AMER. ZOOL., 38:70–81 (1998)

Sexual Dichromatism and Temporary Color Changes in the Reproduction of Fishes[1]

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SYNOPSIS. **Studies on color patterns of fishes have focused on relationships between bright, relatively permanent colors, such as those of fishes inhabiting coral reef and tropical freshwater habitats, and ecological factors, such as competitors, predators, and the visual background. By comparison, the functions of, and hence the selective pressures acting on, temporary changes in nuptial coloration have received much less attention. Temporary color changes associated with reproduction occur in many freshwater and marine groups. Nuptial coloration in fishes functions both in agonistic interactions among males and courtship of females, so that it is subject to both intrasexual and intersexual selection as well as natural selection. Temporal variation in nuptial color patterns is sensitive to temporal changes in the male's physical condition, motivation, and social status. Physiological processes, such as neuronal and endocrine changes, play important roles in the expression of breeding colors, including rapid responses to changes in social conditions. The importance of proximal mechanisms and ultimate selective processes in mediating rapid changes in the blue, melanin-based breeding colors of pupfish, and the red, carotenoid-based color patterns in guppies are discussed in the context of signal function and evolution.**

INTRODUCTION

Fishes are rivaled only by birds in their display of flamboyant colors or combinations of bright hues and elaborate patterns that sometimes approach garishness. Unlike the colors of other vertebrates, the chromatophores of fishes are under neuroendocrine control, so that colors and patterns can be changed almost instantaneously. This ability to change colors rapidly is used by fishes for many kinds of signals in many different social and environmental settings. Changes in coloration, as well as the colors and patterns themselves, have been subject to both natural and sexual selection. It is not surprising, therefore, that the evolution and function of colors in fishes has been the focus of many studies (*e.g.*, Lorenz, 1962).

In this review I focus on the function of temporal variation in nuptial color patterns in otherwise monochromatic and dichromatic fishes of North American freshwaters. I describe the kinds of color changes, and the social and environmental contexts in which they occur. I discuss the role of phylogeny, sexual and natural selection in the evolution of temporally variable breeding coloration. Studies of red, carotenoid-based, and black or blue melanophore-mediated nuptial colors are used as examples. These colors are conditionally expressed, are costly to produce and maintain, and change rapidly to signal a male's social status, reproductive success, motivation, and physical condition. The role of and interaction between proximate physiological mechanisms and ultimate evolutionary selective processes in the expression of temporary breeding colors is discussed.

PATTERNS

Color patterns of fishes vary in their temporal expression. Permanent, or "fundamental" (DeMartini, 1985) sexual dichromatism, usually brightest in males, develops at maturity and is retained for life. Temporary sexual dichromatism is of two types, seasonal and ephemeral. In some otherwise monochromatic species, individuals, usually males, develop distinct color patterns

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[1] From the Symposium *Animal Behavior: Integration of Ultimate and Proximate Causation* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 26–30 December 1996, at Albuquerque, New Mexico.

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during the breeding season. These changes are temporary, since they are associated with reproduction, and only actively breeding individuals express them. Ephemeral color changes occur in both monochromatic and dichromatic species, and function as social signals of motivation. Changes in hues and patterns of individuals may be extremely transitory and persist for only a few minutes or a few seconds. Although they are most often expressed during courtship of females and agonistic interactions between males, they are not always restricted to the breeding season (DeMartini, 1985). They are also important in signaling parental status in species with discrete parenting phases, such as sticklebacks, and in parent-offspring interactions in groups with extensive parental care, such as cichlids. Seasonal and ephemeral dichromatism represent extremes, and there is a wide variety of intermediate conditions. Both permanent and temporally variable nuptial coloration function in the identification of sex, the coordination of breeding activities between males and females, the deterrence of rivals, and the attraction of mates.

Permanent dichromatism

In many groups of marine fishes and some freshwater ones as well, the sexes differ in their color patterns, with males being the more brightly colored sex. Spectacular examples are the diversity of colors and patterns of males in cichlids of the rift lakes of Africa, and many tropical marine groups, such as wrasses, blennies, and parrot fishes. Sexual dimorphism suggests that colors play important roles in the social and mating systems of these fishes (Thresher, 1984; McKaye, 1991). Often they have a dual role, not only in the attraction of mates but also in the intimidation of males, and so they are subject to both intrasexual and intersexual selection. Both forms of sexual selection are important in the evolution and maintenance of permanent sexual dichromatism in fishes. It appears to occur primarily in such groups, such as wrasses, parrot fishes, guppies, and rock-dwelling cichlids, which have prolonged breeding seasons (4–6 months) and may spawn throughout the year (Fryer and Iles, 1972; Colin and Bell, 1991). In some of these groups, such as certain coral reef fishes, males, and often females as well, maintain year-round territories as adults (Robertson and Hoffman, 1977). This pattern has also been documented in some temperate marine species, which reproduce seasonally but hold permanent territories (*e.g., Oxylebius pictus,* DeMartini, 1985). Species that exhibit permanent dichromatism include those with monogamous and polygynous breeding systems.

Seasonal dichromatism

In many groups of fishes, males develop conspicuous coloration only during the breeding season. At other times their color patterns resemble those of females (Table 1). Often these breeding colors are conditionally expressed and reflect a male's ability to acquire and defend a territory or resources essential for female reproduction, such as a nest or a suitable oviposition site. For example, in Pecos pupfish (*Cyprinodon pecosensis*), a small fraction of mature males in the population, only those with breeding territories, develop conspicuous blue colors during the breeding season. Such temporary color changes are equivalent to "badges" of status in birds, and signal dominance or the ability to gain and hold contested resources (Rohwer, 1982). Seasonally expressed sexual dichromatism is favored in environments in which reproduction is limited to certain times of the year by variation in productivity, temperature, and/or other ecological conditions.

Among species of freshwater fishes with seasonal reproduction, there appear to be some recurrent themes of color patterns. One consists of a black body (*e.g.,* Gila topminnow, *Poeciliopsis occidentalis,* Olympic mudminnow, *Novumbra hubsi*), or a black body with contrasting fins (*e.g.,* Brook stickleback, *Culea inconstans,* with red fins, Mexican pupfish, *Cyprinodon beltrani,* with yellow caudal peduncle and fins). Another common pattern is for breeding males to have a red body, head, or fins. For example, in the Duskystripe shiner (*Luxilus pilsbryi*), the head and fins turn red; in the Redbreast sunfish (*Lepomis auritus*), males acquire a bright orange breast

TABLE 1. *Examples of changes in the color pattern of monochromatic or subtly dichromatic species of freshwater fishes from North America that occur during the breeding season.*

Family	Genus/Species	Common name	Color pattern
Percidae	*Etheostoma olivaceum*	Dirty darter	Black[a]
Umbridae	*Novumbra hubbsi*	Olympic mudminnow	Black[a]
Poeciliidae	*Poeciliopsis occidentalis*	Gila topminnow	Black[a]
Cyprinidae	*Luxilus pilsbryi*	Duskystripe shiner	Red[a]
Fundulidae	*Fundulus zebrinus*	Plains killifish	Red[a]
Centrarchidae	*Lepomis auritus*	Redbreast sunfish	Red[a]
Catostomidae	*Moxostoma hubsii*	Copper redhorse	Red[a]
Cyprinidae	*Nocomis leptocephalus*	Bluehead chub	Blue[a]
Cyprinodontidae	*Cyprinodon pecosensis*	Pecos pupfish	Blue[b]
Fundulidae	*Lucania goodei*	Bluefin killifish	Blue[a]
Centrarachidae	*Lepomis machrochirus*	Bluegill	Complex color pattern[a]
Cyprinidae	*Notropis chrosomus*	Rainbow shiner	Complex color pattern[a]
Percidae	*Etheostoma zonistium*	Bandfin darter	Complex color pattern[a]

[a] Page and Burr 1991
[b] Kodric-Brown 1983

and belly, and in the Plains killifish (*Fundulus zebrinus*), males exhibit orange or red dorsal, anal, and paired fins. Blue nuptial coloration, although less frequent in North American freshwater species, does occur (*e.g.*, Pecos pupfish *Cyprinodon pecosensis,* with a blue body, Bluefin killifish *Lucania goodei,* with iridescent blue dorsal and anal fins, and Bluehead chub *Nocomis leptocephalus,* with a blue head). More complex color patterns also occur. In the bluegill (*Lepomis machrochirus*) breeding males have a blue head, a red-orange breast and belly, and black pelvic fins. In the rainbow shiner (*Notropis chrosomus*), the nuptial color pattern consists of a purple head, dorsum, and the base of the fins, and a silver stripe along the side of the body. The nuptial patterns of darters are varied and often colorful. For example, breeding males of the Bandfin darter (*Etheostoma zonistium*) have a bright red body, green head, and blue pelvic and anal fins.

Ephemeral dichromatism

Very rapid color changes are surprisingly widespread in fishes (Tables 2 and 3). Ephemeral colors can be turned on and off

TABLE 2. *Fish families with monochromatic or seasonally dichromatic species that have been shown to exhibit ephemeral color changes during courtship or spawning.*

Family	Common Name	References
Anthiinae	Sea perches	Thresher, 1984
Apogonidae	Cardinalfishes	Thresher, 1984
Aulostomidae	Trumpetfishes	Thresher, 1984
Belontiidae	Gourami	Miller, 1964
Blenniidae	Blennies	Losey, 1976
Centrarchidae	Sunfishes	Page and Burr, 1991
Cichlidae	Ciclids	Beeching, 1995
Cottidae	Sculpins	Morris, 1954
Cyprinodontidae	Pupfish	Kodric-Brown, 1983
Epinephelidae	Groupers	Thresher, 1984
Gasterosteidae	Sticklebacks	McLennan and McPhail, 1989
Gobiidae	Gobies	Tavolga, 1956
Macrorhamphosidae	Longspine snipefish	DeOliveira *et al.*, 1993
Percidae	Darters	Petravicz, 1938
Pomacanthidae	Angelfishes	Moyer *et al.*, 1983
Pteroidae	Lionfishes	Thresher, 1984
Serranidae	Sea basses	Thresher, 1984
Tripterygiidae	Triplefin blennies	Wirtz, 1978
Umbridae	Mudminnows	Hagen *et al.*, 1972

TABLE 3. *Fish families with sexually dichromatic species that have been shown to exhibit ephemeral color changes during courtship or spawning.*

Family	Common name	References
Cichlidae	Cichlids	Voss, 1980
Hexagrammidae	Geenlings	DeMartini, 1985
Labridae	Wrasses	Robertson and Hoffman, 1977, Colin and Bell, 1991
Poeciliidae	Guppy	Baerends *et al.*, 1955
Pomacanthidae	Angelfishes	Moyer *et al.*, 1983
Pomacentridae	Damselfishes	Thresher, 1984
Scaridae	Parrotfishes	Colin and Bell, 1991

quickly, usually within seconds. They are typically expressed by males of species that are otherwise either monochromatic or dichromatic. Ephemeral color changes often signal motivation and intention in the context of courtship and agonistic interactions (Wirtz, 1978; Beeching, 1995). They may function in identifying sex in monochromatic species and in coordinating spawning sequences between males and females in permanently dichromatic species. In the painted greenling (*Oxylebius pictus*), a species in which both sexes maintain year-round territories, males darken completely during courtship but incompletely during agonistic interactions, thereby keeping a barring pattern (DeMartini, 1985). A frequent pattern is intense darkening of the body during agonistic interactions and lightening during courtship (*e.g., Bathygobius soporator,* Tavolga, 1956). In males of many species temporary color patterns developed during courtship also show aggressive components and are used in territorial defense (Colgan, 1983).

Ephemeral changes in the color pattern of permanently dichromatic species either enhance or change their fundamental color patterns (*e.g.,* cichlids: Voss, 1980; McKaye, 1991; wrasses: Robertson and Hoffman, 1977; Colin and Bell, 1991; guppies: Baerends *et al.,* 1955). In guppies, courting males develop large black spots, a horizontal stripe along the side of the body, and often a black caudal fin, thereby increasing the conspicuousness and complexity of their color pattern. Females of a sexually dichromatic damselfish (*Chrysiptera cyanea*) assess male quality by both the vigor of their courtship displays and the development of their temporary spawning colors, especially the extent of orange coloration on the caudal fin (Gronell, 1989).

In otherwise monochromatic species males frequently undergo dramatic, temporary changes in color patterns. For example, in courting males of the longspine snipefish *Macrorhamphosus scolopax,* the posterior part of the body turns brick red (DeOliveira *et al.,* 1993). Ephemeral color patterns that are expressed only during spawning bouts might also be expected to occur in schooling species, but I am unaware of any examples. It appears that ephemeral color patterns function at close range and increase the complexity and showiness of the more invariant elements of a male's color pattern.

Color patterns and behavior

Color patterns enhance the visibility of courtship or agonistic behavior, thereby facilitating assessment of the social status or motivation of the displaying individual by potential mates or rivals. The interaction between behavioral components of displays and nuptial colors is a dynamic one. Both color patterns and behavioral displays enhance the effectiveness of one another in conveying information. Breeding colors and patterns selectively draw attention to the rhythm and tempo of movements during courtship or threat displays. The display movements in turn, enhance the conspicuousness of nuptial colors and draw attention to ephemeral changes during both courtship and agonistic interactions. For example, in Pecos pupfish the figure eight display, made more conspicuous by intense blue nuptial coloration, attracts the female's attention to the territorial male. Contrast against a background also is important in enhancing the visibility of both nuptial coloration and displays. The iridescent blue nuptial coloration of Pecos pupfish provides a striking contrast to the white gypsum substrate and reflects in the sunlight that penetrates the clear, shallow water on the breeding territories (Kodric-Brown, 1983).

Nuptial coloration and breeding systems

Attempts to show a relationship between type of nuptial coloration and breeding system in marine groups have not been very successful. In angelfishes (Pomacanthidae), species with monogamous, polygynous, or promiscuous breeding systems may be either permanently dichromatic, or develop ephemeral nuptial coloration during courtship and spawning (Moyer *et al.,* 1983). In wrasses and parrotfishes, sexual dichromatism is apparently not related to the type of breeding system, since it occurs in species with harems, in which a male monopolizes the breeding activities of several females, with "leks", in which males defend territories that function as breeding sites, or with promiscuous mating, in which males do not defend territories but pursue and court females, either in pairs or groups (Thresher, 1984; Colin and Bell, 1991). Breeding systems of fishes are extremely variable. Individuals typically respond opportunistically, changing both their behavior and color patterns in response to temporal or spatial variation in sex ratio, population density, structure of the habitat, availability of breeding sites, and presence or absence of competing or predatory species. Thus it is difficult, if not impossible, to draw generalizations about the relationship between breeding system, social structure, and type of nuptial coloration.

EVOLUTIONARY MECHANISMS

Sexual and natural selection

Nuptial colors of fishes represent a compromise between the interaction of sexual selection for conspicuous color patterns to signal conspecifics, and natural selection for cryptic patterns to avoid predators (Endler, 1983; Baube *et al.,* 1995). Sexual selection is an important evolutionary force in the development and maintenance of both permanent and temporary nuptial color patterns in fishes. In permanently dichromatic species and some seasonally dichromatic ones as well, nuptial coloration has a dual function in attracting mates and deterring potential rivals, so that both intrasexual and intersexual selection are important in the evolution, maintenance, and expression of color patterns (Robertson and Hoffman, 1977; Kodric-Brown, 1990; McKaye, 1991). Ephemeral changes in the nuptial coloration of both permanently and seasonally dichromatic species often have specific functions in courtship or in agonistic interactions, and have evolved through the action of either intersexual or intrasexual selection (*e.g.,* cichlids: Voss, 1980).

Complex color patterns may consist of distinct components, some of which function in the attraction of mates and others in deterring rivals, so that both intra- and intersexual selection are implicated. In the threespine stickleback (*Gasterosteus aculeatus*), courting males develop an intense red body and a blue eye color. The red coloration of the belly functions both in male-male interactions and in the attraction of females, whereas intersexual selection appears to be primarily important in the elaboration of the blue color of the eye, since males with intense blue eyes are most attractive to females (McLennan and McPhail, 1989).

Clear distinctions between the relative importance of intrasexual and intersexual selection in the evolution of temporary or permanent dichromatism are often difficult (Kodric-Brown, 1996). This is not surprising since the colors are often displayed, sometimes simultaneously or nearly so, to both rivals and potential mates. Even in species such as the guppy (*Poecilia reticulata*), where female choice is clearly an important selective force in the evolution of the complex colors and patterns of males, the influence of male-male interactions cannot be discounted (Kodric-Brown, 1992).

Properties of the physical and biotic environment also influence the type of nuptial coloration that evolves. Spectral properties of the water and of substrates that are backgrounds for displays select for colors that enhance conspicuousness and contrast with the background. The prevailing light of shallow, freshwater environments is green, so red should provide the maximum contrast (Lythgoe, 1979). The nuptial coloration of many groups of freshwater fishes incorporates elements of reds and oranges, typically in the fins or parts of the body. In clear water of intermediate depth, blue and yellow should be the most visible colors. The predominant nuptial colors of fishes on coral reefs and of cichlids in clear freshwater lakes are blue and yellow (Barlow, 1974; Levine and MacNichol, 1979). Predictions as to the types of color patterns favored in turbid water are less clear. Essentially all colors are represented, but red, yellow, and orange appear to be especially common in these environments (Barlow, 1974; Levine and MacNichol, 1979). Black, or patterns that incorporate contrasting elements of black and white, show up well against background light in many environments. Thus it is not surprising that black is a common element of many temporarily and permanently dichromatic color patterns.

Predation is an important selective pressure in constraining the conspicuousness of nuptial coloration and the colors and patterns represented. Environments that provide hiding places tend to reduce the risk of predation and favor selection for conspicuous nuptial coloration both in temporary and permanent dichromatism. Darters (Genus: *Etheostoma*) are a good example of a group where the use of shelters has provided an opportunity for proliferation of color patterns. In marine environments, coral provides hiding places from predators, and species of parrotfish and wrasses that are closely associated with coral are permanently dichromatic (Robertson and Hoffman, 1977; Colin and Bell, 1991). Species living in other types of habitats, such as sandy substrates or benthic plant beds, are more likely to be exposed to predators, and so develop ephemeral nuptial coloration only during courtship and spawning.

The role of predation in the evolution of permanent sexual dichromatism is perhaps best understood for the guppy, which has been studied intensively on the island of Trinidad (Endler, 1983; Endler and Houde, 1994). Guppy color patterns are influenced by the type of substrate, the prevailing quality of light in the habitat, and the presence of predators. Types of predators as well as their abundance affect the conspicuousness of male color patterns, especially the size and number of carotenoid spots. In habitats where piscivorous predators are abundant, mates are drab and color patterns consist of few small spots. In the absence of such predators, sexual selection favors colors and patterns that are conspicuous, complex, and contrast with the background. In these environments color spots are large and numerous, and color diversity is high. Male color patterns also show seasonal responses to changes in predator abundance. At a mainland site in Venezuela, males are more colorful during the wet season, when diurnal piscivores are less abundant than in the dry season when predation pressure is more intense (Winemiller *et al.*, 1990).

Avian predation probably is an important selective factor in the development of permanent sexual dichromatism in fishes, especially in tropical or subtropical freshwater habitats. In such environments predation by species such as kingfishers, herons, and anhingas, can be substantial. In general, only species that are below the size that is profitable for avian predators (*e.g.*, male guppies), or that can take advantage of shelters (*e.g.*, gobies), tend to be permanently dichromatic.

Phylogenetic constraints

It is not clear to what extent phylogeny has constrained the evolution of nuptial coloration in fishes. On the one hand, there are examples where limited variation in patterns and colors of breeding males appears to reflect phylogenetic relationships. In suckers (Family Catostomidae, Genus *Moxostoma*), breeding males of all 17 species that occur north of the U.S./Mexican border develop red, orange or yellow fins (Page and Burr, 1991). On the other hand, many nuptial colors and patterns occur widely across taxonomic groups (Table 1). For example, breeding males with red fins occur in many families of North American freshwater fishes, including minnows (Cyprinidae), suckers (Catostomidae), killifish (Fundulidae), sunfish (Centrarchidae), darters (Percidae), and cichlids (Cichlidae). In darters (Genus *Etheostoma*), the nuptial coloration of males varies from none (mottled brown pattern), to extremely showy, incorporating blues, greens, yellows, reds, and black in complex patterns and combinations. In this group there are no obvious relationships between nuptial colors and patterns, mode of reproduction, type of habitat, and breeding system (Page, 1985). Quantitative, phylogenetically explicit studies are needed before any conclusions can be reached regarding the importance of, and the extent to which, phylogeny constrains nuptial color patterns in fishes (Brooks and McLennan, 1991; Harvey and Pagel, 1991).

PHYSIOLOGICAL AND BEHAVIORAL MECHANISMS

Are nuptial colors honest signals of male quality?

Sexual selection should favor colors and patterns that are not only conspicuous but are also honest because their expression indicates a male's phenotypic and genotypic quality (Zahavi, 1977; Kodric-Brown and Brown, 1984; Grafen, 1990; Michod and Hasson, 1990). Honest signals will be selected because they convey accurate information about a signaler's physical condition, social status, and motivation, and are costly to produce and/or maintain thus preventing "cheaters" (*e.g.*, Knapp and Kovach, 1991). This cost may be reflected in greater energy expenditure (*e.g.*, Vehrencamp *et al.*, 1989) or higher predation on conspicuously colored males (Endler, 1995). Nuptial colors may also function to amplify or accentuate metabolically expensive courtship and agonistic behavior (*e.g.*, Cordts and Partridge, 1996). The colors best studied in the context of honest sexual signals are those based on carotenoid pigments.

Carotenoid-based pigments

Nuptial coloration of males of many seasonally breeding species consists of red or orange colors produced by carotenoid pigments (Goodwin, 1951; Webber *et al.*, 1973; Brush and Reisman, 1965). Detailed studies on the function of carotenoid pigments in mate choice are available for two groups of fishes, guppies and sticklebacks. In both, females prefer to mate with males with well-developed carotenoid-based colors, namely the brightest red or orange patterns (Endler, 1983; Kodric-Brown, 1985; Houde, 1987; Bakker, 1993). Carotenoid pigments also are important in agonistic interactions, and so they are acted upon by intrasexual as well as intersexual selection (*e.g.*, sticklebacks: Rowland, 1994; firemouth cichlids: Evans and Norris, 1996). In fishes, carotenoid pigments are costly to acquire and express. They cannot be synthesized, but must be acquired from the diet. Because invertebrates and other sources of carotenoids are rare in many environments, males with intense red colors signal their superior foraging ability and general state of health (Kodric-Brown, 1989; Frischknecht, 1993). In male guppies, the intensity (brightness) of carotenoid pigmentation is positively correlated with swimming endurance, an estimate of physical condition (Nicoletto, 1993).

In fishes, unlike birds, where carotenoids are deposited in feathers at the time of the molt, carotenoid pigments signal a male's current nutritional state and the quality of his diet. Carotenoids are also important in immune function and enhance B and T lymphocyte production (Lozano, 1994). Depletion of stored carotenoids through their mobilization into nuptial coloration may compromise the immune system (Shykoff and Widmer, 1996). Consequently, expression of carotenoid-based nuptial coloration may represent the outcome of a prioritization of allocation of scarce carotenoids between nuptial coloration, a sexually selected trait that will enhance a male's reproductive success, and the immune system, with potential consequences of increased susceptibility to parasites and pathogens. Individuals in good physical condition with a carotenoid-rich diet, should be better able to produce bright colors without compromising immune competence. The precise mechanisms and interactions between carotenoids, the immune system and the expression of carotenoid pigmentation has yet to be determined (Fig. 1).

The degree of expression of carotenoid pigments also is an indicator of resistance

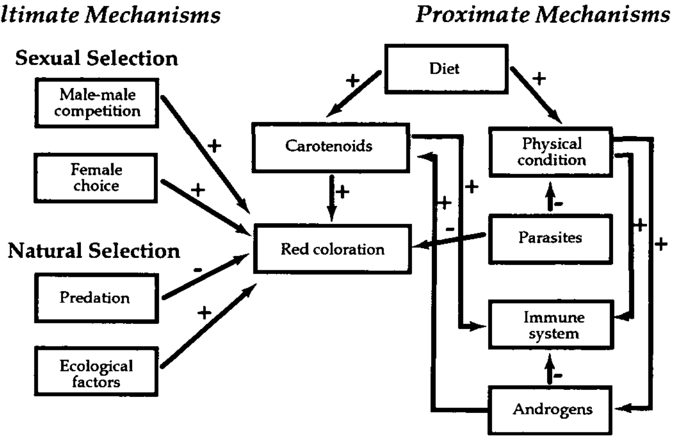

FIG. 1. The role of proximate and ultimate mechanisms in the expression of carotenoid-based red nuptial coloration in fishes. Arrows indicate the direction of effects. The sign above the arrow indicates whether the effect is positive or negative. See text for detailed explanation of interactions between proximate and ultimate mechanisms.

to parasites. Both in guppies and sticklebacks, males infected with a monogenean parasite displayed less intense carotenoid pigmentation and were avoided by females (Milinski and Bakker, 1990; Houde and Torio, 1992). Females preferring intensely pigmented males acquire healthy, unparasitized mates in superior physical condition, and presumably of higher genetic, as well as phenotypic, quality. Carotenoid pigments represent honest sexually-selected signals that are conditionally expressed, because they are expensive to produce and maintain. Bright red, carotenoid-based breeding colors indicate a male's viability traits, such as health, vigor, ability to forage for carotenoid-rich invertebrates and other scarce resources, resistance to parasites and pathogens, and ability to escape predators. Thus it is not surprising that red and orange are important components of nuptial color patterns in guppies, sticklebacks, and salmon, and perhaps many other permanently and temporarily dichromatic species.

Melanins

Many nuptial color patterns are ephemeral signals that can be selectively displayed by briefly changing color patterns (Eibl-Eibesfeldt, 1962). Their expression is mediated through the neuroendocrine action of chromatophores (Fujii, 1993). Rapid changes in black and blue color patterns, such as those in the red hind *Epinephelus guttatus* (Shapiro *et al.,* 1993) or Pecos pupfish *Cyprinodon pecosensis* (Kodric-Brown, 1996) are mediated by the expansion and contraction of melanophores. One common feature of these signals is that they are very transitory and can be turned on or off within seconds. Because of the rapidity with which they can be expressed, they are not very costly. Risk of predation to the signaler is small and, presumably, so is the expenditure of energy required to express or suppress the trait. If such signals are not expensive to produce and maintain, how can they be honest?

The Pecos pupfish (*Cyprinodon pecosensis*) is a seasonally reproducing species inhabiting the Pecos River, its tributaries, and gypsum sinkholes in the southwest. Males defend breeding territories, that are visited by females that deposit one to several eggs and then leave. Only males which are able to acquire territories develop bright blue nuptial coloration, which can be turned off instantaneously, if, for example, fish are frightened by a predator. Males without territories retain the drab olive-brown coloration of females. At the peak of the breeding season favorable oviposition substrates are limited and competition for spawning sites is intense. Only a small fraction of males in superior physical condition can acquire and maintain breeding territories (Kodric-

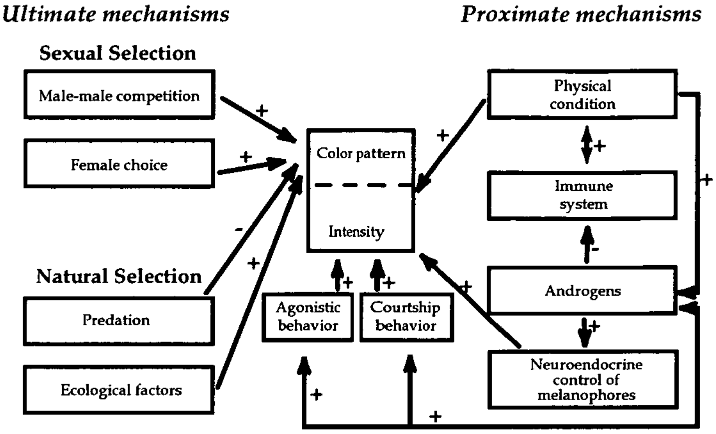

FIG. 2. The role of proximate and ultimate mechanisms in the expression of nuptial coloration in Pecos pupfish (*Cyprinodon pecosensis*). Arrows indicate the direction of effects. The sign above the arrow indicates whether the effect is positive or negative. Both the intensity of intrasexual and intersexual selection and ecological factors, such as presence of predators, water clarity, and prevailing light conditions, influence the expression of male nuptial coloration. The intensity of nuptial coloration is affected by the frequency with which a male engages in courtship and agonistic interactions. Ability to engage in strenuous courtship and agonistic behavior depends on physical condition, which is influenced by the immune system. Androgens are essential for the development of nuptial coloration, courtship, and agonistic behavior. Action of androgens is mediated through neuroendocrine control of melanophores. Androgens tend to compromise (suppress) the immune system, however, so only males in prime physical condition can express full nuptial coloration.

Brown, 1983; Kodric-Brown and Nicoletto, 1993).

Nuptial coloration of pupfish is a conditionally-expressed trait. The intensity of blue color is positively correlated with territory quality (Kodric-Brown, 1983). Females preferentially visit territories of males with maximum development of nuptial coloration. Males darken after winning fights or spawning with females (Kodric-Brown, 1996). Thus the expression of a male's breeding coloration is a good indicator of his recent success in mating and agonistic interactions (Fig. 2). The honesty of this signal is maintained through continuous probing by males, especially neighboring territory owners.

Role of androgens

In seasonally dichromatic species androgens mediate both the expression of ephemeral color changes and the development of nuptial coloration. Circulating androgens are present during the breeding season and increase during episodes of fighting and spawning. Neuroendocrine changes associated with androgen production and release provide a feed-back mechanism between agonistic and courtship displays and expression of nuptial coloration (Wingfield *et al.,* 1990; Brantley *et al.,* 1993). Changes in plasma androgen levels are associated with the development of secondary sexual characteristics and reproductive behavior in many teleost fishes (Sikkel, 1993; Borg, 1994; Oliveira *et al.,* 1996). Increased levels of circulating androgens have been measured in territorial males of bluegill sunfish, parrotfish, wrasses, Atlantic salmon, stickleback and plain midshipman (reviewed in Brantley *et al.,* 1993). It is likely that elevated levels of androgens, such as 11-ketotestosterone, not only stimulate agonistic interactions, but also enhance the intensity of nuptial coloration. Injection of testosterone intensified the body coloration, as well as increased the agonistic and courtship behavior of territorial males (cichlids: Fernald, 1976; pupfish: personal observation). The precise interaction between aggression, development of breeding coloration, and fluctuations in androgen levels requires further investigation. Maintenance of high levels of circulating androgens may be costly not only because they increase the probability that bright males will have an increased risk of predation, and will engage in energetically expensive behaviors, such as fighting, but also because their production may compromise the immune system (Fig. 2). Only males in good physical condition are likely to be able to maintain high levels of circulating androgens and also display intense breeding coloration (Folstad and Karter, 1992; Skarstein and Folstad, 1996).

FUTURE DIRECTIONS

In this review I have focused on the characteristics of temporally variable, sexually dichromatic traits in fishes. Both carotenoid and melanin pigments have been shown to feature prominently in temporary color patterns in fishes. For the carotenoid-based nuptial colors we are beginning to understand the complex interactions between proximate mechanisms (hormones, nutrition, immune systems) and ultimate processes (natural and sexual selection) responsible for their expression. Detailed studies of the function of carotenoid-based pigments in mate choice and male-male interactions have so far been limited to only a few groups, especially sticklebacks and guppies. Other taxa need to be studied in order to determine how general or variable are the phenomena described above.

Although studies on a few model systems have provided some insight into why certain temporary nuptial colors and patterns have evolved and are maintained through the interaction of sexual and natural selection, underlying physiological mechanisms are poorly understood. Studies on the interactions between a male's androgen levels, immune system, and his overall physical condition are practically nonexistent. Although we are beginning to appreciate the complexity of interactions between the neuronal, hormonal, nutritional, and behavioral processes that affect the expression of nuptial coloration, many details of the mechanisms still remain to be elucidated. For example, the role of carotenoids in the immune system of fishes warrants careful, experimental studies. Hypotheses, such as the "challenge" (Wingfield *et al.,* 1990) and the "immunocompetence" hypothesis (Folstad and Karter, 1992) suggest possible interactions and feedback mechanisms between different physiological process; data are needed to test them.

Another focus of studies of nuptial color patterns of fishes should be on the role of androgens in their expression. Very little is known about the action of androgens, and their interaction with other neuronal and hormonal mechanisms, in mediating color changes in fishes.

The role of phylogeny in constraining the evolution of nuptial color patterns also warrants investigation. Why do certain groups show such diversity and flamboyance of colors and patterns while other groups, living in similar habitats and seemingly subject to similar selective pressures, are so conservative? Unfortunately, the nature and scope of comparative studies will be severely curtailed until phylogenetic reconstructions and behavioral and physiological studies have been performed on more species and higher taxa.

Research on the nuptial coloration of fishes provides an excellent opportunity to study the relationship between proximate and ultimate factors in the evolution of signals. The diversity of color patterns, the rapidity with which they change in response to both environmental conditions and physiological state, and the relative ease with which fishes can be kept and experimentally manipulated, make them an excellent system to pursue many of the questions which have been raised, but certainly not definitively answered, in this review.

ACKNOWLEDGMENTS

I thank James Brown, Lee Drickamer, David Gray, Moshe Kiflawi, Craig Sargent, Paul Verell, and an anonymous reviewer for valuable comments on the manuscript. Support from the National Science Foundation (grant IBN-9318217) is gratefully acknowledged.

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Corresponding Editor: Paul A. Verrell