Phenotypic variation in male guppies from natural inland populations: an additional test of Haskins' sexual selection/predation hypothesis

Kirk O. Winemiller[1], Mitchell Leslie[1] & Robin Roche[2]
[1] *Department of Zoology and Texas Memorial Museum, University of Texas, Austin, TX 78712, U.S.A*
[2] *Department of Entomology, University of Arizona, Tucson, AZ 85721, U.S.A.*

Synopsis

In Venezuela, guppies, *Poecilia reticulata*, are found in a diversity of aquatic ecosystems fringing the western slope of the eastern Andes. These inland drainages are associated with large between-site variation in both physical and biotic environments. Numbers of potential guppy predators vary greatly between low diversity piedmont streams and high diversity llanos swamps. We analyze geographic variation in several phenotypic traits associated with conspicuousness of male guppies as an independent test of Haskins' (Haskins et al. 1961) hypothesis of natural balance between sexual selection (driving male conspicuousness) and predation (driving crypsis). Four sites were compared: a diverse llanos swamp (high predation), two Andean piedmont streams (intermediate and low predation), and a spring pool located south of Venezuela's Paría Peninsula (no aquatic predators). Because tropical wet and dry seasons are associated with varying degrees of environmental change at these sites, within-site seasonal samples provided an additional test of the role of selective predation on male phenotypes. Phenotypic traits associated with both size and coloration supported the sexual selection/predation hypothesis. Male guppies from the spring were generally more colorful than male guppies from inland drainages. Males from the diverse swamp site were smaller and less colorful than guppies from other sites. Males from the swamp population were smallest and least colorful during the early dry season, when diurnal aquatic piscivores were more diverse and abundant. Dominant spot pigments at each site were generally those that provided greatest contrast with the predominant environmental background color, lending further evidence that coloration patterns in male guppies enhance conspicuousness.

Introduction

In many organisms, courting males face a conflict between advertizing to females and remaining hidden from predators. Both sexual selection and selection for communication efficiency favor obvious signals. Female choice, for instance, frequently drives evolution of exaggerated male phenotypes or displays (Darwin 1871, Fisher 1958). In addition, apparent signals are more easily detected over background noise and can be transmitted farther than more cryptic displays (Hailman 1977). An obvious signal, however, carries a large risk; the performer advertises himself to predators as well as to potential mates. Many animals lessen this risk by displaying only when courting, rarely revealing brightly colored patches or obvious movements. Other animals are permanently on display, since their coloration or plumage is the signal. In this case, selection for predation avoidance can countervail sexual selection (Endler 1978). The optimal signal, therefore, represents an evolutionary bal-

ance between crypsis and conspicuousness, a balance that varies with risk of predation, optical characteristics of the background, and strength of sexual selection (Haskins et al. 1961, Endler 1978, 1983).

Haskins et al. (1961) and Endler (1978, 1980, 1983) studied the shifting balance between sexual selection and predation in producing coloration patterns of guppies (*Poecilia reticulata*, Poeciliidae) on the island of Trinidad. Male guppies are highly variable in patterns of carotenoid (red, orange, yellow), iridescent structural (metallic, green, blue), and melanistic (black) pigments. Although intensity of carotenoid colors can vary to some degree with diet (Endler 1980, 1983, Kodric-Brown 1985), positions and sizes of spots are genetically determined (Yamomoto 1975, Endler 1978). Sexual selection strongly favors showy, highly-contrasting males in this species. For instance, females choose the brightest and most colorful males against a white background (Kodric-Brown 1985). When the background (e.g., gravel substrate) contains colors found on the fish, males contrasting most strongly in spot color or spot size are preferred (Endler 1983). In the absence of predators, average number of spots per male increases evolutionarily over time (Endler 1980). In the natural setting, colorful males suffer higher risk of predation by diurnal piscivores than less colorful conspecifics (Haskins et al. 1961). For example, Endler has shown that the level of predation affects number and size of spots and frequency of colors, and that these characteristics evolve if predation intensity is altered. Guppies from streams with dangerous predators exhibit smaller spots and fewer spots of structural colors than those from streams with fewer and less dangerous guppy predators (Endler 1978, 1980). Since structural colors are highly reflective, they are probably more conspicuous than carotenoids over long distances (Endler 1983). When guppies were transplanted from streams with dangerous diurnal predators to streams with relatively innocuous predators, spot size, spot number, color diversity, and spot area increased after 15 generations (Endler 1980).

Endler (1978, 1980) investigated guppies from low diversity coastal drainages in Venezuela and Trinidad. Guppies are also found in piedmont streams in western Venezuela (Winemiller 1987a), thus providing independent systems for tests of Haskins' hypothesis. We examined guppies from three sites in western Venezuela and from a spring-head in northeastern Venezuela. The four sites vary greatly in the number of guppy predators and optic properties of the aquatic environment. Additionally, large-scale seasonal changes in habitat and local fish assemblages result in both spatial and temporal variation in predation intensity. We examined the effects of these seasonal changes within sites and the effects of between-site differences in predation pressure on the patterns of coloration exhibited by resident male guppies.

Methods

Study sites

Guppies were collected from four mainland locations in Venezuela during 1984 (Fig. 1). Fishes were seined (20 × 1.8 m, 12.7 mm mesh; 2.5 × 2 m, 3.2 mm mesh) and dipnetted every month from the floodplain and channel of Caño Maraca (abbreviated CM), a lowland creek of the Río Apure-Orinoco drainage in the western llanos (Portuguesa state; 8° 52' 30" N; 69° 27' 30" W). Eighty-eight fish species, including nine visually-hunting diurnal piscivores (Table 1), were collected at Caño Maraca over the course of 12 continuous months. During any given month, 41 to 63 fish species were captured. During the dry season at CM (Jan.–April), guppies achieved their highest densities in shallow vegetation-choked pools on the periphery of the main creek channel. For the most part, only very small fishes and species having special respiratory adaptations remained in deoxygenated pools of the creek channel during extended periods of the dry season (Winemiller 1987b, 1989a). With the initiation of heavy rains in May, the floodplain of CM is abruptly converted into a vast productive marsh. Guppy densities were low throughout the wet season (May–Aug.), although the absolute size of the local population presumably peaks in the newly created aquatic habitat of
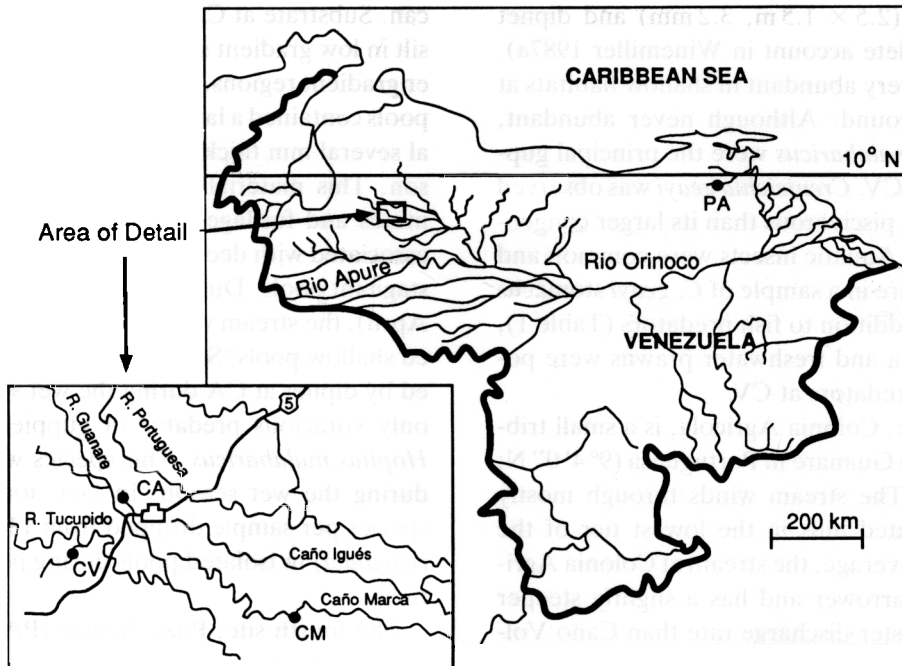
Fig. 1. Map of Venezuela showing location of study sites. Inset shows location of sites CM, CV, and CA in the western llanos (Río Apure drainage). PA is a spring pool of the Río San Juan drainage, Monagas state.

the floodplain. The floodplain gradually dried up from September to December (transition season). During the transition season, fishes (the majority being young-of-the-year) become increasingly concentrated into a smaller area of aquatic habitat. Fish densities in December were among the highest recorded for freshwaters (Winemiller 1987a). Fish mortality from predation is high during the transition season. Piscivorous fishes were diverse and abundant at CM during this time (Table 1). Dense schools of red-belly piranhas, *Pygocentrus notatus* (Characidae), were particularly active in deeper pool regions of the creek. Based on examination of large samples of stomach contents (Winemiller 1987a, 1989b) in which guppies and other small diurnal fishes taken from shallow environments were found, the most dangerous guppy predators at CM are *Hoplias malabaricus* (immature size classes), *Charax gibbosus, Crenicichla saxatilis*, and especially *Caquetia kraussii*. In addition, a number of invertebrates at CM were potential small fish-predators, including dityscid beetles, belostomatid and nepid hemiptera, and palaemonid

prawns. Although plant species relative abundances showed large temporal variation, a diverse assemblage of rooted and floating aquatic macrophytes was present year round at CM. The substrate consisted of mud and detritus, both within the main creek channel and peripheral floodplain (see Winemiller 1987a, 1987b, 1989a, 1989b for further descriptions of the aquatic environment at CM).

The second site, Caño Volcán (CV) is a low gradient tributary of the Río Tucupido (Apure-Orinoco basin). This small creek winds through the lowest tier of the Andean piedmont on the fringe of the western llanos (8° 59' 15" N; 69° 53' 0" W). Pool substrates at Caño Volcán consisted of sand and leaf litter, whereas cobbles and sand covered riffle regions. The creek's watershed was pristine forest in 1984, and aquatic macrophytes were essentially absent at CV throughout the year. Seasonal environmental variation at CV was limited primarily to brief flash floods during wet season downpours. The fish assemblage at CV consisted of essentially the same 20 species throughout the year, based on

monthly seine (2.5 × 1.5 m, 3.2 mm) and dipnet samples (complete account in Winemiller 1987a). Guppies were very abundant in shallow habitats at this site year round. Although never abundant, small *Hoplias malabaricus* were the principal guppy predators at CV. *Crenicichla geayi* was observed to be much less piscivorous than its larger congener, *C. saxatilis*. Aquatic insects were common and guppies were rare in a sample of *C. geayi* stomachs (N = 106). In addition to fish predators (Table 1), nepid hemiptera and freshwater prawns were potential guppy predators at CV.

The third site, Colonia Agricola, is a small tributary of the Río Guanare in Portuguesa (9° 4' 0" N; 69° 49' 0" W). The stream winds through mostly settled, deforested hills in the lowest tier of the piedmont. On average, the stream at Colonia Agricola (CA) is narrower and has a slightly steeper gradient and faster discharge rate than Caño Vol-

cán. Substrate at CA consisted of sand, litter, and silt in low gradient stretches, plus cobbles in steeper gradient regions. In addition, most low gradient pools contained a layer of flocculent orange material several mm thick, especially during the dry season. This material was apparently derived from molds and fusilage from iron-containing bacteria associated with decomposing vegetative detritus in stagnant pools. During the driest months (March–April), the stream was reduced to a series of isolated shallow pools. Sixteen fish species were collected by dipnet at CA during the wet season, but the only voracious predator of guppies present was *Hoplias malabaricus*. This species was found only during the wet season. In fact, total number of species per sample dropped from 13 to 1 (*Poecilia reticulata*) in isolated pools during peak dry conditions.

The fourth site, Pozo Azufre (PA), is a spring-

Table 1. Biotic and physical environmental differences between four Venezuelan sites containing guppies (* = common, W = wet season resident, T = transition season resident, D = dry season resident).

	Diurnal guppy predators	Dominant substrate (color)	Seasonality
CM	(Erythrinidae) *Hoplias malabaricus* WD* *Hoplerythrinus unitaeniatus* D (Characidae) *Acestrorhynchus microlepis* T *Charax gibbosus* WT* *Pygocentrus notatus* WT* (Cichlidae) *Astronotus ocellatus* WTD* *Aequidens pulcher* WTD* *Crenicichla saxatilis* WT *Caquetia kraussii* WTD* several aquatic invertebrate spp.*	mud, silt, detritus, aquatic vegetation (brown, black, and green)	extensive lateral sheet flooding during wet season severe fish crowding during transition season dessication and anoxia during dry season
CV	*Hoplias malabaricus* WD (Lebiasinidae) *Lebiasina erythrinoides* WD* *Aequidens pulcher* WD* *Crenicichla geayi* WD* nepid Hemiptera, prawns*	sand, cobbles, detritus (brown)	brief flash floods during wet season stable dry season flow
CA	*Hoplias malabaricus* W *H. unitaeniatus* W* (D) *Aequidens pulcher* W nepid Hemiptera*	sand, detritus, cobbles, iron-bearing flocculent matter (brown and orange)	stable wet season flow series of small isolated pools during dry season
PA	none	mineral sediments (blue/grey)	stable spring head

fed pool that gives rise to a small stream flowing into the Río San Juan near Venezuela's Paría Peninsula (Monagas state; 10° 17' 0" N; 63° 7' 0" W). The pool's water is rich in sulphur bearing minerals, and its substrate consists of gravel covered by a layer of blue-grey mineral precipitates several centimeters thick. The pool was approximately 30 m in diameter and 1.5 m maximum depth, and serves as a popular bathing area for the local populace. The pool contained no aquatic macrophytes. Only one fish species (*Poecilia reticulata*) was collected or observed on the single date that it was visited (Aug. 30, 1984). The site was surrounded by strong sulphur odor, and we presume other fish species are intolerant of the pool's water chemistry. Only two species, *Caquetia kraussii* (Cichlidae) and *Eleotris amblyopsis* (Eleotridae), were found approximately 0.5 km downstream from PA on the periphery of the Río San Juan's inundated estuary.

Measurements

A sample of fishes collected from each site was preserved in 15% formalin and later transferred to 45% isopropanol for storage. Stomach contents were quantified for a sample of each species taken during each monthly collection at CM and CV (details in Winemiller 1987a, 1989b). Mature male guppies (classified as such if the gonopodium appeared fully formed with a curved, hook-like configuration at the distal tip of the 3rd and 4th anal fin rays) in each sample were measured for standard length and length of the dorsal and caudal fins (straight line measure from base to distal tip of longest fin ray to nearest 0.1 mm). The height and length of each clearly distinguishable spot on preserved specimens was measured (nearest 0.1 mm) using a dissecting scope fitted with an ocular micrometer. Sample sizes for the four sites are CM = 53, CV = 60, CA = 37, PA = 31.

Three types of spots were measured on preserved specimens: black, white, and brown (the latter were actually patches of diffuse dark pigment). The range of living color patterns represented by each type of spot on preserved specimens was determined by photographing eight live male

guppies, preserving and storing them in the same manner as field specimens for 2 months, then matching preserved specimens with their photographs. We obtained highly consistent correspondence between preserved and living colors. Black spots on preserved specimens always corresponded to black spots on living guppies. White spots on preserved specimens corresponded with carotenoid colors: red, orange, and yellow. Brown spots on preserved specimens corresponded with iridescent structural colors: blue, green, and silver. In a few instances, spots associated with structural (and to a lesser extent carotenoid) colors on living fishes were not visible on the preserved specimens. Consequently, our estimates of spotting patterns on preserved specimens should be considered conservative and not absolute measures. All specimens are deposited in the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas.

Analyses

We exploited environmental differences (i.e., predation threat and background color) between sites to test Haskins' (Haskins et al. 1961, Endler 1978) hypothesis. Using the criteria of species richness of piscivores, predatory species' relative abundances, and the relative threat posed by each predatory species (according to stomach content analysis), we ranked the predation threat to guppies at the four sites as (from greatest to lowest): CM >> CV > CA >> PA (Table 1). Based on seasonal and site variation described above, predation threat was ranked transition > dry > wet at CM, dry = wet at CV, and wet > dry at CA. The springfed pool, Pozo Azufre, is expected to show very little seasonal environmental variation. In addition, PA contained no dangerous aquatic guppy predators when sampled in 1984. Given the dominant background color of substrates, we predicted the following spot pigments would contrast greatest at each site: CM (carotenoid), CV (iridescent), CA (iridescent and melanistic), PA (carotenoid and melanistic).

For each male, nine variables were analyzed: number of spots of each color, mean spot area

(= spot height × length in mm²) for each color, dorsal fin length, caudal fin length, and standard length. To equalize variances across groups, number of spots was transformed by $(\chi + 1)^{1/2}$ prior to statistical analysis (Snedecor & Cochran 1980). Log$_{10}$ transformations were applied to mean area of brown and black spots to normalize data. Analysis of variance and covariance were performed on male phenotypic characters, testing first for site effects, then separately for seasonal effects within sites.

Results

Inter-site comparisons

According to Haskins' hypothesis, one would predict that guppies should be least conspicuous at CM, the site containing the most diurnal piscivores, and most conspicuous (i.e., attractive to females) at PA, where no aquatic predators threaten guppies. Coloration and size patterns generally confirm this prediction. CM guppies had fewer and smaller reflective, iridescent (= brown) spots and fewer black spots than fish from other sites (Fig. 2, 3). PA males had more carotenoid (= white) and black spots and larger iridescent spots than males from CM. Since CM guppies were also smallest (Fig. 4), reduced coloration potentially could be influenced by allometric effects on average numbers and areas of spots. To account for potential allometric relationships, Endler (1978, 1980) adjusted his measures by standard length (arc-sin $\sqrt{\text{spot length/body length}}$) and found no qualitative change in results. He concluded that body size was not an important factor in determining spot size. We tested for body size effects with analysis of covariance, using standard length as the covariate. Only one color character, number of iridescent spots per fish, showed significant covariance with length (Table 2). Number of carotenoid spots per fish did not meet the homogeneity of slopes assumption (Sokal & Rohlf 1981) and consequently was not tested for intersite differences. Number of iridescent spots differed significantly between sites when corrected for body size (Fig. 2, Table 2).

Although correction for length removed almost all of the disparity between CM, CV and PA males, CA fish still had the most iridescent spots.

Both dorsal and caudal fins are usually pigmented and contribute to overall male conspicuousness. No significant covariation was found between caudal fin length and SL, whereas dorsal fin lengths were significantly associated with SL (Table 2). Adjusting for SL did not fully eliminate between-site variation in length of dorsal fins. Again, PA fish had largest caudal and dorsal fins, and CM fish had smallest caudal fins. When adjusted for SL, dorsal fins of CM males were smaller than those of PA fish (Fig. 4).

Analysis of variance was used to test for main effects on size-independent variables. Standard length, black spot area, iridescent spot area, and number of black spots varied significantly among sites (Table 2). Contrast analysis (Snedecor & Cochran 1980) was used to test for intersite differences. In every comparison except number of black spots (where CM = CV = CA), CM fish had the lowest values. Guppies from PA had the most and largest black spots, whereas CA fish had the largest iridescent spots. PA males were not significantly larger than CV or CA fish.

Within-site, seasonal comparisons

Because guppies at the relatively constant environment at PA were sampled only once, they are not among the seasonal within-site comparisons. At CM, body size was a significant covariate with number of iridescent spots per fish, and no significant seasonal differences were found after size correction. Number of black and carotenoid spots differed across seasons at CM (Fig. 5). Males had fewer black spots during the transition season of high predator densities. In addition, black spots were significantly larger during the dry season (Fig. 6). Males had more carotenoid spots during the dry season when predators were relatively scarce at CM. SL and dorsal fin length were significantly smaller at CM during the dry season, however mean dorsal fin length showed no seasonal variation when adjusted for SL (Table 3, Fig. 7). In
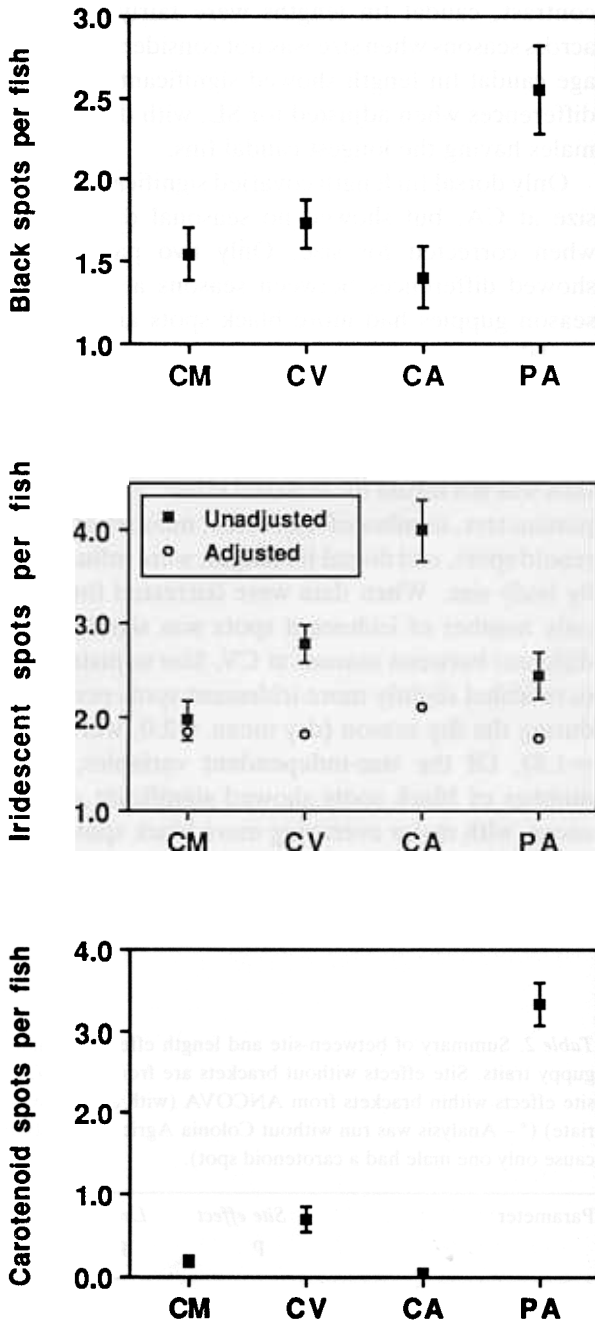
Fig. 2. Average number of spots per fish across four study sites arranged in a gradient of decreasing predation threat. Vertical bars represent ± one standard error. Adjusted means (values corrected for standard length with ANCOVA) are plotted as open circles in the second panel. Iridescent spots correspond to brown patches on preserved specimens, carotenoid spots correspond to white patches, and black spots correspond to black (melanistic) patches.
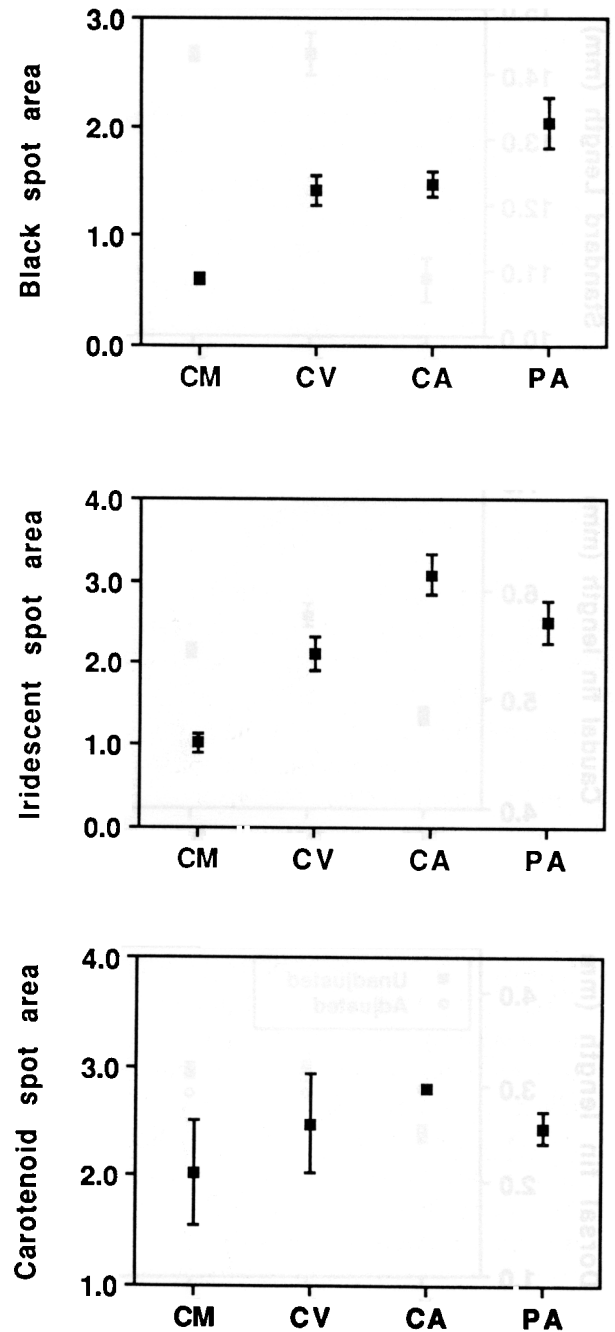
Fig. 3. Average areas of black, iridescent, and carotenoid spots (mm²) on male guppies from four sites. Symbols are the same as in Fig. 2.
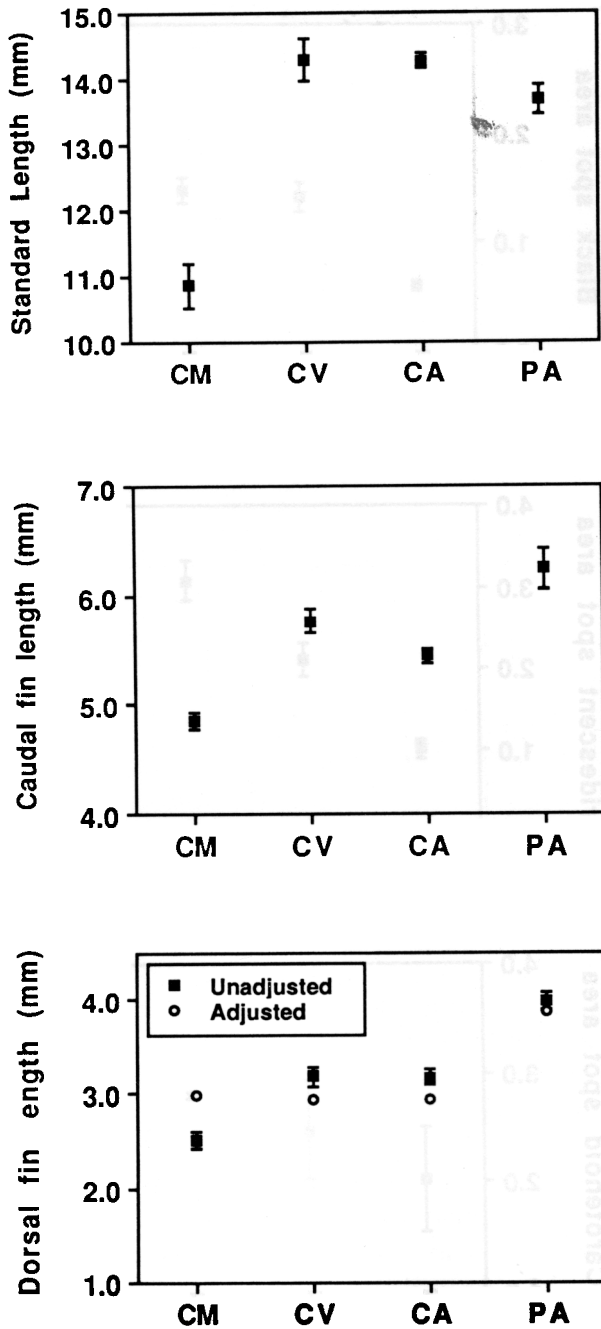
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Fig. 4. Average body length (SL) and fin lengths of male guppies from four sites. Symbols are the same as in Fig. 2 (open circles = mean dorsal fin lengths adjusted for standard length).

contrast, caudal fin lengths were fairly uniform across seasons when size was not considered. Average caudal fin length showed significant seasonal differences when adjusted for SL, with dry season males having the longest caudal fins.

Only dorsal fin length covaried significantly with size at CA, but showed no seasonal differences when corrected for size. Only two parameters showed differences between seasons at CA: dry season guppies had more black spots and longer caudal fins.

CV guppies showed more complex relationships among phenotypic measures. Black spot area showed heterogeneous slopes in ANCOVA, and thus was not tested for seasonal effect. Three other parameters, number of iridescent, number of carotenoid spots, and dorsal fin length, were influenced by body size. When data were corrected for size, only number of iridescent spots was significantly different between seasons at CV. Size adjusted data revealed slightly more iridescent spots per male during the dry season (dry mean = 2.0, wet mean = 1.8). Of the size-independent variables, only number of black spots showed significant differences, with males averaging more black spots during the dry season.

Table 2. Summary of between-site and length effects on male guppy traits. Site effects without brackets are from ANOVA, site effects within brackets from ANCOVA (with SL as covariate) (* – Analysis was run without Colonia Agricola fish, because only one male had a carotenoid spot).

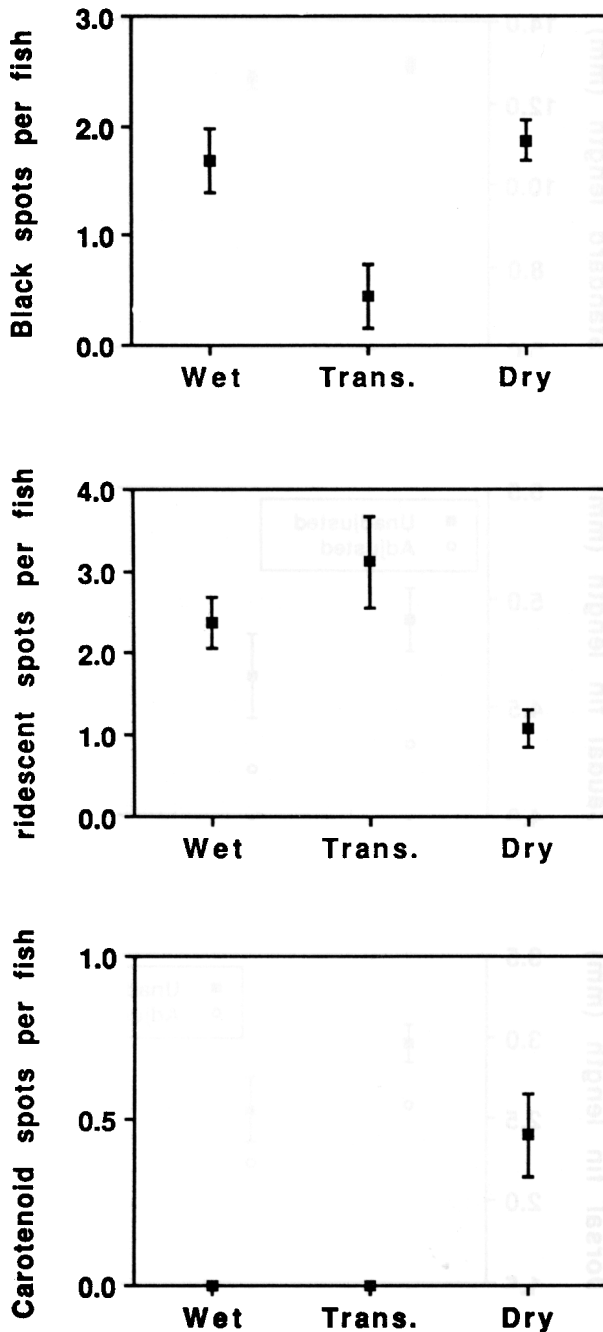| Parameter	Site effect p	Length effect p
No. iridescent spots per fish	[0.002]	< 0.001
No. black spots per fish	0.001	NS
No. carotenoid spots per fish	–	heterogeneous slopes
Mean iridescent spot area	< 0.001	NS
Mean black spot area	< 0.001	NS
Mean carotenoid spot area*	NS	NS
Standard length	< 0.001	–
Caudal fin length	< 0.001	NS
Dorsal fin length	[< 0.001]	< 0.001

Fig. 5. Mean number of spots per fish during three seasons at Caño Maraca. Predation intensity follows the seasonal gradient: Transition season (Trans.) > Wet > Dry.
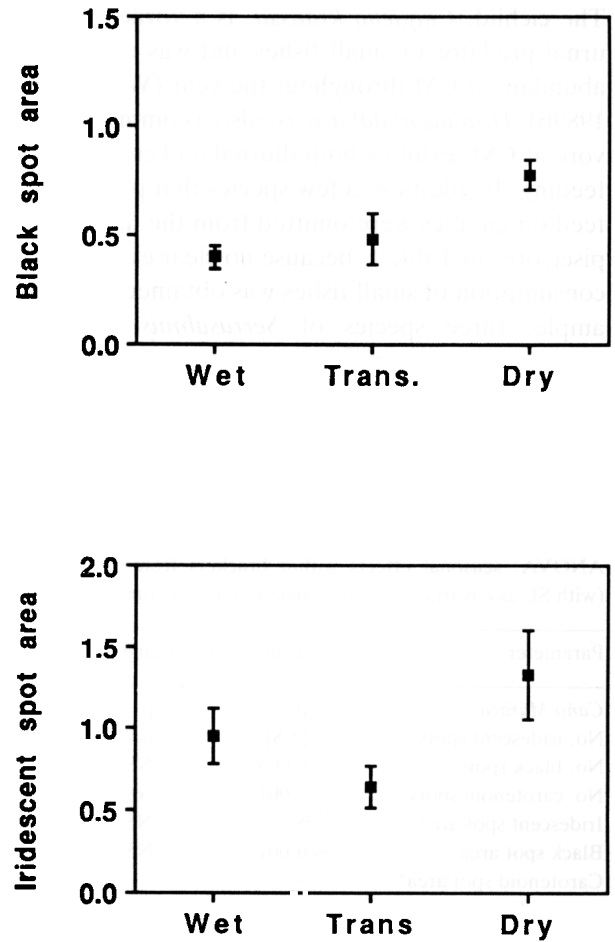

Fig. 6. Seasonal differences in average area of black and iridescent spots (mm²) on male guppies from CM. Carotenoid spots were only present in dry season fish.

Discussion

Both between-site and within-site seasonal comparisons of male guppy phenotypes largely corroborated Haskins et al. and Endler's earlier findings for coastal populations. Even after allometric effects had been adjusted for statistically, between-site variation in coloration and fin dimensions corresponded to a general gradient of larger more colorful fish at sites having fewer dangerous guppy predators. Male guppies from the diverse fish assemblage at Caño Maraca were small and comparatively drab in appearance. At least seven species of visually hunting, diurnal piscivores where present at CM during a major portion of the annual cycle.

The cichlid, *Caquetia kraussii*, is a voracious, diurnal predator of small fishes and was extremely abundant at CM throughout the year (Winemiller 1989b). *Hoplias malabaricus*, also a common piscivore at CM, exhibits both diurnal and crepuscular feeding. In addition, a few species that potentially feed on guppies were omitted from the list of CM piscivores in Table 1, because no clear evidence of consumption of small fishes was obtained. For example, three species of *Serrasalmus* piranhas (Characidae) were predominately fin specialists at CM.

Mean body size and number of spots per fish

Table 3. Summary of within-site seasonal and length effects on male guppy traits. Seasonal effects without brackets are from ANOVA, seasonal effects within brackets from ANCOVA (with SL as covariate) (* – insufficient data for comparison).

| Parameter	Season effect	Length effect
Caño Maraca	p	p
No. iridescent spots	[NS]	0.033
No. black spots	0.003	NS
No. carotenoid spots	<0.001	NS
Iridescent spot area	NS	NS
Black spot area	<0.001	NS
Carotenoid spot area*	–	
Standard length	<0.001	–
Caudal fin length	[0.013]	0.004
Dorsal fin length	[NS]	0.006
Caño Volcán		
No. iridescent spots	[0.019]	<0.001
No. black spots	0.01	NS
No. carotenoid spots	[NS]	<0.001
Iridescent spot area	NS	NS
Black spot area	–	heterogeneous slopes
Carotenoid spot area	NS	NS
Standard length	NS	–
Caudal fin length	NS	NS
Dorsal fin length	[NS]	<0.001
Colonia Agricola		
No. iridescent spots	NS	NS
No. black spots	0.028	NS
No. carotenoid spots*	–	–
Iridescent spot area	NS	NS
Black spot area	NS	NS
Carotenoid spot area*	–	–
Standard length	NS	–
Caudal fin length	0.015	NS
Dorsal length	[NS]	0.005
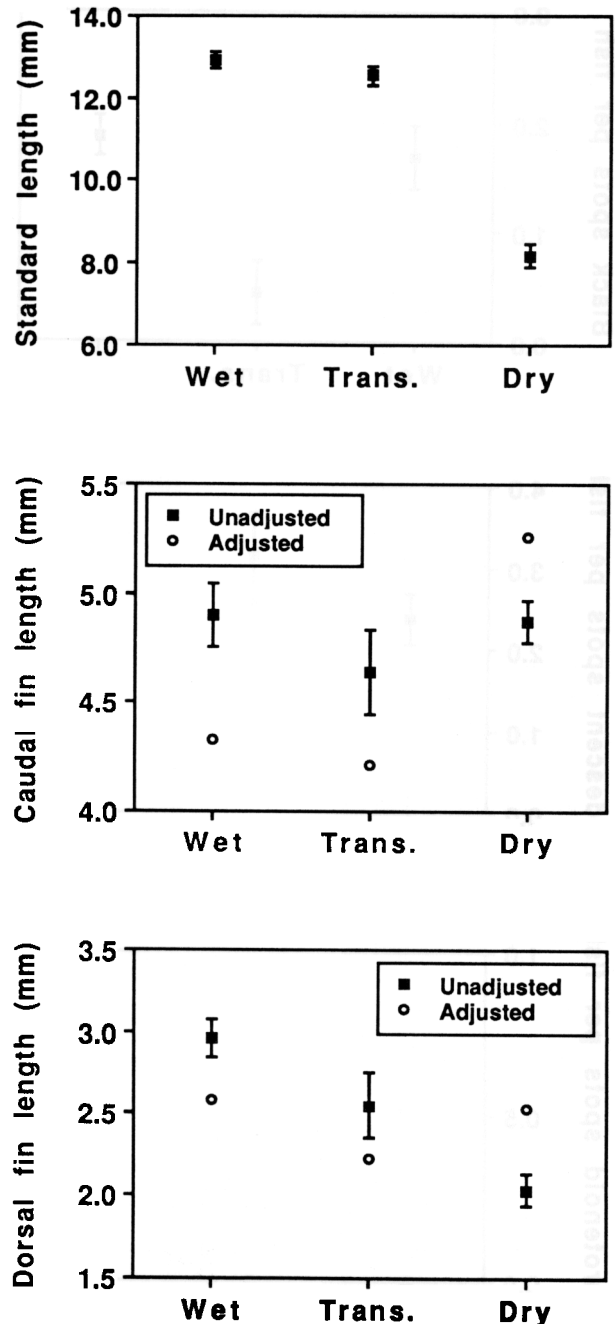
Fig. 7. Seasonal differences in body length and fin lengths of male guppies at CM (open circles = mean fin sizes adjusted for standard length).

were lower for CM males than mean values report-ed by Endler (1983) for coastal Venezuelan and insular guppies. Mature males at CM averaged only 10.9 mm SL (range 6.6–14.6 mm) compared to means of 13.0–15.6 mm at high predation sites in Trinidad (Reznick & Endler 1982). In addition to having a smaller size at maturation, female guppies from high predation sites in Trinidad demonstrated higher relative reproductive investment (Reznick & Endler 1982). High adult mortality from preda-tion may select for life histories associated with early maturation and a high intrinsic rate of pop-ulation increase (Stearns 1976, Reznick & Endler 1982). Not only would earlier maturation increase the likelihood of successful reproduction by an in-dividual prior to it being eaten, but reproducing earlier reduces generation time and functions to increase the intrinsic rate of increase of the geno-type or population, all other factors being equal (Lewontin 1968).

Caño Volcán and Colonia Agricola males had mean spot values similar to the values obtained by Endler (1983) for coastal guppies at high predation *Crenicichla* and *Eleotris* sites. CV was similar in many of its environmental features to Endler's *Crenicichla* sites (e.g., small stream, forested wa-tershed, large guppy population, similar predator assemblages). Pozo Azufre fish had body size and spot numbers comparable to those of Endler's low and intermediate predation populations. PA males averaged more black spots per fish (2.6) than En-dler's lowest predation sites (1.9–2.3 spots per fish), but slightly smaller carotenoid and iridescent spots (Fig. 2, 3 here compared with Fig. 2, 3 in Endler 1983). In addition to the effects of preda-tion, differences in non-melanistic spotting could have been influenced by methodology, since our measurements were made on preserved specimens.

Only three out of nine male traits at CV and one out of nine at CA revealed significant seasonal effects. By comparison, five of nine characteristics showed significant seasonal effects at CM, the most seasonally variable site. CM was a particularly haz-ardous environment for guppies during the transi-tion season when fishes, many of them piscivores, attained high densities in the shrinking aquatic hab-itat of the estero. Demographic effects of intense predation on small, shallow water-dwelling fishes at CM are well illustrated by the killifish, *Rachovia maculipinnis* (Cyprinodontidae). No *Rachovia* were found at CM during the dry season, a period when killifish survive as resting embryos in the substrate. *Rachovia* experienced a rapid popula-tion increase following the initiation of the wet season in late May. In spite of virtually continual reproduction and recruitment during the transition season, *Rachovia* gradually declined from being one of the most common wet season species to a point in which no adults could be found. Because *Rachovia* frequently live for two years or more in aquaria, predation must be the principal agent eliminating the dry season adult stock at CM (*Ra-chovia* were identified in several fish stomachs). Although guppies were abundant and reproduc-tively active in shallow, dry season CM pools, they reached their greatest population size during the benign wet season (collections made during each season by Winemiller (1987a) produced: $N_{dry} =$ 105, $N_{wet} = 111$, $N_{trans} = 97$). Extensive lateral sheet-flooding of the estero should have reduced encounter rates with potential predators. Like *Ra-chovia*, guppies probably suffered greatest expo-sure to intense predation during the later stages of the gradual dessication of the estero, when most fishes at CM were confined to the main creek chan-nel. Guppies were least exposed to aquatic preda-tors during the peak dry season, when many pisci-vores emigrated from the estero region in response to high temperatures and aquatic hypoxia (Wine-miller 1989a, 1989b). Most guppies were found in shallow, vegetation-choked pools scattered along the creek channel during the dry season. Subadult *Hoplias* and *Caquetia* were relatively uncommon and probably the only significant diurnal aquatic piscivores in these microhabitats.

Dry season males were smaller and had more black and carotenoid spots, larger black and iri-descent spots, and relatively longer caudal fins than transition season males at CM. Since diurnal visual hunters were less common during the peak dry season at this site, greater spotting in dry season males is consistent with the sexual selection/preda-tion hypothesis. Yet, smaller males are less con-spicuous and should suffer reduced predation. Be-

tween-site comparisons both here and in earlier studies of coastal guppies show smaller males in association with greater predation threat (Liley & Seghers 1975, Endler 1978, Reznick & Endler 1982). Seasonal size differences at CM run counter to this trend; males were smallest during the period associated with the fewest adult guppy predators. Because the dry season lasted only about four months, it is unlikely that guppies had passed through a sufficient number of generations (two or three at most) to evolve a genetic basis for observed phenotypic differences. One possible explanation is that other kinds of predators were selectively feeding on larger males during the dry season. A variety of birds (e.g., herons, egrets, ibises) and two facultative air-breathing, nocturnal fish predators [*Gymnotus carapo* (Gymnotidae) and *Synbranchus marmoratus* (Synbranchidae)] could have affected guppy populations confined in shallow dry season pools. With respect to body size, terrestrial avian and nocturnal fish predators may have caused a trend consistent with a hypothesis of greater dry season predation on CM guppies. CM guppies were more vulnerable to avian predators during the dry season than any other time of year. Size and motion are important cues for bird predators (Seghers 1974). Guppy color characters probably influence bird attack rates very little, because the dorsal surface is normally dark (countershaded) and spotting is found primarily on the sides of males.

A second hypothesis that may explain smaller dry season males at CM involves nutrition and size of maturation. Male guppies, in fact most male poeciliids, are assumed to have determinate growth (i.e., negligible growth following sexual maturation, Borowsky 1973, Reznick & Endler 1982). Guppies are more resource-limited during the dry season than any other time during the annual cycle of ecological events at CM. Wet season flooding is associated with a bloom of aquatic primary production in a greatly expanded aquatic environment (Winemiller 1987a). Diets of CM guppies were dominated by diatoms and filamentous algae (55% by volume, N = 22) during the wet season. During the dry season, fine detritus was the major diet component (45% by volume, N = 24) with algae forming less than 30% of the diet by volume. Expression of carotenoid pigments in CM fish apparently was not greatly limited by carotenoid compounds in consumed algae (Endler 1980, Kodric-Brown 1985), since dry season males had more and larger carotenoid spots than wet season fish (Fig. 6, 7). The smaller size of dry season males relative to wet season fish was likely due to environmental conditions, either diet or temperature or both. On average, shallow dry season pools inhabited by guppies were 6.1° C warmer than aquatic environments in the flooded estero during the wet season (mid-afternoon samples, N_{dry} = 14, N_{wet} = 4).

Comparison of the dominant spot pigments at each site are consistent with Endler's (1978) observation that conspicuous colors should contrast with ambient optic signals. For example, guppies with large spots should exhibit greatest contrast against fine-grained substrates, whereas small spots should produce greater contrast (hence conspicuousness) against a coarser gravel background. All four of the Venezuelan study sites had fine-grained substrates, ranging from fine sand to mud and smooth flocculent sediments (Table 1). Large spots should enhance visual contrast with the background at each of our study sites. However, the dominant color of substrates varied considerably between sites. At Colonia Agricola, where dominant background colors were orange and brown, spots composed of iridescent structural pigments (blue, green, silver) were most numerous and larger (Fig. 2, 3). CA males displayed virtual absence of carotenoid spots (red, orange, yellow). Blue-grey mineral deposits dominated the visual background at Pozo Azufre, and male guppies had numerous large black and medium-sized carotenoid spots but relatively few iridescent structural patterns (Fig. 2, 3). Clearly, spot pigments most similar to the dominant visual background at two sites with the lowest threat of predation from diurnal aquatic piscivores were not significantly accentuated in males.

Factors shown to influence male size and coloration in coastal guppy populations (Endler 1978, 1980, 1983) appear to operate on distant inland populations of *Poecilia reticulata* in a very similar fashion. Sexual selection and predation yield an

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evolutionary balance in phenotypes involved in male showiness, given the optic properties of local environments. Female choice for large colorful males favors the retention of genes for elements of male conspicuousness in guppy demes. Males that are too conspicuous are eliminated by predation in diverse fish assemblages of the western llanos. Recently, Endler (1987) showed that male guppies can alter components, intensity, or diel timing of courtship displays in response to the relative threat of predation. Where predation is very intense, this behavioral strategy probably can offset the impact of predation to some degree. Independent confirmation of predicted patterns of geographical variation in guppy phenotypes associated with male conspicuousness suggests that behavioral mechanisms do not fully subjugate the evolutionary impact of predation.

Acknowledgements

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