Research

Oikos 000: 000–000, 2008
doi: 10.1111/j.2008.0030-1299.16354.x,

Subject Editor: Stig Larsson, Accepted 30 December 2007

Fish and dragonfly nymph predators induce opposite shifts in color and morphology of tadpoles

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Many prey species, including amphibian larvae, can adaptively alter coloration and morphology to become more or less conspicuous to predators. Despite abundant research on predator-induced plasticity in tadpoles, the combination of color and morphological responses to predators remains largely unexplored. We measured predator-induced morphological and color plasticity in tadpoles. We reared tadpoles of the neotropical treefrog *Dendropsophus ebraccatus* with dragonfly nymph or fish predators, or in a predator-free control. After 10 days, we digitally photographed tadpoles and measured eight morphometric variables and five tail color variables. Tadpoles reared with nymphs developed the largest and reddest tails, but incurred a developmental cost, being the smallest overall. Cues from fish induced an opposite tail phenotype in tadpoles, causing shallow achromatic tails. Control tadpoles developed intermediate tail phenotypes. This provides the first experimental evidence that tadpoles can shift both color and morphology in opposite, predator-specific directions in response to a fish and an odonate predator. Despite mean differences, however, there was substantial variation in the degree of phenotype induction across treatments. Tail redness was correlated with tail spot size, but not perfectly, indicating that color and morphology may be partially decoupled in *D. ebraccatus*. Balancing selection from multiple conflicting predators may result in genetic variation for developmental plasticity.

Many sensory modalities are employed in predator–prey detection and assessment (Barbosa and Castellanos 2005). In both terrestrial and aquatic habitats, prey detect predators with chemosensory, tactile, acoustic and visual cues (Dodson et al. 1994, Chivers and Smith 1998, Barbosa and Castellanos 2005). Upon detecting predators, many invertebrate and vertebrate prey change their phenotype by altering behavior, morphology or chemistry in ways that increase their survival (Tollrian and Harvell 1999, Benard 2004). Plants show a similar ability to alter their chemistry as a defensive response to herbivores (Karban and Baldwin 1997).

Color can have considerable effects on predator–prey interactions. Cryptic phenotypes are common in nature and are presumably strongly selected for by predators (Norris and Lowe 1964). The use of color by animals is highly context dependent; the same color can function for communication or crypticity based on the background environment (Marshall 2000) and the perception of color changes with environmental conditions (Seehausen et al. 1997). Many animals do not use coloration for crypsis, but instead use brightly colored and expendable body parts to direct predator strikes away from more valuable body regions (Castilla et al. 1999, Van Buskirk et al. 2003). Predator-induced color change may thus serve either of two functions; to increase prey crypticity or to create a defensive lure phenotype. Multiple predator hunting strategies, combined with variable uses of induced coloration, will lead to differential selection upon prey species and the evolution of predator-induced color plasticity (McCollum and Van Buskirk 1996, McCollum and Leimberger 1997, Van Buskirk and McCollum 2000a, Van Buskirk and Schmidt 2000, Richardson 2006). We may even expect predator-specific color responses by prey, as has been documented for morphological traits (Relyea 2001, 2003, 2004). What remains less explored, however, is what role color might play in induced phenotypes, and how prey might integrate color into predator specific defensive phenotypes. Color change represents an important phenotypic modification in a broad range of organisms and a more rigorous analysis of predator-induced coloration and morphology, and the link between them, is necessary.

During the past 20 years, it has become evident that animals can dramatically alter morphology in response to cues from predators. For example, aquatic invertebrates such as larval odonates (Arnqvist and Johansson 1998, Dahl and Peckarsky 2002), a snail (Trussell 1996) and a marine bryozoan (Harvell 1998) all develop morphological defenses in response to chemical cues from predators. Amphibian larvae also alter development in response to predators, often developing fine tuned, predator-specific phenotypes that involve morphological and behavioral changes (Relyea 2001, Wilson et al. 2005). In addition, many amphibian larvae can change color (McCollum and Leimberger 1997, Van Buskirk and Schmidt 2000). Until now, most studies of tadpole color plasticity have compared tadpoles to

standardized color plates (LaFiandra and Babbitt 2004), compared the presence or absence of tail spots (McCollum and Leimberger 1997) or used rankings of 'conspicuousness' or 'intensity' (McCollum and Van Buskirk 1996, Van Buskirk and McCollum 2000a, Richardson 2006). These methods can be highly subjective (Endler 1990) and none of these studies quantitatively analyzed induced coloration, limiting our understanding of the potential specificity and ecological role of color change.

High quality digital photography and computer image analysis offers a simple, inexpensive method for measuring color that should be useful to researchers in many fields. Digital images are optimized for the human visual system and represent colors by varying the ratios of red, green and blue (R, G and B, respectively; hereafter 'RGB'), which correspond roughly to our long, medium and short wavelength color photoreceptors (Endler 1990, Fleishman et al. 1998). Thus unlike spectrophotometry, which quantifies reflectance across wavelengths within and outside the human visual spectrum, analyses based on digital images cannot be used to model how animals with different visual systems view color (Fleishman et al. 1998). Likewise, standard digital color images are not appropriate as experimental stimuli for animals with visual systems different from humans (Fleishman et al. 1998) because standard digital cameras do not capture the infrared or ultraviolet spectrum, although it is possible to do so with specially designed cameras, lenses and/or filters. Despite these limitations, our present goal is to classify what colors of the visible spectrum are present and for this purpose digital photography is a suitable method (Gerald et al. 2001).

We measured predator-induced developmental plasticity in tadpoles of the leaf-breeding neotropical treefrog, *Dendropsophus ebraccatus* (formerly *Hyla ebraccata*). We reared tadpoles alone or in the caged presence of either a fish (*Astyanax ruberrimus*; Characidae) or dragonfly nymph (*Pantala flavescens*; Libellulidae) predator and measured body and tail morphology and tail color. Based on prior research, we hypothesized that fish and dragonfly predators would drive phenotypes in opposite directions, such that tadpoles reared with fish would have the smallest, least colorful tails (Caldwell 1982) and tadpoles raised with dragonfly nymphs would have the largest, brightest tails (McCollum and Leimberger 1997). We did not, however, have an a priori hypothesis about the specific color of tails.

Material and methods

Induction experiment

On 17 June 2005 we collected seven amplectant pairs of *D. ebraccatus* adults from Quarry Pond, Gamboa, Panama. Pairs were placed in plastic bags with a small amount of water and allowed to breed overnight in the laboratory. All pairs mated successfully, yielding a total of $\sim$2100 eggs, and were returned to the pond the following day. We hung all egg clutches above a single 6 l container of aged tap water and misted them frequently to maintain hydration. All eggs hatched by 21 June, and families mixed in the water. Because handling new *D. ebraccatus* hatchlings can cause substantial mortality (Touchon pers. obs.), hatchlings were left untouched for two days before beginning the experiment. On 19 June, we collected 20 *A. ruberrimus* (2.67 ± 0.05 mm total length, mean $\pm$ SE) and 20 *P. flavescens* nymphs (1.73 ± 0.05 mm total length). Both predators are common and occur in multiple *D. ebraccatus* ponds in Gamboa, including Quarry Pond where the frogs were collected for this experiment.

The experiment was conducted from 24 June to 4 July in 32 cm round opaque plastic tubs with 5 l aged tap water. A 9 cm diameter container with mesh sides was placed in the center of each container. The outer portion of each tub contained 20 *D. ebraccatus* tadpoles (initial size, 6.28 ± 0.03 mm total length) drawn from the pooled hatchlings, two large leaves and a small amount of filamentous algae. The inner container held a predator (fish or dragonfly nymph) or was a predator-free control ($n = 20$ replicates per treatment). All inner containers contained a stick for predators to perch on. Predators never came into physical contact with test tadpoles. Predators were fed five *D. ebraccatus* tadpoles every three days for the duration of the experiment. Tadpoles in each replicate were fed two pellets of rabbit chow (ca 50 mg) every three days, always on the day after predators had been fed. This amount of food was essentially ad libitum as there was always a small amount of food remaining at the next feeding. The inner containers were checked every day for dead or metamorphosed predators, and predators were replaced as necessary. Control treatments were also checked, to ensure that there was no handling bias between treatments. Predators were also replaced if they had not eaten all of their tadpoles by the next feeding date.

Morphometric and color analyses

On 4 July 2005, we removed all tadpoles and randomly selected ten from each replicate to photograph. Tadpoles were lightly anaesthetized with MS-222 and digitally photographed in both dorsal and lateral views with a Nikon D70 digital camera (6.1 Megapixel) with built-in flash and a Tamron 90 mm macro lens. All photos were manually focused and taken with an F/6.3 aperture, a 1/60th second exposure time, and a +0.7 exposure compensation. Ambient overhead lighting was constant during photography. Anaesthetized tadpoles were held between two stationary pins in a shallow water bath, to allow the body to lay flat naturally. Five tadpoles were photographed at a time. A ruler and white color plate were included in the frame of view for scale and brightness calibration. Anesthesia lasted only a few minutes and no mortality occurred during the process. Morphology and tail coloration were analyzed using ImageJ 1.34s (NIH). Treatments and replicates were fully randomized prior to photography, and image analyses were conducted blindly to ensure no measurer bias.

We measured tadpole total length (TTL), body length (BL), head width at the eyes (HW), tail length (TL), tail muscle width at the base of the tail (TMW), tail muscle depth at the base of the tail (TMD), and maximum tail fin depth (TD) (Fig. 1A–B). *Dendropsophus ebraccatus* tadpoles have a conspicuous pigmented area at the posterior end of

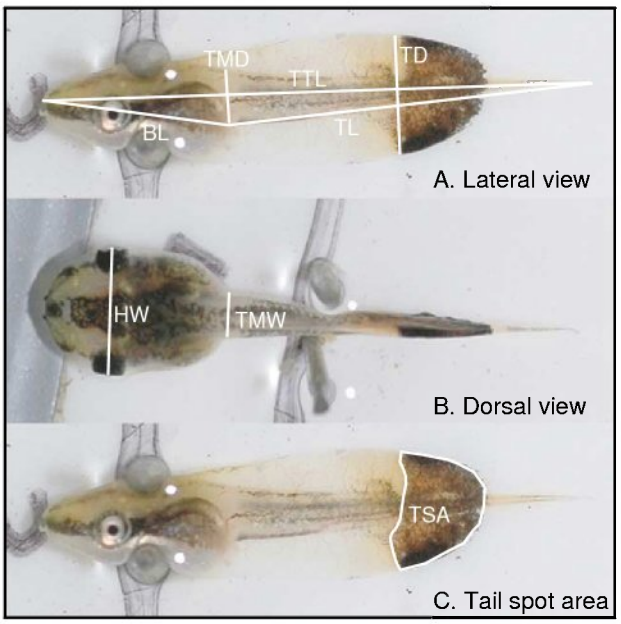

Fig. 1. The eight morphological variables measured, shown on dorsal and lateral views of the same *Dendropsophus ebraccatus* tadpole. Variables were total tadpole length (TTL), body length (BL), tail length (TL), tail muscle depth (TMD), tail fin depth (TD), head width (HW), tail muscle width (TMW), and tail spot area (TSA).

the tail. This spot was outlined using the freehand tool in ImageJ and the area of the tail spot (TSA) was measured (Fig. 1C). Color (RGB) of the entire tail spot was measured using the RGB Measure function and hue and chroma were measured using the HSB Stack and Measure functions. ImageJ measures RGB, hue and chroma values on a scale of 0–255. For hue, zero represents pure red and increasing values represent colors of shorter wavelengths; increasing values indicate yellow, then green and lastly blue. Chroma is the purity of a color; small values indicate achromatic colors (shades of white, gray and black) and larger values indicate purer colors.

Following Gerald et al. (2001), we plotted tadpole tail spot color on axes generated by logarithms of the ratio between B/G (x-axis) and G/R (y-axis). The B/G ratio = $-2.5 \times \log(B/G)$ and the G/R ratio = $-2.5 \times \log(G/R)$. As with other 2-dimensional color spaces, distance from the origin is a measure of chroma and direction from the origin represents hue (Endler 1990). Points falling on or near the origin are highly achromatic (e.g. white, gray or black), while points farther away are more chromatically pure.

Statistical analyses

All statistics were conducted on mean values for each replicate tub in R (R Development Team 2007, ver. 2.6.0). Since morphological measures are inherently correlated, and may be correlated with color as well, we conducted a principle components analysis (PCA) for eight measures of tadpole morphology (BL, HW, TL, TMW, TMD, TD, TSA and TTL) and two measures of tadpole tail color (hue and chroma). The PCA correlation matrix was normally distributed and homoscedastic and therefore data were not transformed. The first two components (PC 1 and PC 2) accounted for 80% of the variance between treatments (Table 1). The eigenvalues of the remaining components were all <1 and these components are thus not reported. As often occurs, PC 1 reflected differences in overall body size (McCollum and Van Buskirk 1996, LaFiandra and Babbitt 2004). PC 2 represented tail shape and color, corresponding to tail fin depth, tail spot area, hue and chroma.

We used a multivariate analysis of variance (MANOVA) to detect overall effects of treatments on the two principal component response vectors. Since the MANOVA demonstrated significant treatment effects, individual principal component vectors were analyzed using univariate ANOVA's and Bonferroni corrected post-hoc comparisons.

To statistically test specifically for predator-induced tadpole tail color we analyzed hue and chroma with univariate ANOVA's and Bonferroni corrected post-hoc comparisons. To test if tail spot color is coupled with tail spot size, we tested for a correlation between tail hue and chroma with TSA using a Pearson's product moment correlation test. To provide a visual interpretation of color variation, we implemented a linear model based on the axes in our 2-dimensional color space. The model utilized the G/R ratio as our dependent variable, the B/G ratio as our independent variable and predator treatment as a covariate. However, since the G/R axis is not actually dependent on the B/G axis, but is instead correlated with it, the linear regression was only used as a visual tool to illustrate the separation of treatments in color space.

Results

Caged predators had a significant effect on the morphology of tadpoles (Table 2), driving tadpole phenotypes in opposite directions (Fig. 2). Tadpoles reared with caged dragonfly nymphs were smaller overall than tadpoles raised alone or with caged fish, which were not different from one another in size (Fig. 2A; post-hoc Tukey's tests, nymph vs fish $p = 0.001$, nymph vs control $p = 0.0005$, fish vs control $p = 0.924$). Fish induced tadpoles to grow shallower tails with smaller tail spots than controls and nymphs induced

Table 1. Factor loadings from a principal components analysis of eight morphological and two color variables for *Dendropsophus ebraccatus* tadpoles raised with a fish or odonate predator, or a no-predator control. Shown are the first two components and the percent of variance they explain. The predominant explanatory variables are highlighted in bold.

Original variable	PC 1 (overall size)	PC 2 (tail shape and color)
Total length	**0.406**	−0.002
Head width	**0.401**	−0.001
Body length	**0.395**	0.116
Tail muscle depth	**0.391**	0.012
Tail muscle width	**0.351**	0.077
Tail length	**0.392**	−0.058
Tail fin depth	0.197	**−0.422**
Tail spot area	0.152	**−0.550**
Hue	0.081	**0.407**
Chroma	−0.140	**−0.574**
% of variance	57.0	23.0

Table 2. Predator effects on morphology of *Dendropsophus ebraccatus* tadpoles. Results of overall MANOVA and univariate ANOVAs testing predator treatment, block and treatment × block effects on the first two principal components of morphology and color. Significant effects are highlighted in bold.

	Wilks' λ	F	DF	p
MANOVA: induced tadpole phenotype				
Predator treatment	0.159	37.749	4, 100	**<0.00001**
Block	0.943	0.749	4, 100	0.561
Treatment × block	0.974	0.163	8, 100	0.995
Univariate ANOVAs				
PC1 Treatment		9.576	2, 51	**0.0003**
Block		1.549	2, 51	0.222
Treatment × block		0.128	4, 51	0.972
PC2 Treatment		54.195	2, 51	**<0.00001**
Block		0.485	2, 51	0.612
Treatment × block		0.294	4, 51	0.881

tadpoles to grow deeper tails with larger tail spots than controls (Table 2, Fig. 2B; post-hoc Tukey's tests, fish vs nymph or control $p < 0.0001$, nymph vs control $p = 0.04$).

Tadpoles also developed predator-specific tail colors and color changed in conjunction with tail spot size (Table 1). Control tadpoles and tadpoles reared with dragonfly nymphs had significantly redder (lower mean hue) tails than tadpoles reared with fish (Fig. 3A; post-hoc Tukey's tests, nymph vs fish $p = 0.001$, control vs fish $p = 0.05$). Tadpoles raised with nymphs had redder tails than controls, although the difference was marginally non-significant (Fig. 3A; post-hoc Tukey's test, nymph vs control $p = 0.062$). Color purity (chroma) varied significantly between all three treatments: tadpoles reared with nymphs had the highest chroma while control tadpoles and tadpoles raised with fish were significantly more achromatic (Fig. 3B; post-hoc Tukey's tests, all $p < 0.0001$). Tail spot chroma was strongly positively correlated with TSA ($r = 0.611$, $t_{58} = 5.89$, $p < 0.00001$), and hue was negatively correlated with TSA ($r = -0.256$, $t_{58} = -2.02$, $p = 0.048$).

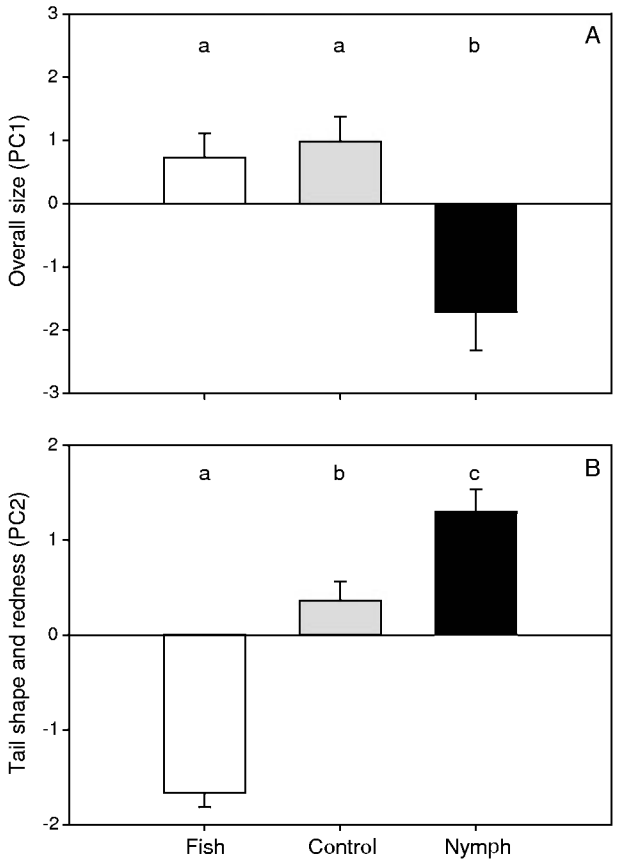

Fig. 2. *Dendropsophus ebraccatus* tadpoles reared with fish, dragonfly nymphs or a no-predator control for 10 days developed predator specific differences in (A) overall size and (B) tail shape and color. Letters above bars indicate significantly different groups ($p < 0.05$) in Bonferroni corrected Tukey's tests. Error bars indicate SE.

As visualized in a 2-dimensional color space, tadpoles reared with dragonfly nymphs had significantly redder tails than either tadpoles reared as controls or with fish (Fig. 4). Fish induced the most achromatic tadpole tails, as evidenced by their close proximity to the origin (Fig. 4). In the 2-dimensional color space, tadpoles reared with dragonfly nymphs exhibited the largest range of variation between chromatic and achromatic tails (Fig. 4).

Discussion

Predator-induced phenotypes are common and often adaptive for many organisms (Tollrian and Harvell 1999, Benard 2004). We examined the effect of two predators, a fish and a dragonfly nymph, on the development of *D. ebraccatus* larvae for 10 days following hatching. Tadpoles developed opposing phenotypes in response to the two predators (Fig. 2–4); dragonfly nymphs caused tadpoles to develop the smallest bodies with the deepest and reddest tail fins whereas fish caused tadpoles to develop shallow, achromatic tails (McCollum and Leimberger 1997, Kraft et al. 2005, Wilson et al. 2005, Benard 2006). Both predators are active hunters, although they differ in their abilities and hunting styles. *Astyanax ruberrimus* is a fast swimming fish that can consume tadpoles much larger than it can swallow whole by pursuing and repeatedly attacking them (Touchon pers. obs.). *Pantala flavescens* nymphs are highly active dragonfly larvae which inhabit the bottom of ponds (Wilson et al. 2005) and will swim through the water column to attack tadpoles (Corbet 1999), but are considerably smaller than

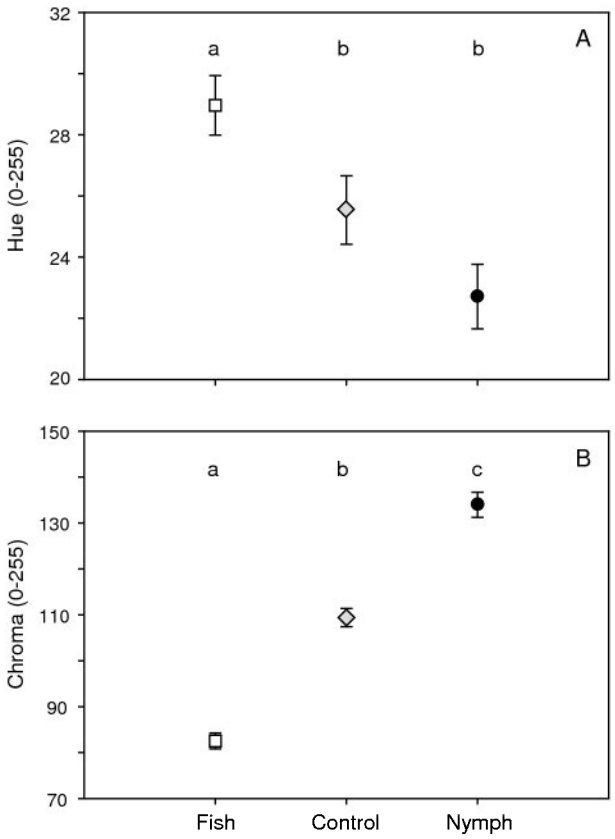

Fig. 3. Tail spot color of *Dendropsophus ebraccatus* tadpoles exposed to fish, dragonfly nymphs, or a no-predator control for 10 days. (A) Hue and (B) chroma. Tadpoles reared with nymphs developed tail spots with the lowest hue (red) and highest chroma, whereas tadpoles reared with fish developed the least red, most achromatic tails. Letters above bars indicate significantly different groups ($p < 0.05$) in Bonferroni corrected Tukey's tests. Error bars indicate SE.

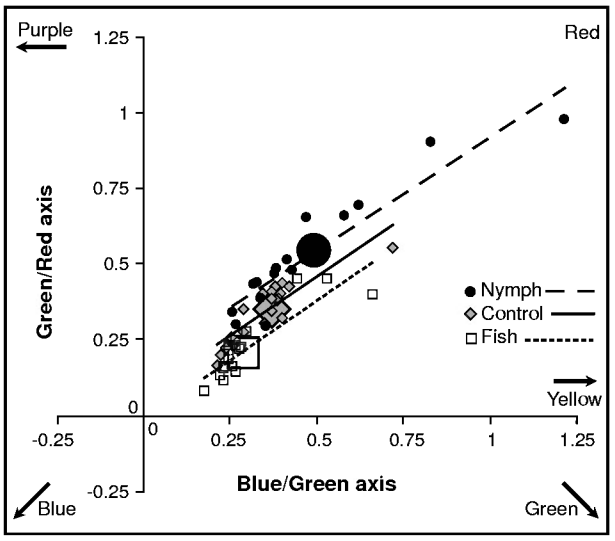

Fig. 4. *Dendropsophus ebraccatus* tadpoles reared with dragonfly nymphs for 10 days developed the reddest tails while those raised with fish developed the most achromatic tails, as plotted in a 2-dimensional color space. Control tadpoles had an intermediate phenotype. Each point is an individual replicate tub mean value. Lines are linear regression lines for each treatment, based on tub mean values. Oversized shapes indicate mean color for each treatment. The color space can potentially plot any color represented by RGB values, and thus axes extend equally in both positive and negative directions. Chroma (purity of color) is indicated by distance from the origin and hue (color) is indicated by direction from the origin. The locations of other colors in the color space are indicated by arrows.

fish. *Astyanax ruberrimus* also hunts in groups, and individual tadpoles can be attacked in rapid succession by multiple individuals (Touchon pers. obs.). In contrast dragonfly nymphs generally hunt alone, so tadpoles that escape an initial attack may often survive (Corbet 1999). The differences in predation style between these two predators may have selected for the predator-specific phenotypes we measured in *D. ebraccatus* tadpoles.

Deep tail fins, such as those induced by *P. flavescens*, decrease overall swimming speed (Van Buskirk and McCollum 2000b, Wilson et al. 2005), but increase maneuverability which may be particularly valuable with dragonfly nymphs (Hoff and Wassersug 2000, Dayton et al. 2005). The red tail spot at the posterior of *D. ebraccatus'* tail may serve as a lure to deflect nymph attacks away from the head (Blair and Wassersug 2000, Van Buskirk et al. 2003, 2004). The spectral sensitivity of *P. flavescens* nymphs is not known, but other dragonfly nymphs see well in the red portion of the visible spectrum (Autrum and Kolb 1968, Horridge 1969, Joop et al. 2006). If *P. flavescens* also sees red well, then *D. ebraccatus* tadpoles may be exploiting this sensitivity by producing a colorful, red tail in concert with an exaggerated tail fin.

The more streamlined tails developed in response to fish predators may enable faster swimming than deeper tail fins, as in *Hyla versicolor* or *Rana lessonae* (Van Buskirk and McCollum 2000b, Wilson et al. 2005), and being clear may attract little attention. While a conspicuous tail spot deflects damage from dragonfly nymphs (Van Buskirk et al. 2003, 2004), it may not work as well with predators such as *A. ruberrimis* that chase their prey if they do not immediately capture it (Touchon pers. obs.). For tadpoles faced with fish predators, rapid escape into refugia may be the only possible option. *Dendropsophus ebraccatus* tadpoles startled in the wild will rapidly bury themselves in the muddy bottom of the pond (Touchon pers. obs.). Having a shallow, achromatic tail fin may thus reduce detection by fish, and when detected, allow fast swimming into a safe habitat.

It is interesting that the terminal filament of the tail is not colored like the tail spot (Fig. 1). Blair and Wassersug (2000) found that pond-dwelling tadpoles with filamentous tails received the majority of damage to the filament while preserving the tail fin. *Dendropsophus ebraccatus* seems primarily to use the terminal filament when holding position in the water column (Touchon pers. obs.). Were it brightly colored, the filament might incur damage from predators as well. Perhaps the terminal filaments' value for maintaining a stationary position outweighs its value as a lure and it is protected, in a sense, by the red spot on the broader portion of the tail fin.

Tail spot chroma and hue were integrated with tail spot size, such that as tail area and depth increased, so did mean

tail spot redness (Table 1, Fig. 2–3). However, color and morphology were not perfectly coupled. Chroma, the purity of color, was strongly correlated with tail spot area. Hue, the shade of color of the tail spot, was negatively correlated with tail spot area (meaning that larger tail spots were redder), but the correlation was weaker. In the 2-dimensional color space, it is clear that there is substantial overlap of tail color between treatments and high variance in color among tadpoles raised with dragonfly nymphs (Fig. 4). Thus, although tail spot size and redness generally increase together, there is clearly variation in phenotype development within environments. This may be relevant for tadpoles developing with different predators, untested here, or in the more natural situation where tadpoles face multiple predators.

Given the amount of variance for tail color within predator treatments (Fig. 4), it appears that not all tadpoles responded to predator cues to the same extent. This might reflect genetic variation in the ability to develop 'fish' or 'nymph' phenotypes and/or potentially variable strength of association between color and morphological plasticity. Some tadpoles reared with dragonfly nymphs had large tails that remained relatively clear, while others raised with fish had fairly red tails (Fig. 4). There were seven different families used in our experiment, but since all tadpoles were pooled at hatching we have no way to directly assess genetic variation from this experiment.

Producing a large red tail may be costly, as evidenced by the fact that tadpoles raised with nymphs were the smallest overall (Fig. 2a). On the other hand, in terms of overall body size, producing a 'fish' phenotype was not costly, relative to control phenotypes (Fig. 2a). Control phenotypes, with intermediate coloration and tail size, likely represent a generalized phenotype that may serve to balance potential costs and threats in the absence of a particular predator cue. Red coloration has long been thought to be costly to produce (Endler 1980, Grether et al. 2001). Maintaining the sensory and regulatory capacity for phenotypic plasticity may also be costly (DeWitt et al. 1998). These costs may create limits in the range of phenotypes a single genotype can produce. For instance, if a particular genotype is good at making a large, red tail in response to dragonfly nymph cues, it may not be as able to create a shallow, achromatic tail in response to fishes. Populations are often variable for plastic traits (Weber and Declerck 1997, Relyea 2005, Kraft et al. 2006). The adults mated for this experiment were from Quarry Pond, which contains multiple species of both dragonfly nymphs and fishes. While both predators are common in Gamboa, each pond in the area has a unique predator community and ponds also vary over time. Genetic variation may result from balancing selection, leading to different strategies for coping with an environment with conflicting selection pressures. It would be interesting to compare the phenotypic plasticity of tadpoles from populations with different suites of predators.

This study represents the first objective quantification of tadpole color change. Previous studies measured color in relation to color plates or subjectively scored if tadpoles were 'brightly colored' or not (McCollum and Van Buskirk 1996, Van Buskirk and McCollum 1999, Richardson 2006). Digital photography and computer analysis remove the potential subjectivity of measuring color by eye (Endler 1990) and provide an alternative to spectrophotometry for many applications. Photographic methods also reduce the amount of time needed for handling of subjects, which can be potentially stressful. Digital image analysis allows measurement of any size color patch, with any shape of border, instead of point sampling as with spectrophotometry. The most substantial drawback of digital images is that they are not receiver-neutral, as are reflectance spectra. Since RGB color is designed for the human visual system, we cannot use digital images to estimate how tadpole tails appear to fish or dragonfly nymph predators (Endler 1990). We can, however, use them to measure differences in animal or plant colors, as we have done here.

In summary, we show for the first time that tadpoles can develop opposing predator-specific morphology and coloration, here in response to cues from predatory fish and dragonfly nymphs. Future work in this system needs to address the function of red coloration in realistic predation scenarios, incorporating environmental complexity and the visual system of predators in question, as well as any behavioral changes that occur in conjunction with morphological and color plasticity. It will only be in natural contexts that we will fully understand and appreciate such inducible phenotypes.

Acknowledgements – We would like to thank the Smithsonian Tropical Research Inst. (STRI) for laboratory space and logistical support. A. S. Rand, W. Wsiclo and M. J. West-Eberhard advised the project. M. Hughey and T. Siok assisted with setting up the experiment and I. Gomez-Mestre assisted with statistical consultation. T. Deboer, I. Gomez-Mestre, M. Caldwell and M. Hughey provided useful comments on the manuscript. J. A. Endler, M. J. Ryan and K. Akre provided helpful advice about measuring and analyzing color. We thank the Panamanian National Authority for the Environment (ANAM) for collection and research permits. This work was funded by an NSF grant to KMW (IBN-0234439), an NSF DDIG to JCT (DEB-0508811), an ASIH Gaige Award, Boston Univ., and STRI.

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