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Selection of substrate type, substrate color, and vegetation by tadpoles of *Dryophytes plicatus*

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Abstract

The characteristics of microhabitats in streams can drive the distribution of tadpoles. We experimentally examined microhabitat selection of tadpoles of *Dryophytes plicatus*. We used a series of choice experiments to test if tadpoles had preferences for particular substrate types, substrate colors, and vegetation. Tadpoles of *D. plicatus* had a strong preference for mud substrates over sand, gravel, and rock substrates and preferred darker substrates over lighter substrates. *Dryophytes plicatus* tadpoles used the non-vegetated side of an aquarium more than the vegetated side. Our experimental results matched previous field observations in the case of the preference for mud substrates but differed from the field observations for substrate color and vegetation, suggesting that basic underlying preferences may be modified by various factors in nature or by learning or conditioning.

Key Words

Arroyo los Axolotes, behavior, Mexico, microhabitat selection, stream, tadpoles

Introduction

In order to assess the consequences of potential degradation of stream habitats (Carpenter et al. 2011; Piñon-Flores et al. 2021) on aquatic species, as well as to develop appropriate habitat management plans for such habitats, greater understanding of how species use or select habitats or microhabitats in streams is needed. The distributions of tadpoles may be a function of a variety of microhabitat characteristics ranging from substrate type to vegetation or habitat structure (Hoff et al. 1999), as well as the result of oviposition site choice by adults (Buxton and Sperry 2017). Experimental investigations in the laboratory may help determine what specific attributes of the environment drive tadpole distributions in nature. For example, some tadpole species prefer vegetated microhabitats or habitats with structure over non-vegetated or simple habitats in the laboratory (e.g., Smith and Doupnik 2005; Chuang et al. 2019), whereas others show a preference for non-vegetated habitats, at least during some stages of development (Smith 1999). Other experimental studies have found tadpoles prefer specific types of substrate, such as rock or gravel (Odendaal et al. 1982; Smith 1999) or have no preferences (Smith and Doupnik 2005).

Several studies have examined a selection of substrates based on color in tadpoles. Some tadpoles show no preference among differently colored substrates (Bishop et al. 2012; Espanha et al. 2016; Eterovick et al. 2018; Melo et al. 2021; Rodríguez-Rodríguez et al. 2021). However, other species of tadpoles show a preference for particularly colored substrates. Some prefer white or light substrates over black or dark substrates (Guimarães et al. 2021; Melo et al. 2021), whereas others prefer black or dark substrates over white or light substrates (Ximenez et al. 2012; Eterovick et al. 2018). The selection of a color

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of substrate often increases crypsis, especially in the presence of predators or predator cues (Eterovick et al. 2010, 2018, 2020); although some tadpoles select backgrounds that create high contrast between the tadpole and its background (Guimarães et al. 2021). It appears color preference of tadpoles, at least in some species, may be innate (Hunt et al. 2020).

Dryophytes plicatus (formerly *Hyla plicata*; Duellman et al. 2016) is an endemic frog found in the mountains of central Mexico (Wilson and Johnson 2010). The Mexican government lists *D. plicatus* as Threatened (SEMARNAT 2019). Adult *D. plicatus* occur more often in sites with longer hydroperiods, and the tadpoles are found more often in sites with less livestock, slower water, and that were wider (Gómez Franco et al. 2023). *Dryophytes plicatus* can be scavengers (Villarreal Hernández et al. 2019). Predators of *D. plicatus* tadpoles include Giant Water Bugs (*Belostoma* spp.) (Villarreal Hernández et al. 2019). *Dryophytes plicatus* co-exist with the snake predator *Thamnophis scaliger* (Villarreal-Hernández et al. 2019); but are excluded from sections of streams where non-native Rainbow Trout (*Oncorhynchus mykiss*) are found (Estrella-Zamora et al. 2018).

We examined microhabitat selection of *D. plicatus* tadpoles using a series of laboratory choice experiments to determine if they prefer specific types of substrates (mud, sand, gravel, and rock), substrate color (dark brown, brown, light brown, and gray), and the presence and absence of vegetation. These experiments were informed by previous field observations of habitat and microhabitat use by *D. plicatus* tadpoles in nature. Visual surveys supplemented by physical probing of substrates (i.e., with a snake hook) indicated that *D. plicatus* tadpoles are often found in sites with mud (Lemos-Espinal et al. 2016; Estrella Zamora et al. 2018). *Dryophytes plicatus* are also found more often in sites with white-yellow and tan-brown substrates rather than those with black substrates (Lemos-Espinal et al. 2016), and use sites with and without vegetation at the same rate (Lemos-Espinal et al. 2016; Estrella Zamora et al. 2018). Based on these field observations, we predicted that *D. plicatus* tadpoles would prefer mud substrates over the other substrates, prefer lighter substrates (e.g., light brown and gray), and show no preference between vegetated and non-vegetated habitats in our laboratory experiments.

Methods

We collected 135 tadpoles of *D. plicatus* from the Arroyo del Axolotes, mpio. Isidro Fabela, Mexico using a dipnet from December 2021 through November 2022. We transported tadpoles to a nearby facility for the experiments. We obtained the tadpoles from a variety of microhabitats; including pools, stream edges, shallows, and at the base of vegetation; along a 1 km stretch of the Arroyo los Axolotes. We pooled individuals into the wet (June to October; N = 100) and dry seasons (November to May; N = 35). Water temperatures are warmer and dissolved oxygen levels higher in the wet season than the dry season (Villarreal Hernández et al. 2020a). We have observed predators, such as *Thamnophis scaliger*, in both the wet and dry seasons along the Arroyo los Axolotes (J.A. Lemos-Espinal pers. observ.). In addition, water depth is greater during the wet season compared to the dry season (Gómez Franco et al. 2022). All tadpoles used in the experiments were premetamorphic and had no obvious evidence of limb buds (i.e., Gosner stage 25–26; Gosner 1960), and were all < 0.8 cm in body length. All tadpoles in our experiment were jet black in color; however, Kaplan and Ramírez-Bautista (1996) described the color of *D. plicatus* tadpoles as dark olive but indicated that some populations are "almost black".

We conducted three choice experiments: substrate type, substrate color, and vegetation. Experiments were begun at around 1400 h, approximately one-four hours after capture. Prior to the experiments tadpoles were temporarily housed in plastic containers. For each experiment, we established multiple test arenas using 36 L glass aquaria (40 cm length × 30 cm width × 30 cm height) with each aquarium divided into sections as described below. We used water from the Arroyo los Axolotes to fill the aquaria. Experiments were run at a water temperature of between 7.3 °C and 8.1 °C; which was similar to water temperatures in the stream. At the start of each trial we placed tadpoles in the center of the aquarium and allowed to acclimate for 5 minutes prior to data collection. We recorded the location of the tadpole every minute for 15 minutes. To minimize the number of tadpoles used in the experiments, we ran each tadpole through all three experiments in the same order for all tadpoles (substrate color, substrate type, and vegetation), with 5–10 minutes between experiments.

For the substrate type experiment, we created four sections on the bottom of the aquaria: mud, sand, gravel, and solid rock, using material collected from the stream. The mud substrate was dark brown in color, the sand brown, the gravel gray, and the solid rock light brown or light gray. We used small rectangular plastic trays to contain the various substrate types and keep them separate. Since our goal was to assess potential preferences for substrate types we used actual natural substrates from the Arroyo Los Axolotes without attempting to control for their color or other aspects, such as the availability of food. For the substrate color experiment, we placed four equal-sized rectangular pieces of colored paper under the clear bottom. We chose colors to approximate the four most common colors of substrates in the Arroyo Los Axolotes using the COMEX color palette (brown color family): dark-brown, brown, light-brown, and gray (Villarreal Hernández et al. 2020a, b). For the vegetation experiment, we divided each aquarium in two, with half containing artificial vegetation to simulate the vegetation in their habitat, and half without vegetation and contained no shelter.

For each tadpole we determined which substrate type or color they used the most. In the case of a tie, we excluded those individuals from the analyses (N = 0 excluded for substrate type; N = 2 excluded for substrate color; N = 0 excluded for vegetation). We used chi-square tests

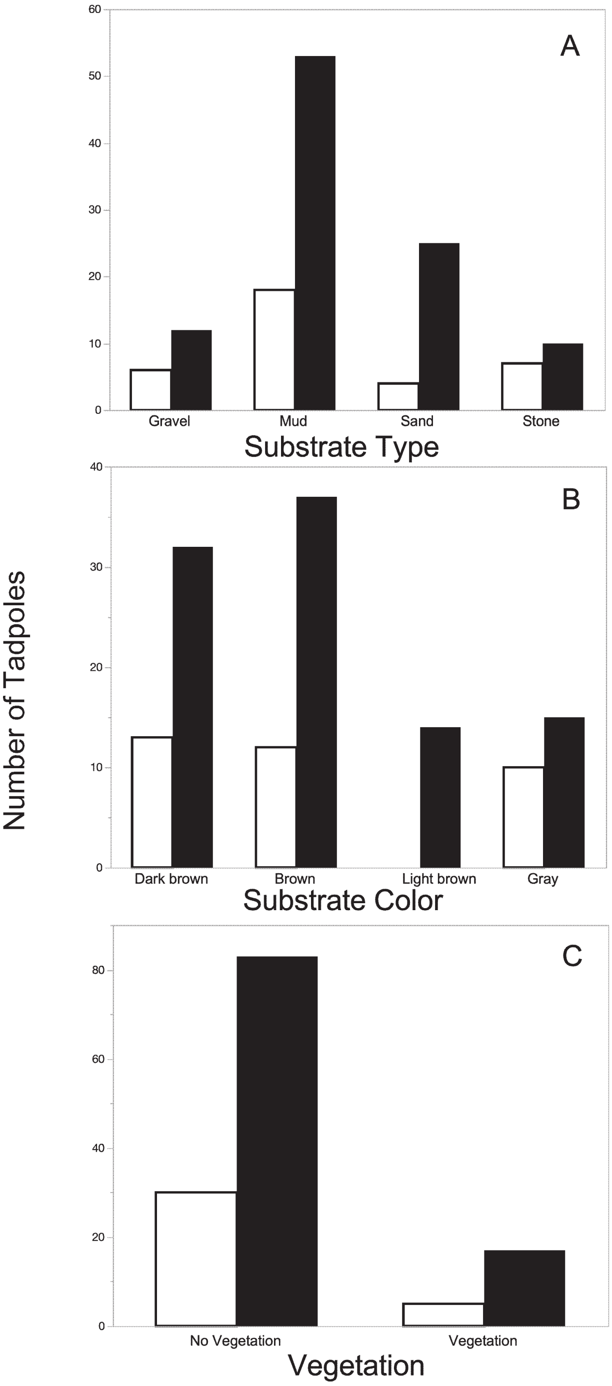

Figure 1. The number of individual *Dryophytes plicatus* tadpoles from the Arroyo los Axolotes that used each **A.** Substrate type; **B.** substrate color; **C.** vegetated or non-vegetated habitat the most in laboratory preference experiments in the dry (white bars) and wet (black bars) seasons

to determine if the numbers of individuals using each substrate type or color the most were different from that expected if the individuals chose substrate types or colors at random (i.e., 25% for each substrate type or color) or vegetated and non-vegetated sides at random (i.e., 50% on each side). We also used chi-square tests (or Fisher's exact test if expected values were < 5 in > 20% of cells) to determine if substrate type and color preferences differed between the wet and dry seasons.

Results

Tadpoles overwhelmingly chose mud substrates over the other substrates (Fig. 1A; $\chi^2_3 = 57.44$, $P < 0.0001$). The substrate type chosen by tadpoles that used a particular substrate type > 50% of the time did not differ between the wet and dry seasons (Fig. 1A; Fisher's exact test: $P = 0.17$).

Tadpoles chose dark brown and brown more than light brown and gray (Fig. 1B; $\chi^2_3 = 24.80$, $P < 0.0001$). There was a nearly significant tendency for the color chosen by tadpoles to differ between the wet and dry seasons, with light brown only used in the wet season (Fig. 1B; $\chi^2_3 = 7.65$, $P = 0.054$).

Tadpoles used the non-vegetated side of the aquarium much more than the vegetated side (Fig. 1C; $\chi^2_1 = 61.3$, $P < 0.0001$). The side of the arena, vegetated or non-vegetated, used by the tadpoles showing a choice of side did not differ between the wet and dry seasons (Fig. 1C; $\chi^2_1 = 0.14$, $P = 0.71$).

Discussion

Our experimental results suggest that tadpoles of *D. plicatus* had a strong preference for mud substrates over sand, gravel, and rock substrates. Our experimental results are similar to those from previous field studies that found mud to be the most used substrate for *D. plicatus* in the Arroyo Los Axolotes (Lemos-Espinal et al. 2016; Estrella Zamora et al. 2018). It is unclear why *D. plicatus* tadpoles prefer mud substrates over other substrates. Possible explanations include the presence of food or that mud correlates with the presence of other resources or conditions. For example, mud may be more present in slower water, a condition correlated with more *D. plicatus* tadpoles (Gómez Franco et al. 2023). Given the preference for mud substrates in both our experiment and our previous field observations (Lemos-Espinal et al. 2016; Estrella Zamora et al. 2018), further experiments or field studies designed to specifically address why mud substrates are preferred would be fruitful.

Tadpoles of *D. plicatus* preferred dark brown and brown substrates over light brown or gray substrates (i.e., they preferred the darker substrates), which is what we might expect given that the tadpoles of *D. plicatus* used in our experiment were jet black. For example, tadpoles of some species have been shown to select substrates that allow them to be more cryptic when disturbed (Eterovick et al. 2010) or in the presence of predator cues (Eterovick et al. 2020). In addition, given the strong preference for mud substrates, the choice of dark brown and brown substrates may reflect a selection for colors that typically match mud, which in the Arroyo los Axolotes is typically dark brown. Alternatively, tadpoles may select mud for its color rather than other characteristics. However, in the Arroyo los Axolotes, *D. plicatus* tadpoles were found more often in sites with lighter substrates than in sites with darker substrates (Lemos-Espinal et al. 2016) which is odd given the very dark color of the tadpoles of *D. plicatus*. Further experimentation is needed to reconcile the results of our experiment and the observations in natural streams. For example, experiments examining substrate color selection by *D. plicatus* tadpoles in the presence and absence of predators or predator cues or an experiment comparing preferences for mud, or other substrates, of different colors but similar in all other aspects would be useful.

In our experiments, *D. plicatus* tadpoles showed a strong preference for using the non-vegetated side of the aquarium over the vegetated side of the aquarium. In nature, *D. plicatus* tadpoles used sites with different types of vegetation, including no vegetation, in the same frequency as their availability along the Arroyo los Axolotes (Lemos-Espinal et al. 2016; see also Estrella Zamora et al. 2018). As with our substrate color results, it may be that the differences between our experimental vegetation selection results and the observations in nature may reflect the additional factors that are present in nature, such as predators or food. For example, some tadpoles increase the time spent hiding in simulated vegetation in the presence of predator cues (Gunzburger 2005; Gregoire and Gunzburger 2008). In addition, the avoidance of vegetation we observed in our experiment may be due to our use of artificial vegetation rather than natural vegetation. However, several experiments examining the behavior of other species of tadpoles that have used artificial vegetation have found no apparent avoidance of or alteration of behavior by using artificial vegetation (e.g., Smith 1999; Smith and Doupnik 2005; Smith et al. 2008a, b; Smith and Awan 2009; Davis et al. 2012), suggesting this is unlikely.

Conclusions

The series of experiments we conducted to examine the elements of microhabitat use in tadpoles of *D. plicatus* suggest that these tadpoles may have preferences for some characteristics of their environment (e.g., mud and darker substrates), but avoid others (e.g., vegetation). In addition, the difference between some of the results we obtained in our experiments for substrate color and vegetation and those from field studies emphasize that basic underlying preferences may be modified by various factors in nature or by learning or conditioning (see Wiens 1970, 1972; Dunlap and Satterfield 1985; Moriya et al. 1996). However, the consistency of a strong preference for mud substrates in our laboratory experiments and in our previous field observations (Lemos-Espinal et al. 2016; Estrella Zamora et al. 2018) emphasizes the potential importance of ensuring that sufficient mud substrates are present when *D. plicatus* tadpoles are found in the streams. Thus, any habitat degradation that may affect the availability of mud substrates with standing water at the appropriate time of year should be avoided or remediated (e.g., reduced water flow, increased scouring events, channelization using artificial substrates). It is our hope that the discrepancies (and similarities) in these sets of results will prompt further investigations into what those factors are.

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