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NATURAL SELECTION ON COLOR PATTERNS IN
POECILIA RETICULATA

JOHN A. ENDLER[1]

Department of Biology, Princeton University, Princeton, N.J. 08540

All too often in evolutionary biology we are led to speculate or infer the mode of action of natural selection; we usually do not know why some individuals are more adaptive than others. Very often attempts to measure natural selection are unsuccessful, leading to heated arguments about the relative importance of selection, genetic drift, and epistasis in evolution (Lewontin, 1974). Until we know more about how and why natural selection occurs, attempts to measure it are quixotic, and discussions of its importance are theandric.

It is no coincidence that most of the successful studies of natural selection have dealt with animal color patterns; it should be obvious which color patterns are more adaptive in the presence of visually hunting predators. The adaptive significance of warning coloration and mimicry of distasteful species has been worked out (Cott, 1940; Wickler, 1968; Edmunds, 1974; Rothschild, 1975; Turner, 1977). But most species are neither distasteful nor mimetic; most have inconspicuous or cryptic color patterns in their natural habitats (Poulton, 1890; Thayer, 1909; Cott, 1940; Endler, 1978).

Most field and experimental studies have shown that the overall color or tone of inconspicuous species matches or approximates the background (DiCesnola, 1904; Sumner, 1934, 1935; Isley, 1938; Popham, 1942; Dice, 1947; Kettlewell, 1956, 1973; Turner, 1961; Kaufman, 1974; Wicklund, 1975; Curio, 1976), but they treated species with solid colors or

have ignored color *pattern*. A color pattern can be regarded as a mosaic of colored spots or patches of various sizes, colors and shapes. Some striking examples of color pattern polymorphisms remain largely unexplained, for example in *Partula* and *Cepaea* (Clarke and Murray, 1971; Jones et al., 1977). In three fish species, the frequency of a color pattern element is correlated with the presence or absence of visually directed predation: *Gasterosteus aculeatus* (McPhail, 1969; Semler, 1971; Moodie, 1972), *Nothobranchius guntheri* (Haas, 1976*a, b*), and *Cichlasoma citrinellum* (Barlow, 1976; Barlow and Ballin, 1976; McKaye and Barlow, 1976). But these simple pattern polymorphisms tell us very little about the factors which determine color patterns as a whole. The purpose of this paper is to show how various aspects of color patterns are moulded by natural selection.

COLOR PATTERNS IN *POECILIA RETICULATA*

Guppies (*Poecilia reticulata* Peters) show a complex color pattern polymorphism which varies with predation pressure, and are excellent for a study of natural selection on a complex character (Endler, 1978). They are native to the mountain forest streams of northeastern Venezuela, Margarita, Trinidad, and Tobago (Rosen and Bailey, 1963; Endler, 1978). Natural populations are highly polymorphic to the extent that no two individuals are alike. The patterns consist of a mosaic of spots or patches varying in color, size, position, and reflectivity, and are controlled by many X and Y linked genes. The color genes are expressed only

[1] Present address: Department of Biology, University of Utah, Salt Lake City, Utah 84112.

in adult males (Haskins et al., 1961, 1970; Yamamoto, 1975; Endler, 1978).

The color patterns in a particular place represent a balance between selection for crypsis by predators and selection for conspicuousness by sexual selection. Males cannot have color patterns which are too conspicuous, or they will be consumed by predators; but they cannot be too inconspicuous, or females will choose other males (Fisher, 1930; Haskins, et al., 1961; Gandolfi, 1971; Greene, 1972; Farr and Herrenkind, 1974; Farr, 1976, 1977; Gorlick, 1976; Endler, 1978).

Direct observations of differential predation on brighter males and differential mating success by brighter males are scanty, and sometimes not found at all (Seghers, 1973). However, a major problem has been that it was difficult to define what was and what 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 natural gravel backgrounds. One fish which may seem more conspicuous than another in the lab may actually be less conspicuous in the field.

In order to be cryptic (inconspicuous), a color pattern must represent or approximate a random sample of the background normally seen by visually hunting predators (Endler, 1978). Any deviation from the background in the distribution of patch size, color, or brightness will make the color pattern conspicuous; and the degree of conspicuousness is proportional to the deviation from the background distributions. In areas of high predation, the background match should be better than in areas with weak predation. On the other hand, sexual selection favors color patterns which deviate from the background. If both sexual selection and predation occur together, then a compromise must be made. Therefore, if we vary predation intensity and background color pattern parameters, then we expect to see parallel changes in the color patterns of the guppies as the balance between sexual selection and crypsis is shifted (Endler, 1978).

Color patterns of natural populations of guppies show a marked change with predation intensity, and appear to fulfill the predictions (Endler, 1978). Moving from places with relatively innocuous predators to places where a large proportion of the predators' diets are guppies, we find a reduction in the number of spots per fish, primarily due to a loss of strongly reflective (bright) structural colors. Increasing predation is also associated with a reduction in color patch size, primarily of the pigment colors (black, red). All of the changes make guppy color patterns less conspicuous at high, compared to low, predation intensities (Endler, 1978).

The field results are striking, but it is possible that some other factor in the environment is affecting the color patterns. In order to provide a more direct test of the hypothesis that the entire color pattern is subject to natural selection, two experiments were set up, one in a greenhouse and one in the field. The experiments were designed to examine the effects of predation intensity and background color patterns on the color patterns of *Poecilia reticulata*.

EXPERIMENTAL DESIGN

Greenhouse Experiment

Ten ponds were constructed in a greenhouse at Princeton University, and their size and contours were designed to mimic natural stream segments of the Northern Range of Trinidad. Four ponds (C1–C4) were made to mimic stream segments containing the dangerous guppy predator *Crenicichla alta* (Cichlidae): 2.4 × 1.2 m with a maximum depth of 40 cm. This is about the normal territory size of *C. alta* in smaller streams. The other ponds (R1–R6) were made to mimic streams with the relatively innocuous *Rivulus hartii* (Cyprinodontidae): 2.4 × 1.2 m with a depth of 15 cm. (Owing to lack of space, R6 was made 1.4 × 1.2 m.) These ponds at normal field density would contain about six adult *R. hartii*. All ponds were connected to a water circulation and sand filtration system to keep the gravel and water clean and clear as in the natural streams. The

temperature was kept at about 25 C, also normal for the natural streams.

The ponds were lined with commercially available dyed gravel in one of two grain sizes, and mixed to give the following color frequencies: 31.4% black, 34.2% white, 25.7% green, and 2.9% each of blue, red and yellow. Although the colors are unnaturally bright, the gravel in Trinidad and Venezuela is also very bright and colorful, though less so. On the other hand, the dyes are excellent approximations to the guppy colors. There are two reasons for using dyed rather than natural gravel: (1) the color proportions are known and constant from pond to pond, and (2) the color proportions are the same with small and large gravel grains; color frequencies of natural gravels change with grain size.

C1, C3, R2, R4, and R6 had a grain size of 2–3 mm, and the remaining ponds had a grain size of 7–15 mm. C1–C4 were destined to have one adult C. alta in each, and R1–R4 to have six adult R. hartii in each pond. R5 and R6 were to be controls with no predators. Thus the experiment simultaneously tests for the effects of predation intensity and background patch size. The factorial design is summarized in Table 1.

In order to ensure a large amount of genetic variation in color patterns in the starting population, an average of ten pairs of guppies were taken at random from stocks originating in 18 localities in 11 streams of Trinidad and Venezuela. The six predator combinations discussed in Endler (1978) were approximately equally represented among the 18 stocks; the fish came from all levels of visual selection intensity. The effective number taken from each stock was actually greater than 20 because most females were already inseminated, and multiple insemination is common.

The foundation population (F) was started by taking five pairs from each stock and placing them together in each of ponds C1 and C2, making 180 fish per pond. (No predators were added until later, as discussed below.) One month later

TABLE 1. *Design of the greenhouse experiment. C1 through C4 simulate stream segments with C. alta. R1 through R6 simulate stream segments with R. hartii.*

	Crenicichla alta (C)	*Rivulus hartii* (R)	No predators (K)
Fine gravel	C1, C3	R2, R4	R6
Coarse gravel	C2, C4	R1, R3	R5

an equal proportion of all size classes from both C1 and C2 was divided among C1–C4, to make 171 fish per pond, and again allowed to build up a large population. Twenty-two weeks after the origin of the foundation population, an equal proportion of all size classes of C1–C4 was divided among all ten ponds to make 200 fish per pond. This repeated mixing among all ponds as the population built up minimized any founding effects among ponds and kept the genetic variation high. Finally, about six months from the origin of the foundation population (F), the predators were placed in the ponds according to Table 1. This is the start of the experiment (S).

Five months after the start of predation (S), a census was taken of all fish and all color patterns, Census I. Fourteen months after the start a second census was taken, Census II. Although there are overlapping generations, guppies can have their first offspring 5–6 weeks after birth, so Census I was at generation 3–4 and Census II at generation 9–10 after the start of predation (S).

The censuses were taken by draining the ponds and scoring all fish. As in the field censuses, males were scored for the number and position of spots, then anaesthetized in MS-222 (Ayerst "Finquel") and photographed with color and scale standards for later measurement of spot and body size (see Endler, 1978, Fig. 7). All fish were returned to their ponds after the census.

The expectations of the greenhouse experiment are: (1) the color patterns should converge on the color patterns of natural populations of guppies living with the same predators; (2) the color patterns

TABLE 2. *Design of the field experiment.*

Purpose	Symbol	Locality	Predators present
Source of guppies	(c)	Aripo *6*	*C. alta* and others*
Introduction site	(x)	Aripo *I*	*R. hartii*
Control	(r)	Aripo *2*	*R. hartii*

* *Astyanax bimaculatus, Hemibrycon dentatum, Aequidens pulchur*

should vary with the background grain; and (3) patch size tracking should be more precise at high, compared to low, predation intensity.

Field Experiment

It could be argued that the greenhouse experiment will yield artifacts because it is so artificial, even though it was designed to be as natural as possible. As an independent test of the effects of predation, a population which evolved naturally under high predation was transferred to a nearby area with low predation.

In August 1974, a small tributary of the Aripo River in Trinidad was found to have *R. hartii* but no guppies. The tributary flows into the main stream over a series of waterfalls, some of which are 5 m drops. The stream was visited in both wet and dry seasons until July 1976, and each time there was no sign of guppies. This is locality Aripo *I*. Approximately 2 km up the mainstream another tributary (Naranjo) joins the mainstream, and this tributary has *R. hartii* and guppies. To a point approximately 1.5 km above the junction with the mainstream, the tributary is virtually undisturbed by man, and physically very similar to Aripo *I*. The sample point at the lower end of the undisturbed area is Aripo *2*. Approximately 2 km below the junction of Aripo *I* and the mainstream, guppies live with *C. alta* and other predators; and in one sample point, Aripo *6*, the habitat is very similar to Aripo *2* and *I*, except that the stream is larger (Table 2).

On July 1, 1976, a sample of about 200 guppies was taken from Aripo *6*, scored for color patterns in the usual way, and introduced into Aripo *I* about 100 m below the road, and well above the first waterfall. The experiment is summarized in

Table 2. The following December the site was visited again; and the guppies had spread upstream and downstream to at least below the first large fall. A sample was taken at the release site on May 4, 1978, approximately 15 generations after the introduction, and scored in the usual way.

The expectation of the field experiment is that color patterns of the transferred population should change from the typical high predation patterns found with *C. alta* to the more complex and colorful patterns found with *R. hartii*. In other words the color patterns should resemble Aripo *2* more than Aripo *6* after 15 generations of relaxed predation pressure.

RESULTS
Greenhouse Experiment

Figure 1 shows the course of change of the total number of spots per fish for each predation intensity level. The ponds with no predators (K) show a steady increase in the number of spots per fish from the foundation (F) to the last census (II). The number of blue spots also increased rapidly, but the number of iridescent spots increased more slowly. After addition of *R. hartii* (R), there was very little change compared to the controls (K), although at Census I the R pools tended to have more iridescent spots than the K pools. The effect of *C. alta* is obvious and highly significant; C pools show a rapid drop in the total number of spots, and this is primarily a loss of blue and iridescent spots.

Figure 2 compares the number of spots per fish at Census II with the field results of Endler (1978). The results for Census I are similar (Fig. 1). The convergence on the natural stream populations is marked.
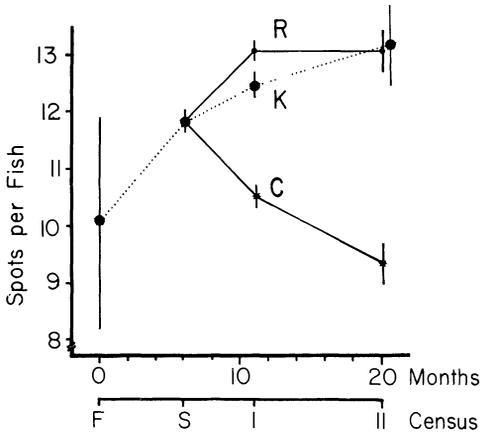
FIG. 1. Changes in the number of spots per fish during the course of the greenhouse experiment. *K*, ponds with no predation. *R*, ponds with 6 *Rivulus hartii* each (weak predator). *C*, ponds with 1 *Crenicichla alta* each (dangerous predator). *F*, foundation population of guppies; no predators. *S*, start of the experiment; predators added to R and C ponds only. Note the rapid change in C ponds after predation began. *I* and *II* are the dates of censuses I and II. Vertical lines are two standard errors.

The only notable difference between the field and greenhouse is that the total number of spots is higher in the greenhouse. Other than that, the results are very similar: the number of black, red, and yellow spots per fish is about the same in high (C) and low (R) predation intensity, while the structural colors (blue, iridescent) drop out in the presence of dangerous predators (C). The differences for blue, iridescent, and total spots between R and C are highly significant, both in the greenhouse and in the field.

Figure 3 presents the effects of predation on spot length, height, and total spot area in the greenhouse populations (shaded bars), and in the field (unshaded bars). Once again the convergences on the field results are striking. In each case (except blue), the spot length in ponds with *R. hartii* is significantly larger than in ponds with *C. alta*. All spots have a significantly greater height (measured perpendicularly to the body axis) in R compared to C ponds. The total area occupied by colored spots is

greater in R compared to C. Note that the standard error of spot size is greater in the controls (K) compared to either predator treatment (R or C), except for black spots. For all characters except black spots, the variance ratios (K/R) are highly significant ($P < .01$ or $.001$).

Figure 3 also presents the effect of gravel grain size on overall mean spot length and height. For both length and height within a given predation intensity, the spots are larger on large grained gravel (*l*) and smaller on small grained gravel (*s*). Table 3 presents the mean sizes for two gravel grains and three predation intensities. In ponds with no predation (K), the spot size is often no different between grains, and often is smaller on *large* grained gravel. Note also that for some characters, especially relative spot height (arc sin $\sqrt{\text{spot height/standard height}}$), the color patterns in R ponds also do not necessarily follow the gravel grain size, but in C ponds they almost always follow the gravel.

Table 4 presents an example of a two-way analysis of variance, and Table 5 presents the results of the significance tests for all characters. The first three columns of Table 5 are the results of analyses of variance excluding ponds with no predation (K) as in Table 4, and the last column gives the interaction term when K ponds are included.

The first column of Table 5 gives the results for the test for the effects of predation intensity. Predators have a significant effect on all characters except color diversity and blue spot length. Guppies are smaller, not as high bodied, and relatively elongated in high (C) compared to low (R) predation intensity. Endler (1978) and Seghers (1973; Liley and Seghers, 1975) also found that natural populations of guppies living with dangerous predators tended to be smaller. Except for blue, spot length significantly decreases with increasing predation. Spot height, spot area, total area, and total spot area relative to body area also decreased significantly with increased predation intensity (Tables 3 and 5; Fig. 3).
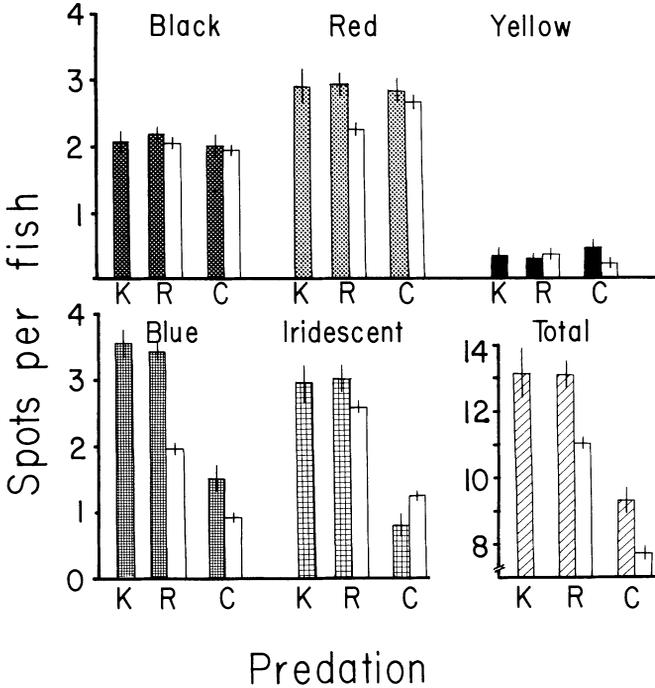
FIG. 2. Number of spots per fish in the greenhouse at Census II and in the field. Small vertical lines are two standard errors. Shaded bars: greenhouse means. Unshaded bars: field results. *K*, ponds with no predation. *R*, ponds with *R. hartii*. *C*, ponds with *C. alta*. Note similarity between field and greenhouse results, and lack of predation effect for pigment colors: black, red, and yellow.

The second column of Table 5 gives the results of the test for the effects of gravel size. Guppies are significantly higher bodied on coarse compared to fine gravel. The total colored spot area and the total area relative to body area are also significantly larger on coarse compared to fine gravel. Black, blue, and overall mean spot lengths are larger on coarse compared to fine gravel. For spot height only black and overall spot height are significantly larger on coarse gravel. Black, red, and overall mean spot area are also larger on coarse gravel. Note that even when the effect of gravel is not significant, spot size is almost always larger on coarse gravel compared to fine, especially in C ponds (Table 3).

The third and fourth columns of Table 5 give the results of tests for interaction between predation intensity and gravel size. When the K ponds are excluded (Table 3, column 3), the interaction term is nonsignificant except for red spot area.

When K ponds are included in the analysis, the significance level for red area increases, and in addition there is significant interaction for color diversity, red and blue lengths (column 4). The interaction arises because spots are larger on small gravel than they are on large gravel. This happens in the ponds with no predation (K) and in some with weak predation (R) (see Table 3). Once again, the effect is consistent among all characters except the iridescent spots, even when not significant.

Because guppies are smaller under more intense predation (C) compared to weak predation (R), it could be argued that some of the differences in spot sizes are due to differences in body size. This might explain why the ponds without predators (K) are intermediate between R and C with respect to color spot size. The K ponds yielded smaller fish (Table 3), probably because they had densities more than
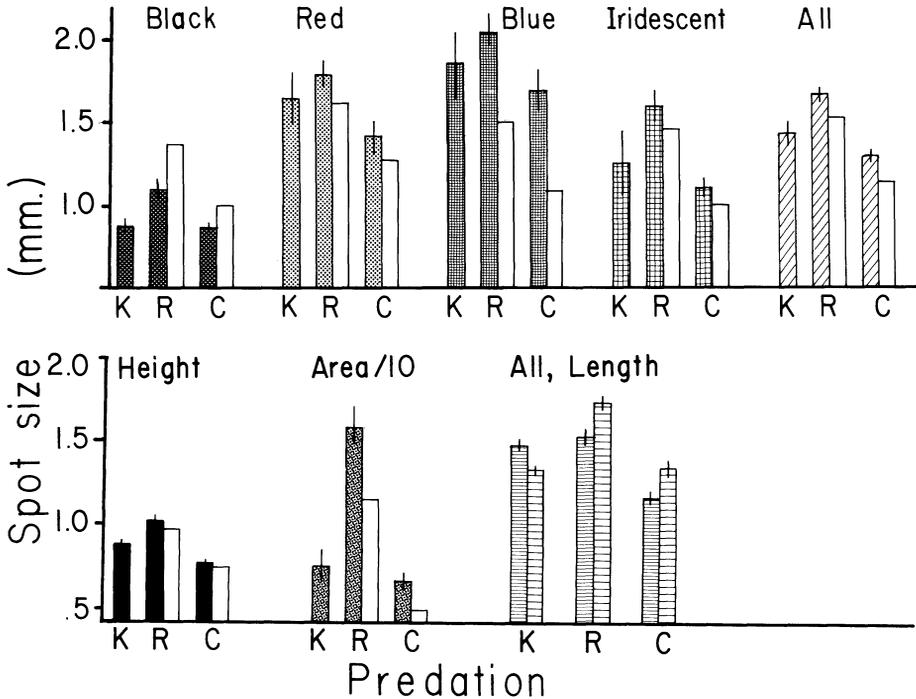
FIG. 3. Spot size in the greenhouse at Census II and in the field. Symbols as in Fig. 2, except for "all, length," lower right. For "all, length," shading is as follows: *fine hatching,* results for fine gravel ponds. *Coarse hatching*: results for coarse gravel ponds. Note the consistent effect of predation and the similarity between the greenhouse and field results. Note also that in the absence of predation, spot length is smaller on large gravel and larger on small gravel (lower right), in contrast to the two levels of predation; see also Table 3.

twice that of the R ponds; crowding restricts body size and growth in fish. However, this is not simply a matter of crowding since the lowest density ponds (C) have smaller fish than the R ponds (Table 3).

In order to correct for the effects of body size on color spot size, the analysis was repeated using spot length relative to body length and spot height relative to body height. As found in the field (Endler, 1978), the results for the effect of predators are unchanged with relative spot size. The reanalysis does affect the results for the effect of gravel on spot height and the interaction terms for both length and height (symbols in parenthesis, Table 5). With relative spot height three more colors—red, blue and iridescent—show the effects of gravel. New interaction effects show in all the spot heights and in overall spot length. There is a tendency

for relative spot height to follow the gravel in C ponds, but to go opposite to the gravel in K and some R ponds (Table 3); this yields the strong interaction between predation and gravel. In general, the background match is best in C, intermediate in R, and worst in K ponds; crypsis is proportional to predation intensity.

Field Experiment

The results for the field experiment are shown in Figure 4, and parallel both the greenhouse experiment and the results from undisturbed streams. During the two years in the absence of dangerous predators, the color patterns of the guppies introduced into Aripo *I* (x, Fig. 4) converged on the patterns characteristic of streams with *R. hartii* the only predator (*r*), and ceased to resemble the parental population living with *C. alta* and other

TABLE 3. *Means from the greenhouse experiment.*

		Black		Red		Blue		Iridescent		All spots*	
		Fine	Coarse	Fine	Coarse	Fine	Coarse	Fine	Coarse	Fine	Coarse
Spot length	C	0.80	0.93	1.47	1.36	1.30	2.15	1.14	1.03	1.17	1.32
	R	1.01	1.17	1.61	1.96	1.97	2.16	1.66	1.51	1.54	1.74
	K	0.88	0.88	1.71	1.60	2.25	1.55	4.18	5.72	1.47	1.34
Spot height	C	0.62	0.74	0.78	0.92	0.79	1.05	0.52	4.26	0.72	0.93
	R	0.80	0.95	1.02	1.08	1.12	1.18	0.90	0.95	0.95	1.06
	K	0.72	0.74	0.92	0.92	0.98	1.05	1.95	4.26	0.82	0.93
Spot area	C	0.53	0.74	1.20	1.10	1.09	2.21	0.61	0.65	0.90	1.12
	R	0.85	1.23	1.66	2.21	2.48	2.91	1.55	1.53	1.59	2.05
	K	0.65	0.72	1.70	1.40	2.48	1.76	2.75	5.46	1.37	1.35
Rel. spot length†	C	12.58	22.11	16.87	13.97	16.00	16.92	14.94	14.62	15.94	16.46
	R	13.99	14.64	17.81	19.19	19.54	19.89	17.91	16.69	17.19	17.88
	K	18.85	13.52	19.51	18.12	21.57	17.99	52.65	72.40	17.49	16.46
Rel. spot height‡	C	26.79	30.89	30.89	31.12	30.45	35.35	24.58	28.43	29.22	31.54
	R	30.41	21.09	34.93	23.35	36.82	25.62	32.47	21.43	33.51	22.63
	K	32.02	30.93	37.04	35.59	37.31	38.75	90.18	160.49	34.31	35.54
Total patch *area*	C	5.99	6.95	*Relative*		20.03	22.11	*Color*		2.69	2.81
	R	12.02	17.52	*patch*		28.18	31.60	*diversity*		3.02	2.62
	K	6.48	8.37	*area*		23.30	24.64			2.29	2.84
Standard body *length* (mm.)	C	16.53	15.76	*Standard*		2.96	2.90	*length/height*		5.59	5.45
	R	16.93	17.51	*body*		3.11	3.38			5.46	5.21
	K	15.12	15.93	*height* *(mm)*		2.52	2.74			6.00	5.86

* Mean spot size per fish for black, red, blue, yellow, gold, cream, green, and iridescent spots.
† Relative spot length = arc sin $\sqrt{\text{spot length/body length}}$
‡ Relative spot height = arc sin $\sqrt{\text{spot height/body height}}$.

predators (c). The size of black, red, blue, iridescent, and other spots increased, color diversity increased, and the total area occupied by colored spots increased as did the number of spots. In each case the increase was highly significant. In some cases, for example blue spot length, the increase went beyond the mean for the

TABLE 4. *Analysis of variance of color spot length relative to body length. Calculated on (arc sin* $\sqrt{patch\ length/body\ length}$).

Source of variation	Excluding ponds with no predators			
	df	SS	MS	F	Sig. level
Pond types	3	69.72	23.24	9.65	***
Predators	1	51.59	51.59	21.42	***
Gravel size	1	16.00	16.00	6.65	*
Interaction	1	2.13	2.13	0.88	n.s.
Error	66	158.95	2.41		
Total	69	228.67			

equivalent R stream, Aripo 2. A comparison of x, the introduction site, with the mean of all streams with *R. hartii* the only predator (Endler, 1978) shows that Aripo *1* falls within the range of variation for streams with only *R. hartii*; the overshoot was probably a result of relatively dull background colors in Aripo 2. Color diversity, measured by $1/\Sigma p_i^2$, where p_i is the proportion of spots (by area) of color i, also overshot Aripo 2 (Fig. 4).

DISCUSSION

The results of both the greenhouse and field experiments are clear and consistent. The convergence between the color patterns in both the experiments and equivalent natural populations is striking. The results are what are expected if the color patterns represent a shifting balance between sexual selection and predator avoidance.

Character	Source of variation			
	Predators	Gravel	Interaction excluding K	Interaction all ponds
Body				
length	**	—	—	—
height	***	*	—	—
l./h.	*	**	—	—
Color area				
total	***	**	—	—
relative	***	*	—	—
diversity	—	—	—	*
Spot length				
black	*	*	—	—
red	*	—	—	*
blue	—	*	—(**)†	**
iridescent	**	—	—	—
all spots	***	*	—	—(*)
Spot height				
black	***	**	—(***)	—(***)
red	***	—(***)	—(***)	—(***)
blue	*	—(*)	—(**)	—(**)
iridescent	***	—(***)	—(**)	—(***)
all spots	***	**	—(***)	—(***)
Spot area				
black	**	*	—	—
red	***	*	*	**
blue	*	—	—	—
iridescent	***	—	—	—
all spots	***	**	—	—

Significance levels· * $P <$ 05, ** $P <$ .01; *** $P <$ 001
† Parentheses indicate significance level when relative spot length or height is different from the same analysis on length or height in mm.

Selection for Crypsis

A reduction in the number and size of spots renders guppies less conspicuous (i.e., more cryptic) to predators. The structural colors (blue and iridescent) are strongly reflective and can be seen from a much longer distance than the pigment colors, so it is not surprising that they reach the lowest frequency under high predation. Thus the brightness distribution is more similar to the background at high (C) compared to low (R) predation.

Spot size is reduced with increasing predation because a small spot will not be as visible as a larger spot at the same distance, especially if the spots are near the limit of the predator visual acuity (Endler, 1978). At high predation intensity (C) it is important to have small spots, while at low predation (R) it is not so critical. In addition, *C. alta* attacks from 20–40 cm, while *R. hartii* attacks from 5–15 cm; differences in spot size make less difference at the close approach distances of *R. hartii,* even though the visual acuity of *R. hartii* is not as good as *C. alta* (Endler, unpubl.).

Within a given predation level (R or C), the spot size is larger when the background gravel grain is larger. This is what we would expect if the guppy spot size approximates that of the background. The guppy spot size is about the same as the background grain for fine gravel (1–3 mm), but although larger on coarse gravel, it is still not as large as the background there. One possible reason for this is that guppies may be genetically incapable of producing colored blotches a centimeter or so in length, at least not in ten generations. Another possibility is that because they are seen several centimeters in front of the gravel, the angle subtended by their spots in the predator's eye can only be the same as the background if the spots are smaller than the background (Endler, 1978). In any case, on coarse gravel guppies with larger spots will be *relatively* less conspicuous than those with smaller spots, so larger spots are at an advantage on coarse gravel.

Guppies are relatively higher bodied on coarse compared to fine gravel (Tables 3 and 5). The whole body may be regarded as a color patch, and on fine gravel the body height is a few millimeters above the background patch size, while on coarse gravel it is several millimeters smaller than gravel grain. As for the individual color spots, it is possible that the body as a whole is less conspicuous if it is of the same order as the background patch size (Thayer, 1909; Endler, 1978).

Background spot size has no noticeable effect on iridescent spots. These spots are the most highly reflective of all spots, and can be seen easily from a distance under water. They are also strongly directional in their reflectivity, hence they give off very strong flashes of white or blue-white light while the fish are moving. The iri-
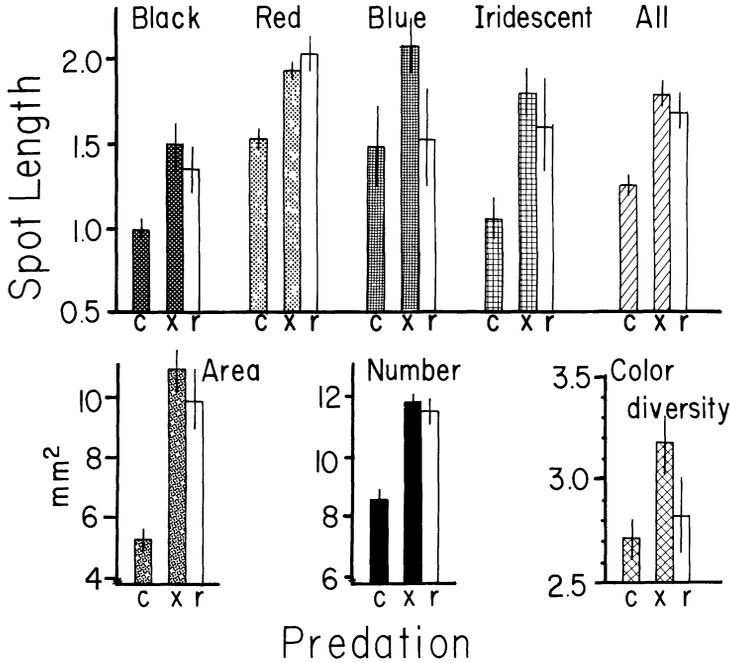
FIG. 4. Results of the field experiment. A population originating in a locality with dangerous predators (*c*) was transferred to a stream having only the weak predator *R. hartii,* and, until the introduction, no guppies (*x*). Another stream nearby with guppies and *R. hartii* (*r*) served as a control. Results shown are from guppies collected at the three sites two years after the introduction. The place of origin and transferred population are shaded for each character. Note the convergence of *x* with *r* and the divergence from *c*.

descent spots are thus extremely conspicuous, and proportionally more conspicuous than any other spots except perhaps yellow, which remains at very low frequency (Fig. 2). There is little advantage to a reduction in size of iridescent spots because even tiny ones can still give off a brilliant flash. This may be the reason they do not seem to respond to size selection.

The effect of gravel on guppy spot size is much stronger in the ponds with dangerous predators than in those with weak or no predators. This is expected if it is more critical to parallel the background patch size distribution in high compared to low predation intensity (Endler, 1978). The effect is greatly exaggerated for relative spot height. This is partly because spot height is correlated with body height, and partly because spot height increases less than the body height on coarse compared to fine gravel. The relationship between spot and body height is complex

and requires more study. It should be remembered, however, that conspicuousness is a function of the deviation from the background of absolute rather than relative spot size.

Guppies forage and escape along their long axis, but sexual displays involve movements which are often along different axes, including the vertical (Baerends et al., 1955; Liley, 1966; pers. observa.). Jackson et al. (1976) and Pough (1976) suggest that color patterns may blend together along the axis of travel if the angular velocity of the spots across the predator's eyes is faster than the predator's flicker fusion frequency. Thus natural selection can act very differently during escape and sexual displays (Endler, 1978). If this were true, then the length of guppy spots should be less critical than the height for background matching. This is supported by (1) most color spots are longer than high, frequently 2 or 3 times longer. (2) Significance levels are higher for spot

height than for spot length, indicating a stronger effect on spot height. (3) The coefficient of variation of spot length is larger than for spot height for all but black spots. The last observation is not found in the K ponds, and is more obvious in C compared to R ponds. Again this is consistent with background matching being more critical under higher predation, and conspicuousness being important in sexual display.

The field experiment provides some evidence that the color patterns of a particular place parallel color frequencies in the background. Aripo 2 and 6 have multicolored gravel, but a large fraction of the grains are relatively pale. Aripo 1 has multicolored gravel similar to Aripo 2 and 6 but in addition has a much higher fraction of brown, dark gray, black, and blue-gray iridescent grains. This is associated with a higher guppy color diversity than either Aripo 2 or 6 (Fig. 4). The greenhouse experiment showed no difference in color diversity between coarse and fine gravel, and this should have happened since the gravels differed only in grain size. The greenhouse guppy color patterns were brighter and more color diverse than the field populations, but this is probably related to the very bright artificial gravel colors in the greenhouse.

In summary, the greenhouse and field experiments are consistent with the hypothesis that the color patterns at a particular place approximate the background color pattern parameters, particularly in spot size, brightness and color frequencies. It is also likely that blending during movement makes matching more critical along the vertical axis compared to the horizontal axis. Background matching is more critical at high compared to low predation intensity. We can easily reject the null hypothesis that the color patterns are random with respect to visual selection by predators.

Sexual Selection

The ponds with no predation (K) provide evidence that sexual selection is operating and that it selects for a mismatch between guppy color patterns and backgrounds.

Figure 1 provides the first evidence: the total number of spots per fish and the number of blue and iridescent spots increased in the K ponds throughout the experiment. If there was no sexual selection, we would expect the number of spots to change at random and stay at about the level of the foundation population (F). It is suggestive that the number of blue spots increased so rapidly; J. Levine (pers. comm.) found that guppies and other Poeciliids have the most blue-sensitive retinae known among the vertebrates. Virtually all males have some blue, so it may be important in courtship.

Figure 3 presents the second line of evidence. The variance in spot size for all but black spots is greater in ponds without predation than those with either low or high predation. If differentiation among ponds were at random, we would expect nonsignificant and significant variance ratios at various levels, but all except black are highly significant ($P < .01$ or $.001$). This is the weakest evidence since it could also simply be a result of relaxed predation, but even with relaxed predation we would expect varying levels of significance, not all or none significant.

The third line of evidence comes from Tables 3 and 5. When K ponds are excluded from the analysis of variance, then the interaction between predation and gravel size is not significant, except for red spot area. When K is included, a significant interaction term appears for color diversity, red and blue spot length, and the significance level for red spot area increases. The reason for the interaction is that the patch size follows the background in R and C ponds, but in K ponds the patch size is larger on smaller gravel and smaller on larger gravel (Table 3), increasing the conspicuousness in K compared to the other ponds.

All three results are exactly what we would expect if sexual selection were operating to make males as different from the background as possible, within the limits of predation. In the absence of pre-

dation, sexual selection favors mismatching in brightness, spot size, and color frequencies. This favors more and larger spots, the bright iridescent spots, and a more even frequency distribution of colors. The greater variance in the absence of predation could come about from the diversifying effects of inter-male competition for mates and frequency-dependent mating (Farr, 1977). If there was no sexual selection, we would not have seen any of the effects described above, with the possible exception of increased variance in the K ponds compared to R and C ponds.

Poecilia reticulata is the first species in which natural selection has been demonstrated for various details of color patterns and certain aspects of color pattern can be predicted. This is the first time we have a relatively complete logical chain for phenotype to fitness; we know *why* some color patterns are more fit than other ones. It is clear that natural selection can act differently on different components of color patterns; spot size may be selected differently than spot color, and some colors are favored differently than others. Certain combinations of color pattern genes will be most adaptive in a particular place, and this favors linkage disequilibrium. This may be one reason that virtually all color pattern genes are together on the X and Y chromosomes; they can act as color pattern "supergenes." The next step will be to measure the differential survival of color pattern classes to enquire whether or not the color patterns which are predicted to be most adaptive on the basis of background matching actually survive better than those which are mismatches to the background.

Possible Reasons for the Polymorphism

An immediate consequence of the predictions about animal color patterns (Endler, 1978) and these observations, is that no single color pattern is necessarily the best in one particular place. Several or many color patterns can be equally good matches to the background, hence equally fit, as long as they approximate the back-ground in patch size, brightness, and color distribution. We do *not* expect selection for any *one* color pattern at a particular place. This allows a lot of variation in the population. Since the least dangerous places are at the highest elevations in the streams, the genetic diversity will be (and is) highest in the headwaters. Gene flow downstream from low to high predation areas will maintain a high degree of polymorphism by a balance between gene flow and a selection gradient for crypsis. Given the possibility that the predators form a search image, and hence exercise frequency-dependent selection (preferentially eating the common forms; Clarke, 1969; Curio, 1976), and that there may be frequency-dependent mating (females choose rare type males; Farr, 1977), we have two additional reasons for the complex color pattern polymorphism in *P. reticulata*. Both frequency-dependent mating and predation favor variation in color patterns because they increase the fitness of rare or unusual color patterns. Color patterns can be different while still being equally cryptic, so a very high color pattern diversity is possible without a loss in fitness.

Granted that these factors favor polymorphism, why are there not more species with the same degree of polymorphism as guppies, and especially, why not within the family Poeciliidae? There are three possible and not exclusive reasons: habitat, species recognition, and automimicry.

Most members of the Poeciliidae live in habitats very different from *P. reticulata*. Although sometimes found in guppy-like habitats, *Poeciliopsis, Xiphophorus, Gambusia,* and Mollies are usually found in larger streams in the lowlands with sand or mud bottoms, often with a heavy growth of algae, and often with silty or green water (Rosen and Bailey, 1963; Rosen, Vrijenhoek, Schultz, *pers. comms.*). Relatively few populations live in clear streams with multicolored gravel bottoms; most live in a visually much simpler and plainer background. If the background is relatively simple, there are fewer ways of being different; and in order to match the

background even crudely, all bright colors are at a strong disadvantage. Consequently the color patterns are simpler and often lack the bright iridescence found in *P. reticulata*. Kallman (1975) summarizes the color patterns in *Xiphophorus,* fish typical of lowland habitats with relatively simple backgrounds.

If a color pattern polymorphism is too complex, and the species depends upon visual cues in species recognition, confusion with other species may result. This is discussed in some detail by Liley (1966), who considers how four species of Poeciliids (including guppies) maintain their integrity in Georgetown, Guyana. Visual species recognition sets an upper limit to the complexity of color polymorphisms in species which are sympatric through most of their geographic range with closely related species. Most Poeciliids are sympatric with one or more congenors, and *P. reticulata* is one of the few species which is the only representative of its family throughout virtually all of its range (Rosen and Bailey, 1963; pers. observ.). Guppies are marginally sympatric (parapatric) with *P. picta, P. parae* and *P. vivipara* at the mouths of rivers where the water becomes brackish, but the area of sympatry usually covers only 5 to 20 m in Venezuela, Trinidad, and Tobago. The populations in Georgetown studied by Liley (1966) were in extremely unnatural habitats (drains and artificial ponds), and the presence of *P. reticulata* there and in Paramaribo, Surinam, probably is a result of the very active and long standing tropical fish trade in the area. Guppies are not found outside these two towns anywhere in the Guyanas (pers. observ.; J. Price, pers. comm.). Guppies may be able to afford the luxury of a complex polymorphism because species recognition is not a problem through virtually all their range. *P. picta* and *P. parae* have simpler polymorphism (3–10 morphs), are found in relatively simple backgrounds, and usually live with congenors.

A third possible reason for the complex polymorphism may result from the combination of sterile streams where guppies are found, and sexual selection on the color patterns. Guppies have three kinds of colored spots: structural, carotenoid, and non-carotenoid pigments. Examples are blue, red, and black respectively. The carotenoid spots are dependent upon the carotenoids taken in the diet, and are brighter when food is very abundant, and can fade and almost disappear when food is very scarce (see Rothschild, 1975, for a discussion). The structural colors and black spots are independent of food. Black spots are good for species recognition and are not as visible to predators as are the other colors. Structural colors are conspicuous like carotenoids, but also very conspicuous to predators. Sexual selection for color patterns would work if there were a correlation between color pattern conspicuousness and some aspect of fitness.

Guppies live in a very sterile environment compared to other Poeciliids, and even in an absolute sense. In streams undisturbed by man, the forest canopy ranges from 50% to 100%, casting deep shade, and algae and other sources of carotenoids are scarce or absent. The gravel is clean and there is very little sediment in which small arthropods can live. Males with the brightest carotenoid spots would presumably be the best choice for females because they were able to obtain the best food. At the very least there would be a correlation between male fitness and carotenoid pigment brightness (excluding the effects of predators, or allowing predation and the "handicap principle"; Zahavi, 1975). This would favor females which chose males with the brightest colors. This is perhaps the only known example where a possible mechanism for the *origin* of sexual selection is known. In other species it is easy to see what maintains sexual selection, but not how it started.

If females simply select on the basis of brightness (not color), then there is a perfect opportunity for mimicry within the species. Males with bright structural colors are as bright or brighter than males with only carotenoid pigments, consequently they would be favored by females

also. Because the brightness of structural colors is independent of feeding success, in some cases, especially low food availability and low predation, males with structural colors will be favored over males with only carotenoids; the structural colors are false advertising for male fitness. But this cannot go too far or the correlation between brightness and fitness will decay, and females may no longer select for brightness. Thus guppies may have an automimicry system where the carotenoid spots are the model and the structural colors are the mimics. In such a system we expect that the mimics should not be more abundant than the models. In guppies we do find fish with carotenoid but no structural colors, but never with structural but no carotenoid pigments. This needs more study, but if true, the effect is to diversify color patterns within a population.

Thus guppies may have such an unusually complex color pattern because: (1) they live against a visually complex background, (2) through most of their range there is no opportunity for confusion with congenors, (3) frequency-dependent predation and mating favors variability, and (4) there may be automimicry between carotenoid and structural colors.

The general conclusion is that natural selection acts in a regular and predictable way on color patterns, though it may act differently among the components of a pattern. Sexual selection and other factors favor color pattern diversity within the constraints of background matching.

SUMMARY

1. It is predicted that the color patterns at a particular place are inconspicuous (cryptic) if they approximate the background in color spot size, brightness, and color distribution, and they are conspicuous when they deviate in one or more of these ways (Endler, 1978). The hypothesis is tested using *Poecilia reticulata,* a Poeciliid fish which is polymorphic for these color pattern parameters.

2. Experiments were set up to examine the effects of predation intensity and background patch size on greenhouse and field populations of *P. reticulata*. The results of the greenhouse and field transfer experiments were consistent and there was a remarkably close convergence on the color patterns of *P. reticulata* living in equivalent natural predation regimes.

3. Background matching is good; populations living on coarse gravel had larger spots than populations living on fine gravel, within a given predation intensity. The effect disappears in the absence of predation. Guppies become less conspicuous at higher compared to lower predation intensity: bright colors drop out and patch size is reduced.

4. Sexual selection increases conspicuousness and color pattern diversity. In the absence of predation, larger color spots were found on fine gravel and smaller spots were found on coarse gravel. Color pattern variation and patch size variation were greater in ponds with no predation compared to either high or low predation.

5. The complexity of the color pattern polymorphism in *P. reticulata* relative to other Poeciliids may result from more complex backgrounds, rare sympatry with congenors, and automimicry among different kinds of color spots.

6. The structural-carotenoid automimicry hypothesis provides one of the few examples in which a possible mechanism for the origin of sexual selection is known.

7. The effects of natural selection on color patterns of *P. reticulata* are predictable and repeatable; this is unusual in studies of natural selection. Natural selection acts differently on different components of the color patterns, hence the usual simplistic models of polymorphisms are not appropriate.

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