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The relationship between body and substrate color for *Ambystoma altamirani* (Caudata: Ambystomatidae) from the Arroyo los Axolotes, Mexico

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Abstract

The relationship between body and substrate color for *Ambystoma altamirani* (Caudata: Ambystomatidae) from the Arroyo los Axolotes, Mexico. To determine whether the coloration of *Ambystoma altamirani* varies and whether the color is related to the color of the salamander's substrate, *A. altamirani* from the Arroyo los Axolotes, state of México, Mexico, was examined. The study was conducted from February 2018 to January 2019, and the colors classified by comparison with a standard color wheel. The most common base color was olive-green (64%) followed by black (21%). The most common color combinations were olive-green with black markings (44%), solid black (14%), and olive-green with black and yellow markings (11%). Olive-green salamanders were present in every month of the study, whereas the other base colors were found in fewer months, with the greatest diversity of base colors being observed from April to July. Olive-green, black, and "light" *A. altamirani* were found on dark substrates more frequently than expected based on availability compared to intermediate or light substrates. Because there is no evidence for substrate color matching, substrate selection likely is based on other environmental features.

Keywords: adult, color, salamander, stream.

Resumen

Relación entre el color del cuerpo y del sustrato de *Ambystoma altamirani* (Caudata: Ambystomatidae) en el Arroyo los Axolotes, México. Examinamos si la coloración de *Ambystoma altamirani* varía y si ésta está relacionada con el color del sustrato usado por esta salamandra, en la población de Arroyo los Axolotes, Estado de México, México. Estudiamos esta

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población desde febrero 2018 hasta enero 2019, y clasificamos los colores comparando a estos con una rueda de color estándar. El color de fondo de cuerpo más común fue el verde olivo (64%) seguido por el negro (21%). Las combinaciones de colores de cuerpo más comunes fueron el verde olivo con marcas negras (44%), negro sólido (14%), y verde olivo con negro y marcas amarillas (11%). Salamandras verde olivo estuvieron presentes en todos los meses de estudio, mientras que los otros colores base se registraron en menos meses, con la mayor diversidad de colores base siendo observada desde abril hasta julio. Individuos de *A. altamirani* de colores verde olivo, negro y pálido, todos utilizaron sustratos oscuros más frecuentemente que lo esperado con base a la disponibilidad comparado a los sustratos intermedios o pálidos. Debido a que no hubo evidencia de coincidencia con el color del sustrato, esto sugiere que la selección del sustrato se base en otras características ambientales.

Palabras Clave: adulto, arroyo, color, salamandra.

Resumo

Relação entre a cor do corpo e do substrato de *Ambystoma altamirani* (Caudata: Ambystomatidae) em Arroyo los Axolotes, México. Examinamos se a coloração de *Ambystoma altamirani* varia e se está relacionada com a cor do substrato usado por essa salamandra na população de Arroyo los Axolotes, Estado do México, México. Estudamos essa população de fevereiro de 2018 a janeiro de 2019 e classificamos as cores comparando-as com uma roda de cores padrão. A cor de fundo do corpo mais comum foi o verde-oliva (64%) seguido pelo preto (21%). As combinações de cores corporais mais comuns foram verde oliva com manchas pretas (44%), preto sólido (14%) e verde oliva com manchas pretas e amarelas (11%). As salamandras verde-oliva estiveram presentes em todos os meses de estudo, enquanto as restantes cores de base foram registadas em menos meses, sendo a maior diversidade de cores de base observada de abril a julho. Indivíduos de *A. altamirani* verde oliva, pretos e de cores claras usaram substratos escuros com mais frequência do que o esperado com base na disponibilidade em comparação com substratos intermediários ou claros. A falta de evidência de correspondência com a cor do substrato sugere que a seleção do substrato é baseada em outras características ambientais.

Palavras-chave: adulto, coloração, riacho, salamandra.

Introduction

Previous studies have shown that the coloration of adult and larval *Ambystoma* can vary with environmental conditions. In some cases, coloration varies with abiotic conditions, such as darkening at colder temperatures in larval *A. barbouri* Kraus and Petranka, 1989 and *A. texanum* (Matthes, 1855) (Garcia *et al.* 2003) or darkening with exposure to UV radiation in larval *A. gracile* (Baird, 1859) and *A. macrodactylum* (Belden and Blaustein 2002) and larval *A. barbouri* and *A. texanum* (Garcia *et al.* 2004). There also is evidence that *Ambystoma* can change color, or at least their darkness or lightness, to match their substrate or environment (Fernandez and Collins 1988, Belden and Blaustein 2002, Garcia and Sih 2003). Such changes seem to be particularly evident in the presence of predators, when salamanders tend to match their substrate or background, thereby increasing their survivorship (Storfer *et al.* 1999, Garcia *et al.* 2009). In addition to changing color, there is also evidence that *Ambystoma* can select substrates that better match their coloration or choose their habitat based on its color. For example, larval *A. texanum* select the substrate that is most similar to their body color (Garcia and Sih 2003). Substrate color is a significant factor in determining the presence or absence of

A. leorae (Taylor, 1943) in sites along the Río Tonatzin in the state of México (Lemos-Espinal *et al.* 2017), and a previous study found that *Ambystoma altamirani* Dugès, 1895 in the Arroyo los Axolotes used black substrates more than expected and white-yellow sites less than expected (Lemos-Espinal *et al.* 2016).

In this study, we examined the base color and color pattern of *A. altamirani* from the Arroyo los Axolotes, state of México, Mexico (Figure 1). Specifically, we quantified the frequency of different base colors by month, and determined whether base color was associated with substrate color. We expected there to be degree of substrate matching by *A. altamirani,* with lighter salamanders using lighter substrates and darker salamanders using darker substrates.

Figure 1. A subadult *Ambystoma altamirani* from Sierra del Ajusco, México City, Mexico, illustrating the species color pattern. Photo by Eric Centenero-Alcalá.

Materials and Methods

Our study took place in the Llano las Navajas in Arroyo los Axolotes, Mpio. Isidro Fabela, Sierra de las Cruces, state of México (19°32'12.2" N, 99°29'52.7" W; 3479 m a.s.l.). Llano las Navajas is an extensive grassland of approximately 100 ha surrounded by a forest of *Pinus hartwegii* Lindl. The Arroyo los Axolotes runs along the southern edge of this grassland. The Arroyo los Axolotes is a permanent stream; however, between December and April it is limited to a main channel that includes several shallow pools ($\leq$ 3.5 m diameter, $\leq$ 1 m depth) connected by branches of the main channel. In contrast, between May and November, surface water flows in two main channels, which are deeper and wider.

We established 25 permanent sites, each 5 m long and 40 m apart, along the Arroyo los Axolotes using a mobile GPS unit. We visited the Arroyo los Axolotes multiple times per month (range: 1–10) from February 2018 to January 2019. Visits took place between 11:00 and 15:00 h. when we visually searched the permanent sites along the stream for *A. altamirani;* we spent about 10 min per site, and used a herpetological hook along the bottom and cavities at the sides of the stream to induce the salamanders to move so that we could see them. In addition, we searched under rocks and other objects in the stream at each site. We captured salamanders with a net. Adult males were identified by the presence of a bulge on each side of the tail near the cloaca and adult females by the absence of such a bulge (Brandon and Altig 1973). We categorized individuals as larvae if they possessed gills and as adults if they lacked gills. The base color (i.e., the color covering the majority of its body) and the colors of any additional markings or patterns were recorded for each salamander captured, with the colors being identified by comparison with the Comex Color Pantone guide (http://tienda.comex.com.mx/familias-de-color). Colors were assessed in natural light in the field. The color of the substrate where the salamanders were originally observed was recorded in the same way as it was for the salamanders. All salamanders were released at the point of capture.

Chi-square tests were used to determine whether there was a correlation between the most common base colors and substrate colors between males and females, and between larvae and adults. To determine the availability of substrate colors, we visited each site monthly

independent of salamander sampling and classified the available substrate colors irrespective of the presence or absence of a salamander. Each substrate color was identified by comparison with a Comex Color Pantone guide. These values were used to calculate average percent availability of each substrate color during the study, and chi-square tests were used to compare the observed frequency of different base colors on different substrate colors. To facilitate this analysis and avoid small sample sizes for some base and substrate colors, we pooled substrate colors into Dark (black, dark brown, brown; 57.2%), Intermediate (light brown, gray; 28.2%), and Light (yellow and white; 14.5%) and limited the analyses to the two most common base colors (olive-green, black) and pooled the "light" base-colored individuals (gray, pale green, translucid, white, yellow).

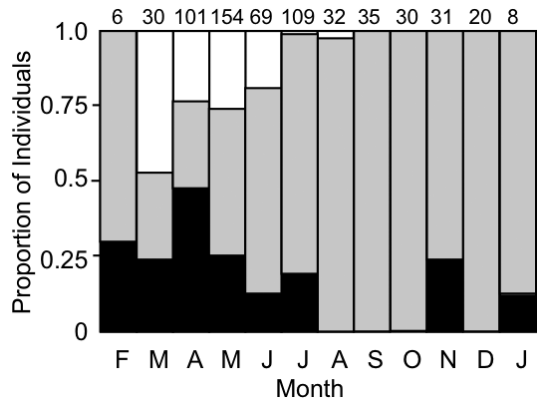

Figure 2. The relative frequency of *Ambystoma altamirani* of the two most common base colors, Black (black portion of bars) and olivegreen (gray portion of bars), from February 2018 to January 2019 in the Arroyo los Axolotes, State of México, Mexico (white portion of bars represents the relative frequency of all other colors combined). Number at top of bar indicates total number of individuals for that month.

Results

The most common base color is olive-green (64%; 397 of 624 observations) followed by black (21%; 132 of 624 observations), with no other base color accounting for > 5% of the observations (Appendix I). The most common color combination is olive-green with black markings (44%; 273 of 624 observations) followed by solid black (14%; 86 of 624 observations) and olive-green with black and yellow markings (11%; 68 of 624 observations) (Appendix II). No other combination accounts for > 5% of the observations (Appendix II).

The abundance of base colors observed in this population of *Ambystoma altamirani* varies during the study period. The most common base color, olive-green, was found throughout the study (Figure 2). The second most common base color, black, was most frequent in April and May, with a few individuals in other months, but mainly from March to July (Figure 2). The other base colors were less common, with the greatest diversity of base colors being observed from April–July (Appendix I).

Males and females do not differ in the frequency of the two most common base colors (black and olive-green; Table 1; $\chi^2_1 = 0.137$, $p = 0.71$). They also do not seem to differ in the less-common base colors, but the sample sizes are too small to analyze the frequencies statistically (Table 1). Males and females do not differ in their use of the most commonly used substrate colors (dark brown, brown, light brown, gray; Table 1; $\chi^2_3 = 0.19$, $p = 0.98$). These two results clearly demonstrate that there is no sexual dimorphism in base color or use of substrate colors in adult *A. altamirani.*

Larval *Ambystoma altamirani* have a higher frequency of black base color and lower frequency of olive-green base color than do adults (Table 1; $\chi^2_1 = 9.32$, $p = 0.0023$). There also are larvae that have some base colors that are rare or not found in adults (e.g., dark gray, green, green yellow, and yellow; Table 1).

Larval and adult *A. altamirani* differ in the frequency with which they use the most common

substrate colors (dark brown, brown, light brown, gray, and white) (Table 2; $\chi^2_4 = 155.9$, $p < 0.0001$). Adults use dark brown and brown substrates slightly more than do larvae. However, adults use white substrates substantially more than larvae do; only two observations of larvae were made on white substrates compared to 177 for adults (Table 2).

Olive-green individuals use dark substrates at a much higher frequency than expected based on availability (Table 3; $\chi^2_2 = 62.81$, $p < 0.0001$). Black individuals primarily are found on dark brown substrates as well, but proportionally fewer individuals are found on other substrate colors and none was found on white substrates. Black individuals used dark substrates at a higher than expected rate compared to the other colored substrates (Table 3; $\chi^2_2 = 39.6$, $p < 0.0001$). Other base colors of salamanders are also found primarily on dark brown—even white and yellow salamanders that were never found on yellow or white substrates. "Light" salamanders used dark substrates at a higher frequency than expected compared to other substrates (Table 3; $\chi^2_2 = 9.57$, $p = 0.0083$).

Discussion

Based on our observations, it is clear that within a single population of *Ambystoma altamirani,* color varies substantially (Appendices I, II); previous studies have documented that color variation in other populations of this species, as well. The base color of larval *A. altamirani* has been described as "yellowish," with "dark dorsal bands" (Brandon and Altig 1973); however, Campbell and Simmons (1962) described a black base color with yellow markings. These authors also described the base color of adult *A. altamirani* as gray with black spots or markings.

Our results suggest that the color of individuals or populations of *A. altamirani* may change during a year. There may also be differences in detectability of different colors at different times of the year. We lack the data necessary to determine which, if either, of these alternatives occurs in the Arroyo los Axolotes. However, these observations do suggest that the *A. altamirani* in the Arroyo los Axolotes may provide a good model system in which to explore the factors driving coloration in populations of

Table 1. The frequency of different base colors of male and female *Ambystoma altamirani* and larval and adult *A. altamirani* in the Arroyo los Axolotes, state of México, Mexico. The identification in parentheses is the color's key number from Comex Color Pantone guide (http://tienda.comex.com/familias-de-color).

Base color	Males	Females	Larvae	Adult
Black (Neg-01)	48	54	68	55
Dark brown (Casob-01)	0	0	1	0
Dark gray (316-07)	3	4	21	1
Dark green (216-07)	1	2	3	0
Gray (316-05)	7	7	2	8
Gray green (316-06)	8	2	3	7
Green (215-06)	2	4	6	0
Green yellow (217-03)	0	0	8	0
Olivegreen (224-07)	138	169	150	229
Pale green (217-01)	0	3	2	0
White (Blco-01)	0	0	1	0
Yellow (AmAle-01)	3	1	19	0

Table 2. The use of different colored substrates by adult male and female *Ambystoma altamirani* and larval and adult *A. altamirani* in the Arroyo los Axolotes, state of México, Mexico. The identification in parentheses is the color's key number from Comex Color Pantone guide (http://tienda.comex.com/familias-de-color). * indicates those colors compared by chi-square tests.

	Black (Neg-01)	Dark brown (Casob-01)	Brown (Chocolate-0013)	Light brown (Pino-0021)	Gray (Cocoa-010	Yellow (Marfil-01)	White (Blco-01)
Males	2	134*	30*	29*	8*	2	5
Females	2	157*	32*	36*	9*	4	3
Larvae	3	184*	30*	58*	21*	4	2*
Adults	0	200*	47*	28*	14*	2	177*

Table 3. Observed and expected frequency of *Ambystoma altamirani* of different base colors using different substrate color categories.

Base color	Frequency	Substrate color category		
		Dark	Intermediate	Light
Black	Observed	110	18	3
	Expected	75	37	19
Olivegreen	Observed	302	73	19
	Expected	227	112	56
"Light"	Observed	34	10	0
	Expected	25	12	6

Ambystoma, especially by gathering data on color in marked individuals over their lifetime.

The differences between larval and adult *A. altamirani* in the frequency and diversity of base colors suggests that there is either selection against certain colors resulting in these colors being less common in adults, or there is an ontogenetic change in coloration in *A. altamirani.* Adult *A. altamirani* seem to be found in or near streams throughout their life (J. A. Lemos-Espinal, pers. observ.), indicating that neither differential migration nor selection in the terrestrial environment is likely in this species. Larvae of both *A. barbouri* and *A. texanum* become lighter as they mature (Garcia *et al.* 2003), suggesting there can be ontogenetic changes in the coloration. A study that follows marked individuals and that tracks their coloration will be required to address these possibilities.

Adults use white substrates more frequently than do larvae and used dark brown and brown substrates slightly more than larvae, thereby suggesting that there is an ontogenetic shift in the color of the substrate used by *A. altamirani.* We cannot determine whether this shift is caused by the color or the composition of the substrate because the color and nature of the substrate are not independent at our study site.

We have only equivocal evidence for substrate matching in *A. altamirani* because both darker and lighter salamanders can be found on darker substrates, but not light substrates.; these results are consistent with those of a more limited study on this population by Lemos-Espinal *et al.* (2016). Thus, it seems likely that *A. altamirani* selects

darker substrates because they provide resources for the salamanders or are correlated with other stream characteristics that are important for them, rather than choosing a substrate color for camouflage. For example, the darker substrates often include mud as the base material, and mud is an important substrate for *A. altamirani* (Lemos-Espinal *et al.* 2016, Villarreal Hernández *et al.* 2020) and other Mexican *Ambystoma*—e.g., *A. leorae* (Lemos-Espinal *et al.* 2017) and *A. rivulare* (Taylor, 1940) (Bille 2009). *Ambystoma altamirani* also seems to avoid gravel or bedrock substrates (Lemos-Espinal *et al.* 2016, Villarreal Hernández *et al.* 2020) that tend to be lighter in color; this may explain the usual absence of salamanders on lighter substrates.

We do not preclude the possibility that base colors may be selected to match available substrate colors because the two most common base colors are black and olive-green and the two most common color combinations are olive-green with black markings and solid black; together, these account for 58% of all observations. The ability to camouflage increases survivorship in the presence of predators (Storfer *et al.* 1999). The color variation may exist, in part, because there are no predatory fish in the Arroyo los Axolotes to select against the more visible color combinations. Although there are predatory snakes, *Thamnophis scaliger* (Jan, 1863), found along the stream (Villareal Hernández *et al.* 2019), it is unclear how they might select prey relative to coloration. A caveat that must be associated with our study is that we only viewed color as perceived by humans, not as perceived by potential predators; see Hantak and Kuchta (2018) for an example involving a terrestrial salamander. Additional studies on color variation in this population are needed to examine how color might change in individuals and how color affects predation risk. It would also be interesting to conduct similar studies on color variation and substrate color use by *A. altamirani* in streams with predatory fish.

The results of this study document the apparent importance of substrate in determining the distribution of *Ambystoma altamirani* in streams, along with ontogenetic variation in substrates that are selected by the salamanders. Although we focused on substrate color, the evidence linking substrate color to the color of an individual salamander is mixed (Lemos-Espinal *et al.* 2016). Substrate selection by these salamanders doubtless is more complex than simple color choice because we know that substrate type (e.g., mud vs. bedrock) seems to be important in determining substrate use in multiple populations of *A. altamirani* (Lemos-Espinal *et al.* 2016, Villarreal Hernández *et al.* 2020). From a conservation standpoint, it seems that conserving darker, muddy substrates may be necessary to maintain populations of this salamander, especially in the larval stage.

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Appendix I. *The frequency of* Ambystoma altamirani *of different base colors in different months from February 2018 to January 2019 in the Arroyo los Axolotes, state of México, Mexico. The identification in parentheses is the color's key number from Comex Color Pantone guide (http://tienda.comex.com/familias-de-color).*

Base color	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Total
Black (Neg-01)	2	7	48	39	9	19	0	0	0	7	0	1	132
Dark brown (Casob-01)	0	0	1	0	0	0	0	0	0	0	0	0	1
Dark gray (316-07)	0	0	5	17	0	0	0	0	0	0	0	0	22
Dark green (216-07)	0	0	0	2	2	0	0	0	0	0	0	0	3
Gray (316-05)	0	1	0	8	5	0	0	0	0	0	0	0	14
Gray green (316-06)	0	0	0	6	4	0	1	0	0	0	0	0	11
Green (215-06)	0	0	4	2	0	0	0	0	0	0	0	0	6
Green yellow (217-03)	0	7	1	0	0	0	0	0	0	0	0	0	8
Olive green (224-07)	4	9	30	72	46	89	31	35	30	24	20	7	397
Pale green (217-01)	0	0	3	1	0	0	0	0	0	0	0	0	4
Translucid (000-27)	0	0	0	1	0	0	0	0	0	0	0	0	1
White (Blco-01)	0	0	0	0	2	1	0	0	0	0	0	0	3
Yellow (AmAle-01)	0	6	9	6	1	0	0	0	0	0	0	0	22

Appendix II. *Summary of the frequency of color combinations (i.e., base color and the color of additional patterns or markings) observed in* Ambystoma altamirani *for the Arroyo los Axolotes, state of México, Mexico. The identification in parentheses is the color's key number from Comex Color Pantone (http://tienda.comex.com/familias-de-color). Percent of observations is given in parentheses.*

Color combination	Number of individuals (%)
Black (Neg-01)	86 (13.8)
Black with green (Neg-01 & 215-06)	1 (0.16)
Black with olive-green (Neg-01 & 224-07)	6 (0.96)
Black with olive-green and yellow (Neg-01 & 224-07 & AmAle-01)	2 (0.32)
Black with transparent parts (Neg-01 & 000-27)	7 (1.1)
Black with transparent parts and olive-green (Neg-01 & 000-27 & 224-07)	1 (0.16)
Black with yellow (Neg-01 & AmAle-01)	28 (4.49)
Black with yellow and white (Neg-01 & AmAle-01 & Blco-01)	1 (0.16)
Dark brown with yellow (Casob-01 & AmAle-01)	1 (0.16)
Dark gray (316-07)	22 (3.53)
Gray (316-05)	1 (0.16)
Gray with black (316-05 & Neg-01)	9 (1.44)
Gray with black and yellow (316-05 & Neg-01 & AmAle-01)	1 (0.16)
Gray with dark green (316-05 & 216-07)	1 (0.16)
Gray with yellow (316-05 & AmAle-01)	1 (0.16)
Gray green with black (316-06 & Neg-01)	12 (1.92)
Dark green with black (216-07 & Neg-01)	3 (0.48)
Green with black (215-06 & Neg-01)	4 (0.64)
Green with yellow and black (215-06 & AmAle-01& Neg-01)	2 (0.32)
Green yellow with black (217-03 & Neg-01)	8 (1.28)
Olive-green (224-07)	20 (3.20)
Olive-green with black (224-07 & Neg-01)	273 (43.8)
Olive-green with black and gray (224-07 & Neg-01 & 316-05)	13 (2.08)
Olive-green with black and white (224-07 & Neg-01 & Blco-01)	6 (0.96)
Olive-green with black and yellow (224-07 & Neg-01 & Blco-01)	68 (10.90)
Olive-green with gray (224-07 & 316-05)	2 (0.32)
Olive-green with yellow (224-07 & AmAle-01)	12 (1.92)
Olive-green with yellow and transparent parts (224-07 & AmAle-01 & 000-27)	3 (0.48)
Pale green with black (217-01 & Neg-01)	4 (0.64)
Translucid (000-27)	1 (0.16)
White with black (Blco-01 & Neg-01)	3 (0.48)
Yellow with black (AmAle-01 & Neg-01)	22 (3.53)