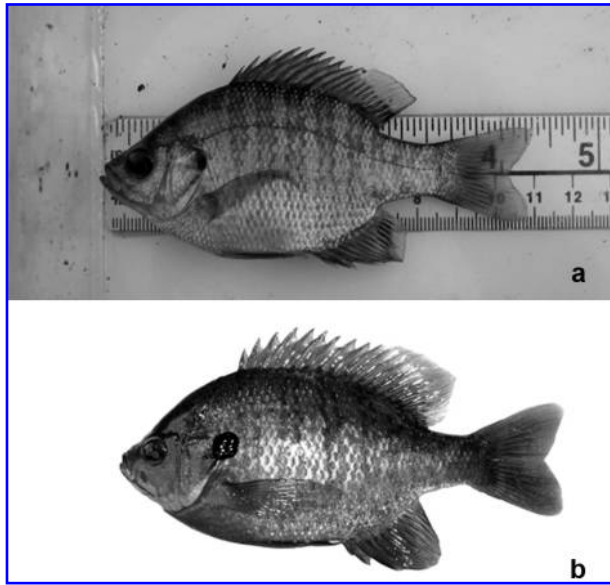


FIG. 5. Melanic patterning in the male bluegill sunfish (*Lepomis macrochirus*). (a) Vertical bars on satellite male bluegill. (b) Parental male bluegill does not express vertical bars. (Photos by K. Cogliati.)

mimicking their own eyes.^{10,68} Because the eyes, or the rostral end of the fish in general, are often the target of attacks, deflecting a predator's attention toward a less critical part of the body could have obvious benefits. There are examples in cichlids where the caudally located eyespots deflect attacks not only from predators but also from conspecific competitors as well.⁶⁸ While many fish species' dark spots are located posteriorly, there are exceptions. Some species possess eyespots curiously close to their actual eyes, and it is unclear what their function might be.⁶⁹

Another form of this intraspecific mimicry is the presence of false egg spots on the fins of some spawning fish, in particular among mouthbrooding haplochromine cichlids (Fig. 3).^{70,71} These cichlids have orange/yellow egg spots on their fins that are colored by pigment that occur in the xanthophore (top layer of pigment). Females in these species lay eggs and immediately take them up into their mouths. The male then presents his anal fin with egg spots to the female, who tries to pick up these eggs bringing her mouth close to the male's genital opening from which he releases sperm and fertilizes the eggs in her mouth.

Another general class of mimicry occurs where color pattern elements induce mating behavior in potential mates. An interesting version of this is a signal used by a nest spawning species, the striped darter (*Etheostoma virgatum*).⁷² In this species, males develop white, pigment-based spots on their pectoral fins that are thought to mimic eggs. In some species with paternal care, females prefer to spawn in nests that already contain eggs; it therefore seems likely that these white patches help males to entice females to lay in their nests. A number of other darter species also have patches of color, and some even develop fleshy masses, on their fins that seem to mimic egg spots.

There is evidence that visual mimicry is involved, through sensory biases, in other aspects of fish reproductive behavior. Garcia and Ramirez⁷³ provide a wonderful example based on



FIG. 6. Terminal yellow band on caudal fin of male Goodeinae fishes attracts females and is thought to mimic invertebrate prey. (Photo by A. Valero.)

a comparative study of Goodeinae fishes. The terminal yellow bands on the caudal fins of males, which they suggest mimic invertebrate prey, attract females (Fig. 6).

Pigments and Vision

There is considerable interest among evolutionary ecologists in determining how patterns shape, and are shaped by, sensory systems, especially with regard to sexually selected color patterns (reviewed in Horth⁷⁴). While this paper has focused primarily on the role pigments play in fish color patterns, pigments are also involved in the visual detection of these patterns. Photon capture in the rod and cone photoreceptor cells is mediated by light-sensitive retinal pigments, and a variety of pigments are responsible for selective filtering of incoming light in many species of fish.

Visual pigments are photosensitive complexes of an opsin protein and a chromophore (retinal, an aldehyde of vitamin A) that is ultimately derived from dietary carotenoids. Free retinal absorbs light most strongly in the UV, but upon binding to the opsin protein via a Schiff's base linkage this value shifts to the blue. This value is further modified by the amino acids of the opsin binding pocket, producing a wide diversity of visual pigments with spectral sensitivities ranging from the UV to the far-red.¹⁷ Two related forms of this chromophore are found in fish, A1 and A2. A2-type pigments tend to be more red-sensitive than A1-type pigments,⁷⁵ and are more common in fish from freshwater environments⁷⁶; turbid freshwater environments, typically murkier than marine environments, scatter short-wavelength light more strongly and consequently contain proportionately more long-wavelength light. Shifts between A1- and A2-type pigments, or up- or downregulation of different opsin proteins, are common occurrences in certain species of fish, and likely relate to changes in local light environment and visual requirements.¹⁷ Treatment with thyroid hormone can induce an A1–A2 shift in some species (including zebrafish⁷⁷), and mate choice experiments with thyroxine-treated and -untreated guppies suggest a link between long-wavelength spectral sensitivity and the color pattern of preferred mates.⁷⁸

Pigments play a second role in fish eyes; they are often distributed throughout the eye where they selectively filter incoming light before its arrival at the retina (reviewed by Douglas and Marshall in Archer *et al.*⁷⁹). Typically these pigments absorb short-wavelength light, though there is considerable variation among species in both the amount and composition of pigments employed (e.g., Losey *et al.*⁸⁰). The

corneas and lenses of many fish contain carotenoid-based and amino acid-based pigments, especially in the dorsal regions that receive strong downwelling light. Some species impose physiological control over corneal pigmentation, inducing dispersion of carotenoid-containing chromophores in response to increased ambient light intensity.^{81,82} Orlov and Gamburtzeva⁸² treated masked greenling (*Hexagrammos octogrammus*) corneas with colchicine and reported a decreased capacity to alter corneal pigmentation, a result consistent with microtubule-dependent pigment migration, which occurs in zebrafish melanophores.⁸³

When present in the cornea and lens, filtering pigments will have broad effects on light detection at the retina, but more local filtering effects can be mediated by the presence of pigments within specific photoreceptor cells. Pigmented oil droplets, commonly found in the photoreceptor cells of birds, are found in the Australian lungfish (*Neoceratodus fosteri*), but not in any bony fishes studied to date.⁸⁴ However, superficially similar structures, ellipsosomes, have been found in several species (e.g., MacNichol *et al.*⁸⁵). Ellipsosomes appear to be derived from mitochondria and contain large amounts of short-wavelength-absorbing cytochrome c pigment. Several hypotheses have been posed to explain the widespread distribution of pigmentation in fish eyes (reviewed by Douglas and Marshall in Archer *et al.*⁷⁹); such pigmentation may protect the sensitive retina from damaging, high-intensity light; improve visual acuity by reducing glare; or, in the case of oil droplets and ellipsosomes, improve color discrimination by reducing the effective bandwidth of cone photoreceptor cells.

Honesty in Signaling: A Comparison of Carotenoid and Melanic Coloration

The maintenance of honesty in signals is of great interest, especially when cheating can potentially lead to great rewards in terms of mates or resources. Some generalizations have been made about honesty in different kinds of signals. For example, signals that are expensive to produce should be more honest than those that are cheap (Tinbergen 1953 in Bedini *et al.*⁶³). However, tests of honesty in signaling must look at all of the costs associated with the trait of interest, and this includes both the costs of producing the signal, as well as the social and behavioral costs of displaying the signal.⁸⁶ It has been generally assumed that, in vertebrates, carotenoid-based traits are more costly to produce and are more likely to be condition dependent than melanin-based traits (but see Griffith *et al.*⁸⁷ for a review of this subject in avian systems). Recent debate on this topic has called these generalizations into question, especially given the relative paucity of studies on the condition dependence of melanin-based traits. We will discuss some of the evidence on the costs and honesty of carotenoid- and melanin-based signals in fish.

Carotenoids

In addition to sexual ornamentation, carotenoids also have many other functions (reviewed in Olson and Owens⁸⁸ and Kolluru *et al.*⁸⁹). Carotenoids are thought to provide an honest signal because they cannot be synthesized *de novo*, must be obtained exclusively through the diet, and are limited in availability.^{90,91} In guppies, males fed on a low-carotenoid diet have orange spots that are duller than those of their

brothers fed on a high-carotenoid diet. Females prefer males raised on a high-carotenoid diet.^{3,92} Males fed on high levels of carotenoids were better also able to reject interspecific allographs of scales and to resist parasite infection, suggesting that they have better immune function.^{4,89} Male guppies, on standard diets, that had been cured of a recent external parasite infection showed both less chromatic orange spots and reduced attractiveness to females.^{67,92,93} Together, these results suggest that male guppies must make complicated trade-offs between allocating carotenoids to their orange spots and to immune function.

This trade-off between functions for carotenoids has been observed in other fish species, including *Betta splendens*, where individuals of the genetically fixed-color morphs (red vs. blue) given supplemental carotenoids exhibited differential responses. When provided a carotenoid-rich diet, blue morphs showed a significantly greater increase in immune response than red morphs, likely because red morphs, which became redder after the dietary treatment, were allocating much of the carotenoids to their integument.⁹⁴ Similarly, in a cichlid (*Pundamilia nyererei*), males that had larger patches of carotenoid-based color produced fewer antibodies when immunochallenged.²⁷

Candolin⁹⁵ found that breeding, male sticklebacks often maintain sexual ornamentation at the expense of body carotenoids when dietary carotenoid intake is limited, leading to susceptibility to oxidative stress and reduced reproductive investment. Although the evidence suggests that carotenoids should be an honest signal in fish, in a rigorous test of the indicator hypothesis, Grether³ found no evidence in guppies of a genetically based divergence in preference strength among females from habitats varying in carotenoid availability. Instead, he and his coworkers found that female mate choice preference for orange coloration on males varied with their own carotenoid intake.⁴

Melanin

Melanic coloration is quite widespread in fishes. Melanic patches can be genetically determined and/or influenced by the environment. For example, in mosquito fish (*Gambusia holbrooki*), temperature is important in the expression of melanism, but there are also genetic influences (sex-linkage and autosomal modifiers).⁹⁶ Pigmentation in shallow water fishes could conceivably provide protection from damaging UV light (by preventing high-energy photons from reaching deep into the organism) or play a role in thermoregulation (by increasing photon capture).⁹⁷ UV treatment experiments with heavily and lightly pigmented *Xiphophorus* hybrids showed that melanin pigmentation can indeed play a protective role, with darker fish having less light-induced DNA damage.⁹⁸ A variety of coral reef fishes secrete a pigmented mucus that likely serves a similar, protective role, though in this case the pigment appears to be amino acid based rather than melanin based.⁹⁹ As for thermal melanism, though it appears to be widespread in insects,⁹⁷ we are unaware of any examples of its action in fish. Garcia *et al.*¹⁰⁰ discuss thermal melanism in regard to larval amphibians, and note that while small aquatic organisms are unlikely to realize a thermal benefit directly owing to melanic pigmentation, melanin may facilitate behavioral thermoregulation by providing protection from UV light in shallower waters.¹⁰¹ Research on fish

color patterns is often focused on the common conflict between natural selection to reduce predation and sexual selection to increase mating success; selection for thermal or UV-protective reasons is understudied in fish, and could conceivably interact antagonistically with these other pressures (e.g., Zamzow and Losey⁹⁹), favoring plasticity.

Previously, it had been assumed that melanic displays were not honest signals of quality because it was thought that melanin was not costly to produce,¹⁰² although this has not been rigorously tested.⁸⁷ Several lines of evidence from recent work suggest that melanic signaling may be more costly than previously thought, for example, because so many important physiological pathways are linked to the complex melanocortin system (e.g., immunity, reproduction, stress, energy expenditure, and feeding rate).⁴⁹ Additionally, fish, like insects,¹⁰³ can melanize parasites.¹⁰⁴ This may mean that there are trade-offs between the allocation of melanin to sexual displays and immune function. Melanin is involved in other pathways that may influence the costs of bearing melanic coloration. For example, a recent study in salmonids suggests that there may be different, melanin-linked metabolic strategies that are determined by stress levels experienced by the fish.¹⁰⁵ In both rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*), melanic individuals had a reduced cortisol response to stress.

It is possible that the cost of dark coloration comes from the social cost of bearing the display rather than the cost of producing it (as in carotenoids). For example, there is evidence that melanic individuals are more aggressive than non-melanic forms; in mosquitofish, melanic males are more aggressive than the silver morph, even to potential mates.⁴⁸ In barn owls, melanic morphs provide less parental care; this could also be related to aggression.¹⁰⁶ An individual need not necessarily be in good condition to display a patch, but may pay a severe cost when attacked by an aggressive competitor.⁴² Finally, it is thought that melanic signaling may be honest because there is some evidence that it accurately communicates an individual's motivation and/or competitive ability.⁴⁷

Conclusion

Much is left to learn about pigment-based color patterns in terms of their composition, expression, and evolutionary history. The broad classes of fish coloration fall into the same kinds of categories that apply to other taxa (camouflage, mimicry, etc.), but the specific functions of some patterns (e.g., why longitudinal stripes seem to enhance shoaling) are still not fully understood. Evolutionary geneticists will continue to ask classic questions such as what genes underlie the traits of interest and what forces are shaping genetic variation in these traits (over all time scales). For behavioral ecologists studying fish, the usual issues apply: does this trait enhance the ability to obtain resources, get mates, avoid predators, etc.? But the variety of aquatic environments and the diversity of species of fishes seem to have scaled up the number of possible color pattern solutions.

Pteridines, in particular, are poorly understood, despite being common in many of the taxa that exhibit carotenoid-based color patches, including fish, reptiles, amphibians, insects, and birds. Do carotenoids have important spectral properties that cannot be mimicked by pteridines? Is the

synthesis of pteridines constrained by body condition and the availability of dietary precursors? Do different taxa (e.g., among fish or among vertebrates) bear different costs of these pigmentation displays? It would be interesting to consider the evolution of pteridines pigments as signals, especially in the context of what is known about carotenoids and melanins.

Organisms that inhabit aquatic environments can be particularly vulnerable to environmental change. The transmission and interpretation of pigment-based signals among conspecifics can be distorted by changes in the optical environment. For example, when the turbidity of the aquatic environment is increased (as with pollution, eutrophication, or run-off), male sticklebacks can misinterpret aggressive signals, with profound consequences for this species' mating system.⁸⁶ In African cichlids, the loss of species through hybridization has been attributed to increased water turbidity.¹⁰⁷ In addition to these effects on signal transmission, anthropogenic changes to the environment can affect the production of pigment-based signals. When exposed to a common pesticide, the sexually dimorphic, yellow coloration of the Amarillo fish (*Girardinichthys multiradiatus*) is reduced.¹⁰⁸ Fish like these could become model systems for studying the effects of environmental degradation on animals.

Pigment-based coloration in fish can be expressed permanently or flexibly, changing gradually in a manner dependent on season, age, or mating status, or nearly instantaneously, depending on an individual's motivational state. The wealth of knowledge provided by geneticists, physiologists, and developmental biologists studying pigmentation in fish model systems will continue to provide an ideal opportunity to link among- and within-species variation in pigmentation to variation in the underlying genetic and physiological processes. Linking such fitness-related traits to their proximate influences is a major goal in evolutionary research, and efforts to foster such collaborations should be encouraged. Studies like Engeszer *et al.*'s¹⁰⁹ work on the role of visual cues in the shoaling behavior of zebrafish, using engineered color pattern mutants, have begun to take advantage of new molecular techniques. The diversity of pigment patterning present in any one model system cannot compare to the diversity found throughout the fishes, and crosstalk among disciplines may well lead to the identification and development of new model systems. African cichlids and threespine sticklebacks (*Gasterosteus aculeatus*), for example, display striking variation in various anatomical features (jaw shape in cichlids, and degree of armor plating in sticklebacks), and both have recently emerged, in conjunction with the genomic resources now available for these species, as model systems for skeletal developmental biology.^{110,111} The relative ease with which genomic resources can now be developed for ecological and behavioral model systems will undoubtedly motivate further collaborative research dedicated toward explaining the fantastic diversity of fish pigment patterns.

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