Natural and sexual selection on color patterns in poeciliid fishes

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Synopsis

In poeciliid fishes, sexual dichromism is associated with larger size and larger broods, but there is no relationship between sexual size dimorphism and sexual dichromism, or between degree of dichromism and color pattern polymorphism. Factors are discussed which influence the evolution of color pattern polymorphisms, sexual dimorphism and dichromism. Detailed studies of South American species have shown that the color patterns of poeciliid fishes have predictable effects in (1) avoiding diurnal visually hunting predators; (2) mating success; and (3) species recognition. Data from some Central American species indicate that some color pattern elements may be closely linked to physiologically variable loci, which further affect the variation in color patterns. Different elements of any given color pattern can be influenced by different modes of natural selection; in guppies the relationship between predation intensity and color pattern is different for melanin, carotenoid, and structural colors. Different color patterns have different degrees of conspicuousness on different backgrounds, and may appear differently to predators and mates with differing visual abilities.

Introduction

Natural selection is a major component of the theory of evolution, yet little is known about its function or magnitude (Lewontin 1974, Endler 1980). Sexual selection is a subject of great interest because it may result in genetic change which has little to do with environmental factors (Lande 1980, 1981, Kirkpatrick 1982). The best examples of both phenomena are in studies of color patterns because they are relatively easy to measure, and their adaptive significance is usually obvious (Endler 1978, 1980). Discussion of natural and sexual selection will be limited to the Poeciliidae; data from other families are very scanty (see Endler 1978).

The teleost family Poeciliidae is distributed from Delaware and southern Arizona through north-eastern Argentina and Ecuador (Rosen & Baily 1963). It is found in most fresh and brackish water habitats, but tends to be absent from very fast flowing mountain streams, large rivers, and far inland. Poeciliids are primarily fish of shallow waters, and except for the piscivorous *Belonesox*, are omnivorous.

Sexual dimorphism and dichromism

Male poeciliids are usually smaller than females; the ratio of male to female maximum observed sizes (TL) averages 0.7, and ranges from 0.4 in *Poecilia scalpridens* and *Poeciliopsis gracilis* to 0.9 in *Neoheterandria cana* and *Priapella bonita*, and about 1.0 in *Poecilia petenensis* (data from Jacobs

1971). Sexual dimorphism in color patterns (dichromism) is also highly variable in the family, although some genera tend to be more (*Poecilia, Xiphophorus*) or less (*Gambusia, Girardinus, Poeciliopsis*) dichromic than the family as a whole. The female color patterns are generally simpler and less developed than in males. If we split the species into those which are strongly, weakly, or not sexually dichromatic, there appears to be no relationship between the degree of size dimorphism and the degree of dichromism [$F(2,123) = 0.4$, $P \gg 0.05$, data from Jacobs 1971].

Ghiselin (1974) suggests that in species with small males, females invest energy in producing eggs and males invest energy in seeking out females rather than in gonadal development. The differences in size may arise because energy for growth is shunted into swimming and sexual displays in males, while female energy allocation is towards growth of body and gonads, egg production (in terms of total weight of eggs), and food transfer to developing embryos (Balon 1975, 1983, Wourms 1981), which is proportional to female size. There is a significant correlation between female size (TL) and brood size among species [$r = 0.35$, $P < 0.02$, data of Jacobs 1971], and within a species (Reznick & Endler 1982). Male poeciliids spend much more time on reproductive activity than females (Baerends et al. 1955, Liley 1966, Constantz 1975 & unpublished manuscript), probably because there are very few females receptive and fertile at any one time and place (Liley 1966, Seghers 1973, Balsano et al. 1981). Gestation time may be an additional indicator of female 'investment', but curiously enough, it is positively correlated with the male/female size ratio [$r = 0.40$, $P < 0.02$], the ratio is closer to 1.0 in species which take longer to mature their broods.

Baylis (personal communication 1982) has suggested an alternate hypothesis to explain why males are usually smaller than females, based upon the energetics of livebearing. Poeciliids have greatly reduced fecundity relative to other fishes by bearing offspring and supplementing embryonic yolk with maternal nutrients (Balon 1975, 1983, Wourms 1981). The advantage of a longer gestation time is a higher 'quality' offspring – able to eat larger food items, better able to maneuver in streams, avoiding predators and rapidly flowing water. Larger females produce larger broods. But there are energetic and predator risk costs to bearing young for long periods. Smaller females may be more efficient in bearing young (lower somatic maintenance costs), so it is possible that smaller females would be favored in areas with either low food availability or very high predation. This predicts less size dimorphism in species and areas with high predation compared to low predation, and in areas with little or no predation, the fecundity-size relationship favors larger size (Baylis, personal communication 1982). This appears to be true for two species: In *Poecilia reticulata* the ratio of male size at maturity to minimum gravid female size is 1.01 in areas of high predation and 0.94 in areas of weak predation (Reznick & Endler 1982). In *Phalloceros caudimaculatus* the mean adult size ratios are 0.98 ± 0.12 and 0.98 ± 0.08 in dangerous and intermediate predation areas, 0.87 ± 0.12 and 0.82 ± 0.05 in arthropod-only and safe areas (Endler 1982). Baylis's predictions are independent of sexual selection, so it is consistent that there was no correlation between sexual dimorphism and dichromism among species. An additional reason for smaller females under high predation is that larger females take longer to mature. If the mean date of maturity approaches or exceeds the mean life expectancy, then this favors earlier maturity. This predicts smaller size at maturity in areas with high predation, which has been found in guppies (Reznick & Endler 1982) and *P. caudimaculatus* (Endler 1982). Males are also smaller at maturity in areas with high predation, but their size does not decline as rapidly with increased predation, hence the smaller size dimorphism in areas with high predation. There are presently insufficient data to know whether this applies among species.

There is a significant relationship between the degree of sexual dichromism and the number of young per brood [$F(2,49) = 3.75$, $P < 0.05$, data of Jacobs 1971]; species which have a greater difference between male and female coloration tend to have a larger brood size ($r = 0.39$). In addition, the strongly dichromic species also tend to be those with larger female size; sexually monochromic or

weakly dichromic species tend to be small [F(2,123) = 4.62, P <0.025]. It is possible that these relationships result from differences in predation intensity among species. The stronger the dichromism the brighter the males, which means greater risk to predation (Fisher 1930, Cott 1940, Haskins et al. 1961). In addition, larger species are preyed upon by larger more dangerous predators than smaller species. Those individuals with larger broods (larger individuals), have a greater chance of leaving reproducing offspring than those with genetically smaller broods, and therefore will be more successful in places with dangerous predators. This may explain the size variation among species and does explain the variation among populations of *P. caudimaculatus* and guppies living with differing predator communities. In guppies the differences are heritable (Reznick 1980, Reznick & Endler 1982). Dichromism may result in relatively more predation on males than on females. Females which are able to suppress the expression of color pattern genes will be at an advantage to those which do not, favoring dichromism. Males cannot suppress their colors or their mating will be impaired, either through poorer species recognition or sexual selection. It is interesting that many of the known color pattern genes are sex limited (color pattern genes not expressed in normal females) and sex-linked in sexually dichromic species which have been examined. The correlation between dichromism and brood size may have arisen because both may be affected independently but in parallel by predation.

Color pattern polymorphisms in poeciliids

Color patterns may be polymorphic (variable among individuals) in sexually dichromic or monomorphic species, for example *P. reticulata* and *Phalloceros caudimaculatus*, respectively. Color pattern polymorphisms are uncommon in the family as a whole, but are relatively common in the genera *Poecilia* and *Xiphophorus*. *P. reticulata* is one of the most color polymorphic vertebrates, and one of the first to be studied genetically. The genetics of the color pattern polymorphisms of *P. reticulata* and *Xiphophorus* species are fairly well known and are

similar, though much more complex in *P. reticulata* (Kallman 1975, Yamamoto 1975). Genes which control the presence or absence of particular colored spots are usually sex-linked and often sex-limited. As with sexual dichromism, color pattern polymorphism tends to be found in larger species. Polymorphism may in fact be more common and well developed in the family than appears from the literature, merely because most species have not been examined, for example, *Phalloceros caudimaculatus* (Endler 1982).

Color patterns serve three major functions in animals: (1) thermoregulation, (2) reduction of predation, and (3) intra- and inter-specific communication (Cott 1940, Endler 1978). Although dark coloration is known to increase temperature in some cold water copepods and mosquito larvae (Byron 1981, L.T. Nielson, personal communication 1982), this has not been studied in fish, and warm water may minimize the importance of colors in the heat balance of neotropical fishes. It is interesting that the black forms of *Gambusia* are found in the north of the distribution of the genus, though they are not necessarily correlated with temperature regimes within species (Martin 1977). Color patterns may serve to hide fish from predators (crypsis, Cott 1940, Wickler 1968, Endler 1978), or to make distasteful or mimetic fish more conspicuous (aposematism, Cott 1940, Wickler 1968, Keenleyside 1979). Color patterns or pattern elements are used by many species during mate recognition, courtship, and in other social contexts (Baerends et al. 1955, Liley 1966, Rosen & Tucker 1961, Constantz 1975). Variation in color patterns will affect their efficiency in one or more of these functions, so color pattern polymorphisms allow us to study the function and adaptation of color patterns.

A complicating factor in the study of color pattern polymorphism, and in fact all polymorphisms, is the possible effects of linked genes with strong affects on fitness, and of pleiotropic effects of particular loci affecting fitness in unexpected ways. Examples are found in *Xiphophorus* species. Kallman & Borkoski (1978) found a sex-linked gene *P* which controls growth and the onset of maturity in *X. maculatus* because it was initially linked to a

color pattern gene. Later investigations revealed the effects of other loci (Schreibman & Kallman 1978). *X. helleri* (Peters 1964), *X. maculatus* (Borowsky 1981), *X. montezumae* (Zander 1965), *X. pygmaeus* (Rosen & Kallman 1969), and *X. variatus* (Borowsky 1978) show a dimorphism in male size and color pattern development which may be associated with this gene complex. It is unclear in many cases whether the differences in size and color patterns among the different male types result from close linkage with *P* genes, or pleiotropic effects of the color pattern genes themselves. Except for Kallman, no one has looked for recombinants. These effects complicate studies of the functions of color patterns because it is difficult to disentangle the direct and indirect effects of each allele.

Some color pattern variation may be a function of, or even result in, differences in social status. For example, compared to subordinates, dominants of the following species are characterized by: young *P. reticulata* - black iris (Martin & Hengstabuck 1981); male *Poeciliopsis occidentalis* - darker (Constantz 1975); male *Gambusia heterochir* - paler (Warburton et al. 1957); male *X. variatus* - yellowish-red (Borowsky 1973). Such differences may or may not be influenced by a genetic polymorphism, and this must be considered in all polymorphism studies.

Color pattern polymorphisms may be found only in males (for example, *P. reticulata*), or in both sexes (*Ph. caudimaculatus*); sexual dichromism is independent of color pattern polymorphism within the family. This makes interpretation of the effects of predation on dichromism and polymorphism complicated. For example, as predation increases, we expect color patterns to be less conspicuous as a result of a decline in the frequency of conspicuous color pattern elements. But it is not clear if there should also be a decline in dichromism with increased predation. The relationship between sexual dichromism, crypsis, and predation may not be obvious, and may not necessarily run the same way. At intermediate predation intensities, sexual dichromism may be stronger than at very high or very low predation: At low predation there is little selection for crypsis in either sex. At high predation, selection for inconspicuousness may be so strong that suppression of certain color pattern elements in

females together with selection against conspicuous pattern elements in males results in very small differences in color patterns between sexes. At intermediate predation intensity, suppression of colors in females encourages dichromism, but the balance between sexual selection and predation encourages polymorphisms. Of course the direct effects of sexual selection may entirely obscure this relationship. The interrelationships between dichromism and color pattern polymorphism need much more work.

Color pattern polymorphism in *Poecilia reticulata*

Guppies, *Poecilia reticulata* Peters, show a complex color pattern polymorphism, and enough is known about their ecology, behavior and genetics to make significant progress in understanding the polymophism (Haskins et al. 1961, Farr 1976, 1977, 1980a, b, Yamamoto 1976, Endler 1978). Natural populations in Trinidad and northeastern Venezuela are so polymorphic that no two males are alike (Fig. 1a-c). The color patterns consist of a mosaic of patches varying in color, size, position and reflectivity, and are controlled by many X- and Y-linked genes. These genes are expressed only in adult males, and female genotypes can be revealed by testosterone treatment (Haskins et al. 1961).

The color patterns in a particular population represent a balance between selection for crypsis by predators and selection for conspicuousness by sexual selection (Fisher 1930, Haskins et al. 1961, Gandolfi 1971, Greene 1972, Farr & Herrnkind 1974, Farr 1976, 1977, Gorlick 1976, Endler 1978, 1980). Two exceptions are the studies by Farr (1980a) on sexual selection, and by Seghers (1973) on predation, in which color patterns had no effect. A significant problem in these and most other studies is the lack of control for the visual background against which mates or prey are seen, and also the difficulty in defining what was and was not conspicuous to predators and mates. A color pattern on a bare laboratory background can be quite conspicuous, yet be quite cryptic against the gravel backgrounds of their native streams (Endler 1978). One guppy which seems more conspicuous than

another in the laboratory may actually be less conspicuous in the field. In the studies described below, background color patterns were taken into account.

In order to be cryptic (inconspicuous), a color pattern must represent a random sample of the background normally seen by visually hunting predators at the time and place at which the prey are most vulnerable to predation (Endler 1978). Any deviation of the whole pattern from the background in the distributions of patch size, color, or brightness, will make the color pattern conspicuous, and the degree of conspicuousness is proportional to the deviation between animal and background distributions. In areas of intense predation, the background match should be better than in areas of weak predation. On the other hand, sexual selection favors color patterns which deviate from the background. Sexual selection and predation occur together in natural guppy populations, so a compromise is achieved which depends upon the relative intensities of the two processes. The compromise will be different for pattern elements which certain predators cannot see, and if the dominant predator has very different vision than we do, our estimate of conspicuousness may be wrong or misleading. Similarly, if predator's and prey's vision differ, the same pattern may differ in conspicuousness for predators and mates (Endler 1978).

Predation intensity in natural guppy populations

Within the natural geographical range of guppies, it is possible to choose localities where the diurnal visually hunting predators are common and well defined (Haskins et al. 1961, Endler 1978, 1980). By careful choice of localities, one can eliminate the effects of diurnal fish-eating insects, snakes and birds (see Endler 1978 for details). The aquatic diurnal visually hunting predators (fish and crustaceans) are easily censused because the study streams are clear, have gravel bottoms with no aquatic vegetation, and owing to the lack of human activity, the animals are relatively tame. The predators are: *Rivulus hartii* (Cyprinodontidae), *Aequidens pulcher*, *Cichlasoma bimaculatum* and *Crenicichla alta* (Cichlidae), *Hemibrycon dentatum* and

Astyanax bimaculatus (Characidae), and the freshwater prawn *Macrobrachium crenulatum* (Palaemonidae). These are found in the south-draining streams of the Venezuelan Paria Penninsula and Margarita Island, and the Northern Range of Trinidad (Endler 1978). A second predator fauna is found in the north-draining streams in these areas, also at the narrow eastern extremity of the Paria Penninsula, and Tobago Island: *R. hartii* (as before), *Agonostomus monticola* and possibly *A. microps* (Mugilidae), *Eleotris pisonis* and an unidentified *Eleotris* (Gobiidae), occasionally *Centropomis unidecimalis* (Centropomidae), occasionally *Gobiomorus dormitor* or *Dormitator maculatus* (Gobiidae), *Macrobrachium crenulatum* and *M. faustinum* (Palaemonidae). Because the first fauna consists primarily of mainland families and the second mostly of marine families, I will refer to the two predator faunas as the Mainland and Caribbean faunas, respectively.

The predators are distributed in a number of characteristic assemblages as a result of habitat choice and requirements, predation by other species, and chance events. In the Mainland fauna the assemblages and their codes are: (R) *R. hartii* alone; (M) *R. hartii* + *M. crenulatum*; (A) *A. pulcher* alone or with *R. hartii* uncommon or rare; (K) Characins: *A. bimaculatus* and/or, *H. dentatum*; (A + K) *A. pulcher* and characins together; (C + A + K) *C. alta*, *A. pulcher* and characins together, occasionally *Cichlasoma bimaculatum* (Endler 1978). In the Caribbean fauna: (R + M) as M, but often with *M. faustinum* in place of *M. crenulatum*; (Ag) *A. monticola* and occasionally *G. dormitor*; (E) *Eleotris* species with *Agonostomus* species and occasionally *C. unidecimalis* or *D. maculatus*. Both sets of assemblages are roughly in order of decreasing elevation. As in many other freshwater stream systems (Hynes 1970, Whitten 1975), the number of species and the number of predators increases downstream in both faunas.

From stomach-content analysis of several populations and 39 h of direct observation of two populations in the upper El Cedro river, Trinidad (Endler 1978, and unpublished) it is possible to rank the Mainland predators by increasing danger to guppies: *R. hartii* < *A. pulcher* = *C. bimaculatus* < *H.*
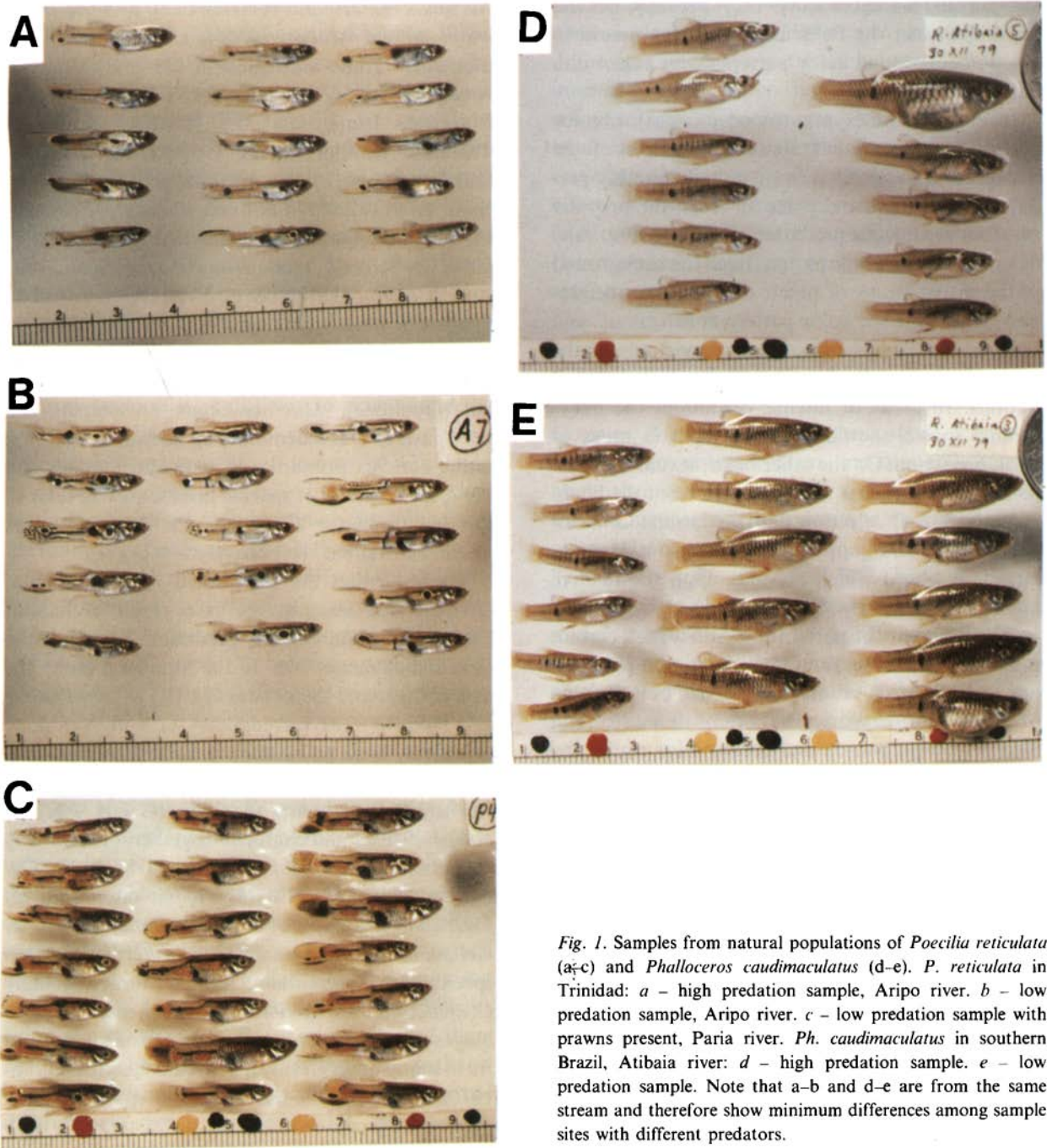
Fig. 1. Samples from natural populations of *Poecilia reticulata* (a–c) and *Phalloceros caudimaculatus* (d–e). *P. reticulata* in Trinidad: *a* – high predation sample, Aripo river. *b* – low predation sample, Aripo river. *c* – low predation sample with prawns present, Paria river. *Ph. caudimaculatus* in southern Brazil, Atibaia river: *d* – high predation sample. *e* – low predation sample. Note that a–b and d–e are from the same stream and therefore show minimum differences among sample sites with different predators.

dentatum < A. bimaculatus ≪ C. alta. The attack rate on guppies per hour was about 3 for C. alta, 1 for the characins, and less than ½ for A. pulcher and R. hartii. Casual observations of M. crenulatum suggest that it attacks at least as often as R. hartii. Aquarium observations indicate that prawns are more dangerous predators than R. hartii; they will eat all guppies in a 38 l tank in much less time than does a R. hartii. On the basis of stomach contents, the Caribbean predators may be ranked by increasing danger: R. hartii < A. monticola = G. dormitor ≪ E. pisonis. A. monticola is similar to A. bimaculatus and E. pisonis is similar to C. alta in danger to guppies.

Because the predator assemblages vary in the number of predators and their degree of danger to guppies, it is possible to choose various points on a visual selection intensity gradient; as one moves downstream and among valleys, one shifts from few species which rarely eat guppies to many species, some of which commonly eat guppies. Thus we can rank the predator assemblages by increasing visual selection intensity: Mainland A ≤ R ≤ M < K < A + K < C + A + K, and Caribbean R + M < Ag < E. The streams also vary in background, and there is a tendency for the more dangerous predator assemblages to be found in places with sand and small gravel, but it is possible to control for background among predator assemblages by careful choice of sampling sites.

Guppy color pattern polymorphisms and predation intensity

The a priori knowledge of visual predation intensity gradients provides an opportunity to test the theory of color pattern and background matching. As visual selection intensity increases, we expect the balance between crypsis and sexual selection to shift. In places with little predation the effects of sexual selection should predominate, favoring relatively conspicuous coloration. In places with intense predation, the effects of predation should be stronger than sexual selection, favoring relatively cryptic coloration. This is exactly what appears to be happening. As predation intensity increases, the number and size of patches decreases (Fig. 2, 3).

The differences and trends for most colors are highly significant (Endler 1978). The new data from the Caribbean predator fauna (Fig. 3) are very similar to the Mainland results (Fig. 2).

The reduction in number of patches with increasing predation is primarily a result of the decrease in frequency of structural colors (blue, iridescent, bronze). Structural colors work on refraction, interference and differential reflection, and are therefore much more conspicuous than the pigment colors, which work on differential absorption. In addition, structural colors tend to reflect maximally at a particular angle, and flash during movement of the fish. This can be very conspicuous from a long distance and hence especially bad in a high predation area. There are several reasons why the size of spots should decrease with increasing predation: (1) the background color pattern patch size tends to be smaller at lower elevations, where more dangerous predators are found; (2) a smaller patch will be below the visual acuity angle threshold or the color detection angle threshold more often than a larger spot; (3) the distance to first detection will be larger for a smaller than a larger spot. For further details, see Endler (1978).

Experiments on predation, and the effects of backgrounds

The concordance between the Mainland and Caribbean fauna results is strong inferencial evidence that predation has a significant effect on guppy color patterns. Experimental manipulation is a direct method of demonstrating that the color patterns at a particular place are an evolutionary response to sexual selection and predation. Experiments were performed in artificial streams in a greenhouse and by field transfer experiments.

Greenhouse experiments. — A large outbred population was derived from 18 localities in Trinidad and Venezuela and distributed among ten segments of an artificial stream system in a temperature controlled (25° C) greenhouse. Four of the segments were made as physical full scale replicas of a typical *Crenicichlia alta* territory (C pools), and the remaining six were replicas of streams containing
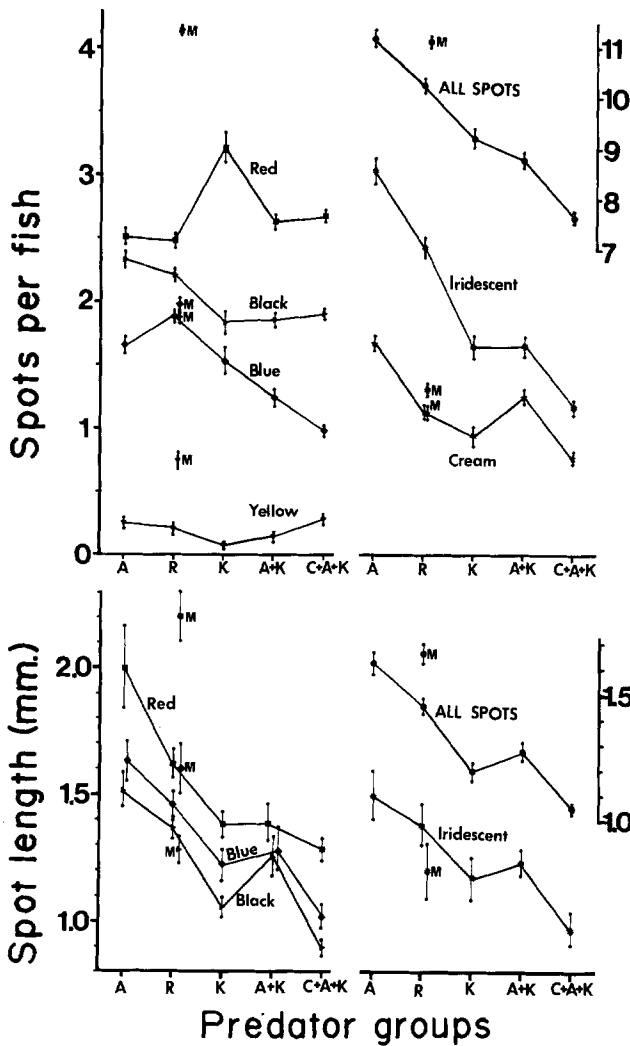
Fig. 2. Numbers of spots per fish and spot length as a function of rank predation intensity in the Mainland predator fauna. The predator groups are ranked in order of increasing predation intensity. For details see text. M stands for localities with freshwater prawns and *Rivulus hartii* rare. The vertical bars include two standard errors around the mean. Note the different scale for all spots pooled (from Endler 1978).

Fig. 3. Numbers of spots per fish and spot length for the Caribbean fauna. The predator groups are ranked in order of increasing predation intensity, as in Figure 2. Color symbols: R-O – red-orange, DR – dark red, Bk – black, Bl – blue, G – green-bronze, Cr – cream-white, Ir – silver- iridescent, Y – yellow, T – all spots. All show significant trends except for Bk, Cr spot number, and DR, Bl, Ir spot size. Note the separate scale for all spots pooled.

Rivulus hartii (R pools). Half of the C and half of the R pools had coarse gravel, and the remaining pools had fine gravel, with the same color and brightness frequency distributions. After six weeks, a *C. alta* adult was placed in each of the four C pools, six *R. hartii* were introduced into each o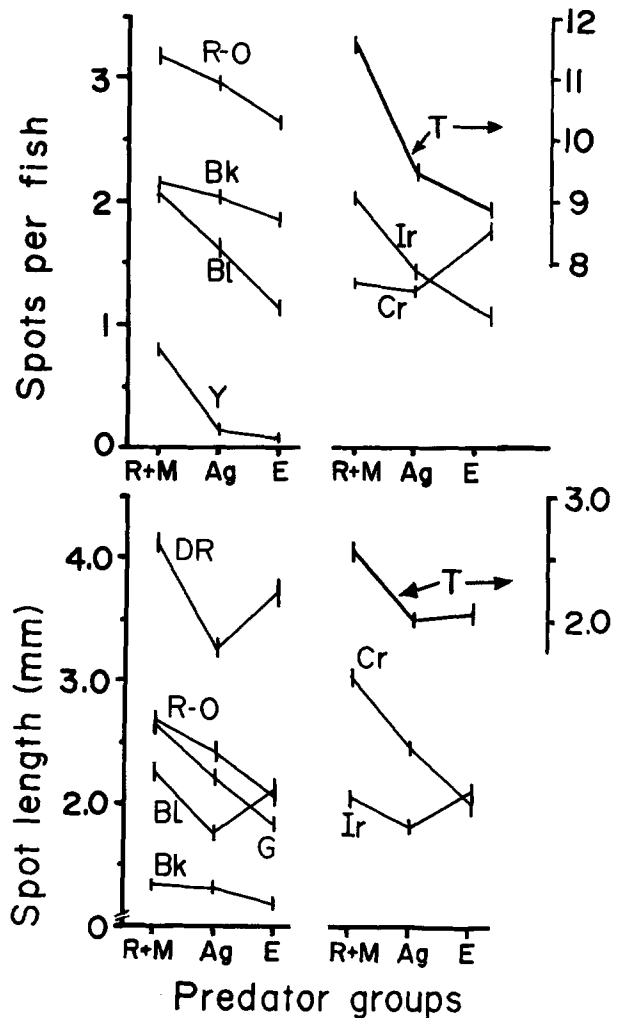f four of the R pools, and the remaining two R pools had no predators. This is a 3 × 2 factorial design, testing simultaneously for the effects of background patch size (fine and coarse) and predation intensity (none, low and high). Complete censuses of all fish were taken at 5 and 14 months (about 3 and 9 generations) after the predators were introduced. For further details, see Endler (1980).

The null hypothesis is that there will be no effect either of predation intensity or background color patch size.

The color pattern characteristics of each predation intensity treatment diverged significantly from the starting values, converged remarkably on the field results, and there was a significant effect of background (Fig. 4). There were smaller and fewer spots per fish in high compared to low predation, and this was primarily due to a reduction in the number of structural colored spots and a reduction in the size of the pigment color spots. In the two predation intensity levels, spot size was larger on large gravel and smaller on small gravel. The similarity to the actual background grain was greater in the pools with *C. alta* (high predation). Note that the effect of predation intensity was much greater than that of background (Endler 1980).

There were direct signs of sexual selection favoring males which contrast with the background rather than resemble it. First, in the control and *R. hartii* pools, there was a steady increase in the number and size of spots. Secondly, in the absence of predation the spot size became larger on small gravel than it became on large gravel (Fig. 4). Males can contrast with the background by having spots either larger than or smaller than the background grain, and the direction of the deviation seems to depend upon the initial difference between the guppy spot size and gravel size. Since these results were all highly significant (Endler 1980), it is clear that the color patterns in a particular place are affected by sexual selection and predation, with a complicated but predictable balance between the two and interaction with the background grain. Experiments are in progress which test for the effects of gravel color frequencies rather than patch (grain) size.

Field experiments. — Additional tests of the effects of predation and sexual selection were performed in the field. A smalll tributary of the Aripo River in Trinidad contained *R. hartii* but no guppies. Two hundred guppies were taken from the main stream, which contained *C. alta* and other predators (C + A + K) and introduced into the tributary (R). A second tributary nearby was physically and

biologically very similar to the first, except that it had guppies; this served as a control (R). Thus guppies were moved from a place with intense predation to a place with little predation. A sample was taken from all three localities 23 months or about 14 generations later. The null hypothesis is that there should be no change in the introduced population, and the alternative hypothesis is that, under reduced predation, the effects of sexual selection should increase the conspicuousness of the introduced guppies. The null hypothesis was rejected; all color pattern characteristics diverged from the mainstream (ancestral) population and converged on those typical of low predation populations, including the control. The color patterns became more conspicuous by an increase in the size and numbers of spots and a shift towards structural
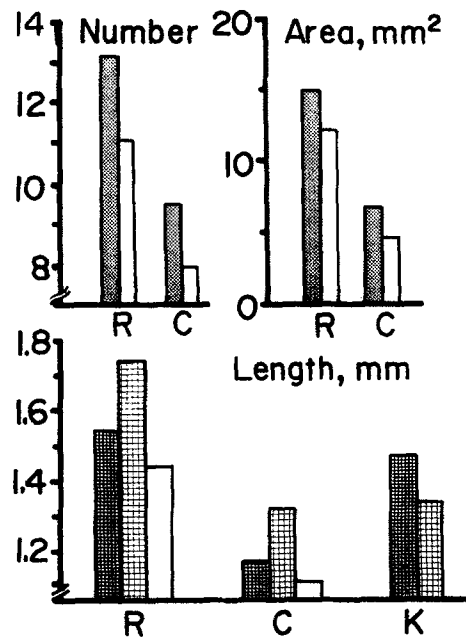

Fig. 4. Summary of the results of the greenhouse experiment: total number of spots, total area of spots and mean spot length per fish. C – high predation, R – low predation, K – no predation. Shaded bars are the greenhouse results and open bars the field results with the same rank predation intensity. Fine hatching – fine gravel. Coarse hatching – coarse gravel. Differences between treatments are highly significant. For further details see text.

colors (Endler 1980). The inverse experiments, introducing *C. alta* into low predation areas and following the color pattern changes in guppy populations, are in progress in two streams.

Background color pattern and female choice

What is conspicuous to a predator will also be conspicuous to a female. By the same arguments used for crypsis, we would expect that the success of males with particular color pattern characteristics will depend upon the background against which they are seen by females, and a given male will not be equally successful on all backgrounds.

The sexual behavior of guppies has been described in detail (Haskins & Haskins 1949, 1950, Clark & Aronson 1951, Baerends et al. 1955, Liley 1966, Farr & Herrnkind 1974, Farr, 1976, 1977, 1980a,b, Kennedy 1979). Males constantly search for receptive females. If a female remains relatively stationary, then the male will go through a series of displays in which his body is placed 30°–35° away from directly in front of her, and presented with fins spread and body oriented so that maximum surface is presented to one of her eyes. During part of the display (usually the S shaped 'sigmoid' part) his body is moved rapidly up and down and through a small angle along his long axis. The displays are followed by copulatory attempts if she remains stationary. Fertilization is internal, by means of a modified anal fin or gonopodium (Rosen & Gordon 1953). Copulation requires active cooperation by the female. Females copulate more often with males with conspicuous color patterns and higher courtship rates. During and immediately following copulation, males usually exhibit rapid 1–4 mm movements ('postcopulatory jerking'), and this appears to be associated with spermatophore transfer. Multiple insemination is common, but in general, the last male to mate prior to zygote formation is responsible for most of the zygotes (Winge 1937, Hildemann & Wagner 1954).

There is a second mode of male behavior called gonopodial thrusting (Baerends et al. 1955) or rape (Farr 1980b) in which a male tries to inseminate a female without first displaying to her. It is most common when females are not receptive, and appears to be independent of prior experience (Farr 1980b). If thrusting always resulted in insemination, then this would weaken the effects of female choice of males with particular color patterns. However, thrusting rarely results in successful genital contact, and the percentage of actual fertilization is even rarer (Clark & Aronson 1951, Baerends et al. 1955, Liley 1966). The evidence for successful fertilization is anecdotal, and in the published experiments, there was no opportunity for subsequent copulation with another male. In natural populations subsequent copulation is possible and probably frequent. Farr (1980b) mentions that thrusting can potentially lead to insemination during any part of the ovarian cycle, while standard courtship is presumably only successful at the appropriate period for fertilization in the cycle. But in the rare instance when a thrust actually results in a spermatophore transfer, the sperm may have to wait until the eggs are mature. If the female is inseminated during standard courtship after a thrust by another male, the new spermatophores will contain younger sperm (presumably more viable), a greater concentration of sperm, and they will be at an advantage compared to the older sperm because they were the last ones in. Thus, the probability that thrusting actually leads to a significant percentage of the fertilizations, hence of importance to the evolution of female choice, is very low. In addition, since the female has little opportunity to choose between different males attempting to thrust, its direct effect on the evolution of color patterns may be small. Much more work needs to be done on the actual fertilization success rate of gonopodial thrusting, and whether or not males which thrust can or cannot be chosen or resisted by females.

Sexual selection appears to be mediated through choice by females of males rather than choice by males or inter-male competition (references above, also Greene 1972, Gandolfi 1971, Gorlick 1976). Inter-male competition frequently occurs in small experimental aquaria (Gandolfi 1971, Farr 1976, 1977, 1980a,b, Gorlick 1976, Kennedy 1979), but is absent in very large aquaria at low densities, in the artificial greenhouse streams (Endler, unpublished), in small artificial streams (Liley, personal communication 1978), or in natural populations in

Trinidad (Endler unpublished, Liley personal communication 1978). The reasons for dominance hierarchies and inter-male aggression in spatially restricted artificial populations and in juveniles (Martin & Hengstebeck 1981), are unknown. During courtship display by two (or rarely more) males to a single female, each displays maximally to the female. If one male tried to interact with the other in some way, it would lose time in displaying to the female, and she might then chose the other male, or move off to another area. One does see males jockeying for best display position, but these are almost always cases in which the female is unreceptive, but being followed by several 'hopeful' males. It is arguable whether two males are trying to maximize their display to a receptive female, or take the female's attention away from another male. I will therefore regard the system as primarily one of female choice rather than inter-male competition.

In order to investigate the factors influencing female choice, guppies were taken from the R pools of the greenhouse population. Males were drawn at random, matched for size and age, and ranked with respect to number and size of (a) red and orange spots, (b) blue spots, and (c) all colors. The matched males were then presented to virgin females in the greenhouse with the following gravel backgrounds: (i) black & white; (ii) black, white, & red; (iii) black, white, & blue; (iv) multicolored bright. The fish were watched for an hour, recording their behavior. The preliminary results are quite interesting (Fig. 5) and show unequivocally that background affects mating success. A male whose main color is predominant in the background will be at a sexual disadvantage to males whose main colors are rare in the background. Males which contrast more with their background are at an advantage to males which contrast less, but the contrast depends upon the particular background against which they are seen.

As shown by all experiments, males can be successful by contrasting with a given background by having spots which are a different size from the background as well as having colors which are uncommon in the background. Conspicuousness also applies to the predators, and there are five ways in which males manage to increase their conspicuousness to females, while minimizing their visibility to predators: (1) some of the colored spots are found in the dorsal fin, which is erected during courtship, but is partially or wholly folded at other times, hiding the colors. (2) Some of the colored spots may be small enough to be below the visual acuity or color detection threshold of the predators at their attack distance of 10–15 cm, but all spots can be seen by females (Endler 1978). (3) There is some nervous control over the size of some black spots; they are enlarged during courtship (Baerends et al. 1955) and are relatively small at other times. (4) Spots are often longer than high (Endler 1980); most foraging movements are along the long axis of
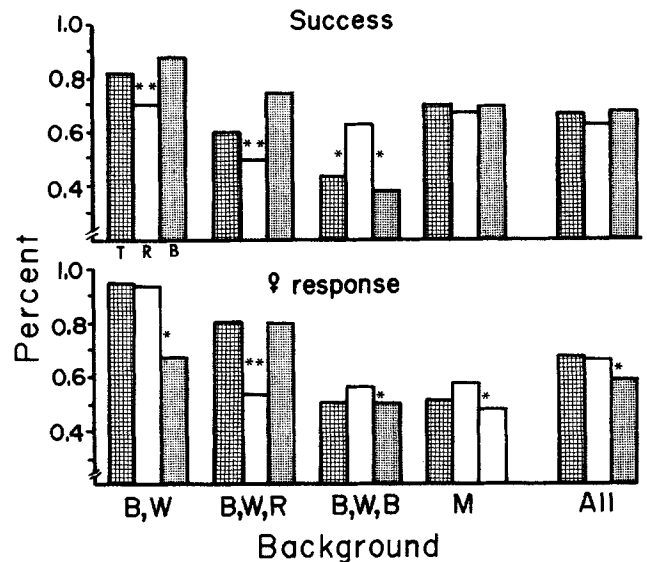

Fig. 5. Preliminary results of mate choice as a function of background color patterns. Vertical axes: percentage of presentations of two males to a single female which resulted in a successful copulation (above) or a significant female response (below). The backgrounds and number of trials (one trial per virgin female) are: B,W – black & white gravel (63). B,W,R – black, white & red gravel (45). B,W,B – black, white & blue gravel (48). M – multicolored gravel (75). All – all experiments pooled (231). The hatched bars (T) are for the male of a pair with more spots and the open bars (R) for males with more red or orange spots, and the shaded bars (B) for males with more blue spots. Asterisks indicate that adjacent bars are significantly different from each other. Note that having red on a non-red background, or blue on a non-blue background is better than having a color which is common in the background.

the body, whereas the sexual display consists of rapid vertical movements. During body movement, and aided by flicker fusion, the spots appear smaller during normal movement, and much larger during courtship. This predicts that it is more critical for patch height to match the background than patch length, and this is supported by the results of the greenhouse experiment (Endler 1980). (5) 'Private wavelengths', colors which can be seen by females, but not by predators.

If the most dangerous predators are incapable of seing certain wavelengths, then those colors should be more developed than the colors which the predators can detect (Endler 1978). This is borne out by a comparison between guppies living with *Rivulus hartii* alone (R), and with *R. hartii* and *Macrobrachium* (M or R + M). Prawns are relatively insensitive to long (red) wavelengths and more sensitive to short wavelengths. When *Macrobrachium* is present (and *R. hartii* uncommon to rare), there is a significant increase in the size and frequency of red, orange, and yellow spots, and a great reduction in the structural colors (Fig. 1, 2), relative to the localities with *R. hartii* alone but otherwise ecologically and visually similar (Endler 1978). The much greater abundance of diurnal *Macrobrachium* in the Caribbean than the Mainland fauna may explain some of the differences in color variation in their guppy populations (Fig. 2, 3).

Carotenoid versus structural colors and the basis for female choice

An interesting result of the female choice experiments (Fig. 5) is that red is apparently at an advantage in the initial stages of courtship (female response), while blue is better once the female's attention is gained, correcting for the background effect. This may result from the differing properties of structural and carotenoid colors. The brightness of carotenoid colors (red, orange, yellow) depends upon diet while structural colors are independent of diet (Fox & Vevers 1960, Rothschild 1975, Davies 1976). If fish are fed a carotenoid-free (or carotenoid-poor) diet, then these colors fade over a few weeks, and if carotenoids are provided again, the

colors become bright and intense.

Since they depend upon diet, carotenoid colors can be a direct indication of food finding ability (Endler 1980). In undisturbed habitats, guppies live in oligotrophic streams with clean gravel bottoms in montane forest, and there is a premium on food, especially food containing carotenoids such as algae. Natural populations in Trinidad eat mainly benthic, algae and invertebrates (Dussault 1980); algae are a major source of carotenoids. Any male which consumes more carotenoids during foraging will have brighter carotenoid colors. Thus male brightness, at least with respect to carotenoid colors, is a direct indicator of feeding success. This makes no assumptions about males specifically seeking out carotenoid-rich foods, but merely that a male with a faster ingestion rate per day will incidentally pick up more carotenoids and become brighter. Carotenoid colors vary in brightness in natural populations, especially in streams through the densest forest. This has a profound implication for sexual selection. If carotenoids were used as indicators of food finding ability, then females may prefer males with brighter, more, or larger carotenoid patches.

If females simply select on the basis of brightness, or absolute contrast with the background (Fig. 5), then males with bright structural colors will be favored by females also. Structural colors are based upon refraction and reflection through guanine crystals and are independent of feeding success. Thus, in some cases, especially in areas of low food availability and low predation, males with structural colors will be favored over those with carotenoid colors. But this cannot go too far because then the correlation between male brightness and male fitness will decline to zero. As long as there is predation, females which waste time choosing males (courtship is a predation vulnerable time) and obtain nothing in return, will be at a disadvantage, and the frequency of discriminating females will decline until an equilibrium is reached. The system is analogous to a Batesian-Mullerian mimicry system (many spots of all classes) in that the structural colors are false advertising for male fitness (Endler 1980); the brightness of structural colors is frequently greater than the carotenoids

and diet independent. Thus, in a sense the carotenoids are the model, and the structurals the mimics.

The mimicry analogy predicts that we should never find guppies with only structural colors (mimics), but we should find guppies with only carotenoids (models) or with both color classes. In more than 10^5 guppies scored, I have never seen guppies with only structural colors, but I have seen some with only carotenoids and most with both. In addition to the analogue of the equilibrium between models and mimics, there is a second prediction. It would be good for females to favor males with more carotenoid colors, but a genetic tendency to select for structural colors would be disadvantageous. This is supported by the mate choice experiments, which indicate that males with more carotenoids are more successful in the early stages of courtship (Fig. 5).

The second stage in courtship, copulation, appears to be dependent upon structural as well as carotenoid colors (Fig. 5). It should be emphasized that it is the subset of males which have been successful in gaining the female's attention, and have more structural colors, that are more successful in copulation, and these do not necessarily have more structurals than the general population. There are two possibilities for structural colors functioning in female choice: (1) Structurals may be more efficient in communication during sexual display in the low light intensity in undisturbed streams: structural colors reflect more light than carotenoids, and thus may be more 'stimulating'. (2) Because structural colors reflect the highest proportion of incident light at a particular angle, females see a flashing of light from the blue and silver spots during the male's vibrating display. The flash frequency is a direct and efficient estimate of the speed and duration of vibration. It is possible that healthier males can vibrate, hence flash, more rapidly and longer than less healthy males. Thus the flicker from structural colors may also be an indicator of male fitness. This is currently being investigated.

Although incomplete, the data on sexual selection and female choice clearly show that female choice depends primarily upon absolute criteria

(contrast with a particular background) rather than relative criteria (contrast between males), and that some aspects of male color patterns may be direct indicators of male fitness. The fitness-indicating hypothesis is reasonable.

The Fisherian models of sexual selection (Lande 1980, 1982, Kirkpatrick 1982) are possible alternative hypotheses to explain sexual selection in guppies. The basic model assumes that there is genetic variation in a male character, and genetic variation among females in their willingness to accept a male with any given character value. This sets up a correlation between male character and female choice criteria which can evolve rapidly, by a correlated response among the male and female characters. Males with more extreme values may be favored by females, which in turn favors females which choose more extreme males, and the system may 'runaway' to extreme values of male characters and female choice criteria. The model makes no assumptions about the fitness of the male character, and the male character may even be maladaptive. Females choosing less viable males are as likely to evolve as females choosing more viable males.

The main problem with the Fisherian models is the problem of what starts the process, and why the female should use a particular criterion to begin with. Once there is a correlation between the male character and female criterion, then the system will rapidly evolve. In guppies the system could have been started by chance and by chance lead to selection by females of males on the basis of absolute contrast with the background. Alternatively, absolute contrast may have been initially favored because such males were simply easier to see in the dark streams. But these models do not explain why carotenoid colors should be favored over structural colors in courtship, or the observed carotenoid/structural color ratios in natural populations. This is easier to explain on the basis of direct fitness indication by males through their carotenoid colors, with the structural color mimics tagging along. Of course a hybrid model is possible in which fitness indication is allowed in a Fisherian model, but computer simulations (Endler unpublished) indicate that the effects of fitness indication and predation overwhelm the effects of the Fisher

runaway process. When fitness indicating genes (such as those controlling carotenoid spots) are present, then the females choosing 'better' males win at the expense of those choosing 'poorer' (duller) males. Finally, all of the variation in guppy color patterns can be explained by the fitness indicating model in the absence of the Fisher runaway process. Therefore, the Fisherian model is either superfluous, or in the absence of fitness indication does not explain as much of the data as does the fitness indication hypothesis.

Summary of guppy data

The evidence strongly supports the hypothesis that the extensive color pattern polymorphism in *Poecilia reticulata* is affected by predation and sexual selection, interacting with background color patterns. These factors interact in predictable ways. The color patterns in a particular place represent a balance between sexual selection, which tends to increase conspicuousness against the local background, and visually mediated predation, which tends to decrease conspicuousness. The balance is very different between the three classes of colors. Melanin spots (black) are voluntarily increased in size during courtship, but reduced in size and intensity at other times. Carotenoid spots (red, orange, yellow) genetically decrease in size and frequency with increased predation. They are often longer than high, making them more conspicuous when movement is vertical than when it is horizontal, and are difficult for arthropod predators to see. Carotenoid colors may also be a direct indication of how well fed a male is and has been for the past few weeks. Structural colors (blue, iridescent, silver, bronze) genetically decrease in frequency with increased predation, are sometimes found in the folding dorsal fin, may be longer than wide, and may be direct indicators of male physical fitness during their flicker in courtship. Because these three classes of colors differ in properties, functions and mode of natural selection, they cannot be treated as equivalent color pattern elements in any evolutionary study.

Color pattern polymorphism in other species

Only three other species have been examined in any detail: *Phalloceros caudimaculatus*, *Xiphophorus maculatus* and *X. variatus*. *Phalloceros caudimaculatus* is ecologically similar to *Poecilia reticulata*, but lives in southeastern South America, chiefly southern Brazil (Rosen & Bailey 1963, Endler 1982). Like the guppy, it is the only member of its family through most of its natural range, and tends to be found in small creeks and streams, though they tend to be sandier and slower moving than guppy streams. As with guppy populations, it is possible to rank stream segments for visual predation intensity by the number and kinds of predators present. Unlike guppies, there is very little sexual dimorphism, and the color pattern polymorphism is much simpler (Fig. 1d,e). *P. caudimaculatus* varies in the number and size of black spots, and in the frequency of colored dorsal and caudal fins. The dorsal and caudal fins are either clear or various shades of red or orange. Unfortunately, the genetics of these characters is unknown. In spite of these limitations, there is a highly significant correlation between rank predation intensity and the color pattern characteristics. As predation intensity increases, the number and size of black spots decreases and the frequency of fish with colored fins decreases (Endler 1982). The results exactly parallel the results for guppies at the other end of South America, living with entirely different predators.

A comparison between streams with weak or no predation (the latter not found with guppies) and streams with only arthropod predators (freshwater prawns, dytiscid beetles, belostomatid beetles, large odonate larvae) shows that black spots are large and the proportion of colored fins is high in places with no or weak predators, but where there are only arthropod predators the black spots are tiny and the frequency of colored fins is high. By contrast, whenever there are intermediate or dangerous fish predators present, the black spots are tiny and the frequency of colored fins is low. As with guppies living with prawns, the only cryptic color patterns are those which the predators can see (Endler 1982). There appears to be good reason to believe that the

relationships between color pattern characteristics, predation and sexual selection is a general one, and not just limited to guppies.

Xiphophorus are morphologically, geographically, and ecologically quite different from *Poecilia* and *Phalloceros* (Rosen & Bailey 1963, Miller 1966, Rosen 1979). In contrast to guppies and *P. caudimaculatus*, *Xiphophorus* species live in a greater variety of habitats and elevations, and usually with a variety of other Poeciliids, and sometimes with congeners. Thus species recognition may limit or affect the development of their color patterns. The background color patterns may also be very different, because *Xiphophorus* live in streams, lakes, and ponds with silty and muddy beds, as well as places with dense growths of aquatic and semi-aquatic vegetation – these habitats are very rare for guppies and *P. caudimaculatus*.

Xiphophorus maculatus and *X. variatus* have a similar but simpler polymorphism than guppies (Kallman 1975), and something is known about social behavior in relation to color pattern (Borowsky & Kallman 1976, Borowsky & Khouri 1976, Borowsky 1978a,b), but little is known about their predators or ecology. This is complicated by the fact that most of their natural habitat is extensively disturbed by man. To make matters more complicated, the differences between color pattern morphs are correlated with differences in body size, and it is body size which determines mating success (Borowsky 1981). Thus, in *Xiphophorus* we do not know whether there is natural selection for color patterns or for body size and growth rate; one or the other characters may be 'hitch-hiking' on the gene frequency changes of the other (Thomson 1977). This is because genes for some color pattern elements are closely linked with growth and maturation genes (Kallman & Borkoski 1978). There are also some fascinating correlations between some of the color pattern element genes and apparent resistance to environmental stress (Borowsky 1978a, 1981); whether or not these are a result of closely linked genes or pleiotropic effects, or are primary results of the color pattern genes, this is obviously worth further research.

The *Xiphophorus* results are in strong contrast to those for guppies and *P. caudimaculatus*. Although

there is a suggestion that size may influence mating success in guppies (Kodric-Brown personal communication 1976), there is little body size variation within natural guppy populations (see Fig. 1, and color plates in Haskins et al. 1961, Endler 1978); most variation is between populations with differing predation intensities (Liley & Seghers 1975, Endler 1980). There is no correlation between color morphs and body size (Endler unpublished), and Farr (1980a) and I found that courtship display rate and color pattern are the major determinants of courtship success in guppies. In guppies and *P. caudimaculatus*, predation and sexual selection are the main determinants of color patterns, while in *Xiphophorus* physiological effects, possibly at closely linked loci, seem more important.

It would be of very great interest to investigate the predator communities of *Xiphophorus* streams for any effects on the color patterns. There is the barest suggestion that predation is important. There is a positive correlation between adult male size and the proportion of *crescent* (C) alleles in natural populations, and C males tend to be larger than the allele *cut-crescent* (Ct, Borowsky 1978). This is complicated by the fact that C males tend to be more variable than Ct males. In addition, the spot size of Ct is smaller than C. In both guppies and *P. caudimaculatus* male size is consistently and significantly smaller in high predation areas than in low predation areas (Liley & Seghers 1975, Endler 1980, 1982). The positive correlation between mean male size and proportion of males with C means that there is a positive correlation between male size and mean spot size among *Xiphophorus* localities. This is entirely consistent with geographic variation in predation intensity: as predation intensity increases, males become smaller and the proportion of males with smaller spots (Ct) increases. This is worth further investigation.

Conclusions

Although a casual glance at the color patterns of poeciliids may make one think that the color patterns are random, detailed study of South American species has shown that the color patterns are

very important in (a) avoiding diurnal visually hunting predators, (b) mating success and (c) species recognition. Data from Central American *Xiphophorus* indicate that some color pattern elements may be closely linked to physiology-affecting loci, which further affect the variation in color patterns.

Using the theory of color pattern and background matching (crypsis) and conspicuousness (Endler 1978) it is possible to predict in detail the kinds of color patterns that will best serve various purposes on particular backgrounds. These tests have been quite successful in poeciliids. It is important to note that different color patterns have different degrees of conspicuousness on different backgrounds, and their degrees of crypsis may be different to predators and mates with different visual abilities.

Acknowledgements

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