
ABUNDANCE, DISTRIBUTION, POPULATION STRUCTURE, AND SUBSTRATE USE OF *AMBYSTOMA ALTAMIRANI* ALONG THE ARROYO LOS AXOLOTES, STATE OF MEXICO, MEXICO

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Abstract.—Ambystomatid salamanders in central Mexico are confronted by anthropogenic threats that can limit their distribution and abundance. *Ambystoma altamirani* (Mountain Stream Siredon) is listed as Endangered by the International Union for Conservation of Nature (IUCN) Red List and as Threatened by the Mexican government. We report on the distribution, abundance, occupancy, population structure, and substrate use of *A. altamirani*, a stream dwelling salamander, along the Arroyo los Axolotes, Sierra de las Cruces, Mexico. We observed *A. altamirani* at least once during repeated surveys between February 2018 to December 2018 in 24 of 25 permanent 5-m long reaches separated by 40 m. The best model for occupancy had constant occupancy, detection, extinction, and colonization probabilities. Sites that dried at some time during the study had fewer observed individuals than those that did not dry. Size structure was relatively constant throughout the year, except for the appearance of small larvae in May, June, and July. Proportion of gilled individuals (larvae) peaked from March to May with very few or none from August to October. Mud substrates were the most commonly used, and rock related substrates were relatively rarely used. Our observations and those of previous studies suggest critical stream characteristics for *A. altamirani* include sites that do not dry, presence of mud substrates, and the absence of fish..

Key Words.—*Ambystoma altamirani*; Ambystomatidae; Mountain Stream Siredon; occupancy; salamanders; sex ratio; size structure; stream

Resumen.—Las salamandras ambystomátidas en la parte central de México enfrentan amenazas antropogénicas que pueden limitar su distribución y abundancia. *Ambystoma altamirani* (Ajolote de Arroyo de Montaña) está considerada como en peligro de extinción en la lista roja de la Unión Internacional para la Conservación de la Naturaleza (UICN) y como amenazada por el gobierno mexicano. Reportamos la distribución, abundancia, porcentaje de ocupación del hábitat, estructura poblacional, y uso del sustrato por *A. altamirani*, una salamandra que habita en arroyos, a lo largo del Arroyo Los Axolotes, Sierra de las Cruces, México. Observamos a *A. altamirani* por lo menos una vez durante muestreos repetidos entre febrero y diciembre 2018 en 24 de 25 sitios permanentes cada uno de 5 m de longitud separados por 40 m lineales. El mejor modelo para la ocupación tuvo probabilidades de ocupación, detección, extinción y colonización constantes. Los sitios que se secaron algún tiempo durante el periodo de estudio tuvieron menos individuos observados que aquellos que no se secaron. La estructura de tallas fue relativamente constante a través del año, excepto por la aparición de larvas pequeñas en mayo, junio y julio. La proporción de individuos branquiados (larva) mostró un pico de marzo a mayo con muy pocos o ninguno de agosto a octubre. El sustrato de lodo fue el más comúnmente utilizado, y sustratos relacionados con rocas fueron relativamente raramente utilizados. Nuestras observaciones y aquellas de estudios previos sugieren que características del arroyo críticas para *A. altamirani* incluyen sitios que no se secan durante el año, presencia de sustratos de lodo, y ausencia de peces.

Palabras Clave.—*Ambystoma altamirani*; Ambystomatidae; Ajolote de Arroyo de Montaña; arroyo; estructura de tallas; ocupación; proporción de sexos; salamandras

INTRODUCTION

In central Mexico, salamanders in the genus *Ambystoma* are confronted by a variety of anthropogenic threats that limit their distribution and abundance, including habitat loss, urban development, expanding agriculture, pollution, and climate change (Soto-Rojas et al. 2017; Escalera-Vázquez et al. 2018; Hernández-Guzmán et al. 2019). In addition, salamanders in the Trans-Mexican Volcanic Belt may be prone to exposure to *Batrachochytrium salamandrivorans* and *B. dendrobatidis* due to the suitability of the habitat for the pathogens (Frias-Alvarez et al. 2008; Basanta et al. 2019a; Bolom-Huet et al. 2019), and *B. dendrobatidis* has been detected in *Ambystoma* in Mexico (Frias-Alvarez et al. 2008; Basanta et al. 2019b). It is therefore important to gain a better understanding of the biology and natural history of these species to provide a basis for creating effective conservation and management plans for these salamanders.

The Mountain Stream Siredon (*Ambystoma altamirani*) is currently listed as Endangered by the International Union for Conservation of Nature (IUCN) Red List (IUCN 2019). In Mexico, *A. altamirani* is categorized as Amenazada or Threatened under the NOM-059-SEMARNAT-2010 norm NOM-059-SEMARNAT-2010 norm of the Natural Resources and Environmental Secretariat (SEMARNAT; Secretaria de Medio Ambiente y Recursos Naturales [SEMARNAT]. 2010. Norma Oficial Mexicana NOM-059-SEMARNAT-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio. Lista de especies en riesgo. Diario oficial. http://www.profepa.gob.mx/innovaportal/file/435/1/NOM_059_SEMARNAT_2010.pdf [Accessed 2 July 2019]). *Ambystoma altamirani* has an Environment Viability Score of 13, indicating they are at the high end of the medium threat category (Wilson et al. 2013). *Ambystoma altamirani* is found in, or in close proximity (usually < 1–2 m) to, high mountain streams in the State of Mexico, Morelos, and Mexico City, where it is subject to threats from the expansion of Mexico City and its effects on the environment (Lemos-Espinal et al. 1999; Woolrich-Piña et al. 2017). In addition, some populations of *Ambystoma altamirani* appear to be threatened by introduced Rainbow Trout (*Oncorhynchus mykiss*; Estrella Zamora et al. 2018) and may experience genetic bottlenecks due to the isolation of populations in different streams or watersheds (Parra-Olea et al. 2011; Heredia-Bobadilla et al. 2017; Monroy-Vilchis et al. 2019).

The largest concentration of populations of *A. altamirani* is in the Sierra de las Cruces in the State of Mexico; however, anthropogenic degradation of

the region (García-Romero 2001) is likely negatively affecting populations of *A. altamirani* there. It is therefore particularly urgent to study life history and habitat associations in this region to be able to propose sustainable practices that preserve the natural resources of the Sierra de las Cruces. Previous studies suggest that *A. altamirani* tends to occur in portions of a stream that have greater volumes of water (i.e., deeper and wider) with faster currents and higher dissolved oxygen content compared to areas where they do not occur (Lemos-Espinal et al. 2016). They also tend to occur in reaches with open canopies, low human disturbance, grassy aquatic vegetation, and a mud or sandy substrate (Lemos-Espinal et al. 2016; Villanueva Camacho et al. In press). Male *A. altamirani* are larger than females (Lemos-Espinal et al. 2016). Eggs have been observed in April to August and December to January (Lemos-Espinal et al. 2016; Villarreal Hernández et al. In press; Villanueva Camacho et al. In press). The diet of *A. altamirani* includes primarily ostracods and gastropods, as well as insects (Lemos-Espinal et al. 2015). The only known predators of *A. altamirani* is the Short-tailed Alpine Garter Snake (*Thamnophis scaliger*; Villarreal Hernández et al. In press).

Here we report the results of a study of *Ambystoma altamirani* from the Arroyo los Axolotes in the Sierra de las Cruces that expands on previous work on *A. altamirani* from the Arroyo los Axolotes (Lemos-Espinal et al. 2015, 2016). In contrast to our previous studies of *A. altamirani* along the Arroyo los Axolotes (Lemos-Espinal et al. 2015, 2016), the present study followed specific permanently established stream sections as opposed to stream sections randomly selected each sampling visit. This change allowed a more rigorous examination of stream use and occupancy, as well as a better understanding of temporal variation in population structure and abundance (i.e., use of different, randomly selected sampling sites did not allow for the separation of site selection from temporal variation). We considered substrate use, size structure, and the proportion of gilled individuals for this population. We placed particular emphasis on monthly variation in these parameters. In particular, we hypothesized that the hydroperiod of the site might affect the abundance of salamanders. This information, along with previous studies on *A. altamirani*, should help to determine the stream characteristics that may be needed to allow this endangered species of salamander to persist in the Arroyo los Axolotes and other streams.

MATERIALS AND METHODS

Study area.—The Sierra de las Cruces is located in the extreme northwestern part of the State of México, with the Cerro de las Navajas its highest peak (3,710

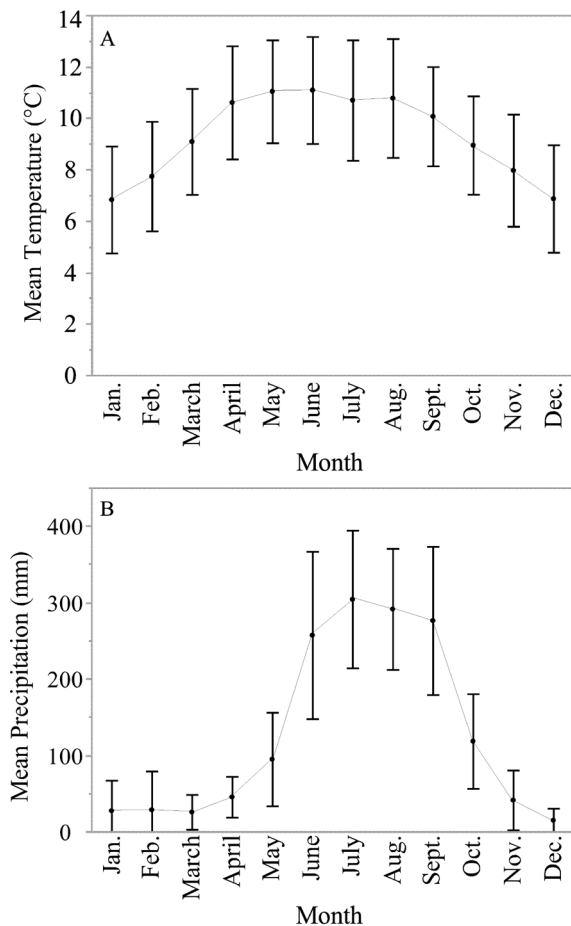


FIGURE 1. (A) Mean (\pm one standard deviation) monthly precipitation and (B) mean monthly temperature 1977–2015 for the meteorological station 15231- "Presa Iturbide" (<https://smn.conagua.gob.mx/tools/RECURSOS/Mensuales/mex/00015231.TXT>).

m altitude). The runoff from this summit drains in a series of permanent streams that run through meadows and canyons surrounded by stands of *Pinus hartwegii* (Hartweg's Pine) and mixed forests of *P. hartwegii*, *P. montezumae* (Montezuma Pine) and *Abies religiosa* (Sacred Fir). The meadows occupied by these streams occur from 2,830 to 3,460 m above sea level. The first meadow that receives the runoff waters of the Cerro de Las Navajas is the Llano Las Navajas, which is an extensive (about 100 ha) grassland (vegetation mostly the grasses *Bouteloua* spp., *Festuca* spp., *Mühlenbergia* spp., and *Stipa* spp.) surrounded by a *Pinus hartwegii* forest.

Our study population was located in the Arroyo los Axolotes found in the Llano Las Navajas, municipality of Isidro Fabela, Sierra de las Cruces, State of México (19°32'12.2"N, 99°29'52.7"W, 3,479 m elevation). The Arroyo Los Axolotes is a permanent, first order stream that runs along the southern edge of the grassland. Between December and April, the Arroyo los Axolotes

is limited to a main channel that includes several shallow pools (≤ 3.5 m diameter, ≤ 1 m depth) connected by branches of the main channel. In contrast, between May and November, the Arroyo los Axolotes consists of two main channels, which are deeper and wider than from December to April. Several marshy areas as well as small streams occurred on the northwestern side of the grassland. Human activities, such as of grazing cattle and sheep, and recreational activities on weekends, were concentrated on the northern edge of the grassland. Most human activities were limited to the banks of the grassland and did not seem to directly affect the stream or, if they did, only small sections of it were affected, which were outside the study area.

At our study site, sporadic rains started in April, gradually increased in intensity in May and June, with maximum mean monthly precipitation from July to October (Fig. 1). From November to March, the mean monthly precipitation was lower and the flow of water in the stream was often reduced to thin strands of water that flow between pools. The average monthly air temperature was relatively constant, fluctuating between 6.8° and 11.0° C with a peak in June (Fig. 1).

Field work.—We established 25 permanent study reaches, each 5 m long and 40 m apart, along the Arroyo los Axolotes (Fig. 2) using a mobile GPS unit (Garmin Etrex Venture GPS, Olathe, Kansas, USA; accuracy to within < 15 m). We visited the Arroyo los Axolotes multiple times per month with a mean of 7.6 ± 0.5 (standard error) visits per month (range, 5–10 visits) from February 2018 to December 2018. Each visit took place from 1100 to 1500. During each visit we visually searched the permanent reaches for *A. altamirani*, using a herpetological hook to check the bottom of the stream and the cavities along its sides to induce movement by salamanders to make them more apparent. In addition, we searched under rocks and other objects in the stream at each site. Surveys lasted about 10 min per site. We captured salamanders with a dipnet and measured snout-vent length (SVL) to nearest mm using a plastic ruler. We also noted whether an individual possessed gills or not (for the most part we assumed the gilled individuals were larvae and not paedomorphic adults based on their size). We recorded the substrate where the salamanders were originally observed. We categorized substrates as being mud, bedrock, clay, sand, gravel, or rocks, as well as combinations of these substrate types. We also measured dissolved oxygen and water temperature at each reach during each survey using a YSI model 85 Handheld Dissolved Oxygen, Conductivity, Salinity, and Temperature System (YSI Incorporated, Yellow Springs, Ohio, USA). We released all salamanders at the point of capture.

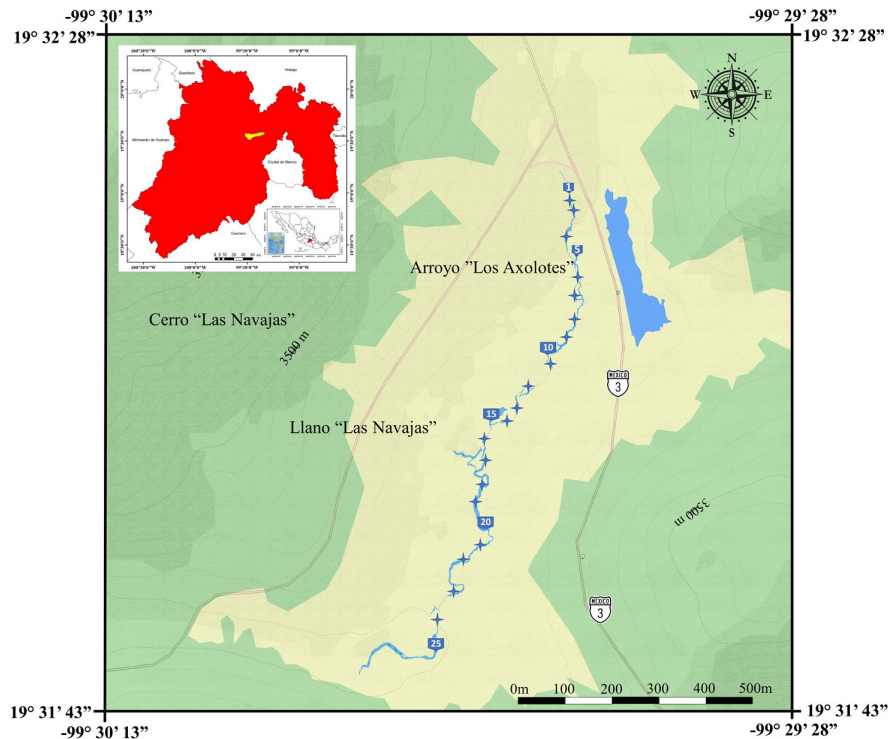


FIGURE 2. Map of the study area showing the 25 sampling sites of the Arroyo Los Axolotes, Sierra de las Cruces, municipality of Isidro Fabela, State of Mexico, Mexico. The sites are separated from each other by 40 m (contiguous sites) making a total of 1,000 m of stream sampled.

Data analysis.—We used the program PRESENCE (Version 2.12.26; www.usgs.gov/software/presence) to estimate occupancy, detection probability, colonization probability, and extinction probability (see MacKenzie et al. 2003; Mazerolle et al. 2007 for details of these methods) using a multiple season model (MacKenzie et al. 2003), treating each month as a season for a total of 11 seasons. We also used models with mean monthly temperature and mean monthly precipitation as covariates (see Table 1 for list of models examined). We used the Akaike Information Criterion (AIC) to select the best model from among candidate models (Burnham and Anderson 2002). Given the distance between reaches (40 m), we assumed there was minimal movement between reaches and thus treated them as independent.

We checked the assumption of normality using Shapiro-Wilks tests and homoscedasticity of variances using Leven's test. If the assumptions of parametric tests were violated, we used either non-parametric tests or rank-transformed the data. We used a Kruskal-Wallis test to compare the mean number of observed individuals and mean SVL among months. We used non-parametric Kruskal-Wallis analyses to compare the proportion of individuals with gills and the proportion of males among months. We used a repeated measures ANOVA on rank-transformed data to compare mean

number of individuals observed per month between sites that dried at least once during the study and sites that never dried. We used JMP Pro 14 (SAS Institute, Cary, North Carolina, USA) for statistical analyses, and for all tests, we used an α -value of 0.05.

RESULTS

Mean dissolved oxygen ranged from 2.5 mg L⁻¹ in March to 6.5 mg L⁻¹ in August. Mean water temperature ranged from 13.6° C in November to 18.7° C in August. We observed *A. altamirani* at least once during the study period in 24 of the 25 permanent sites (Table 2). The best occupancy model (out of eight) based on the AICc model selection procedure was the model with constant occupancy, detection, extinction, and colonization probabilities (Table 1). For this model, occupancy rate was $0.14 \pm$ (standard error) 0.07 , colonization rate was 0.35 ± 0.05 , extinction rate was 0.29 ± 0.05 , and detection rate was 0.30 ± 0.02 .

The mean number of observed individuals differed among months with a peak in July and lows in February, March, and August through December ($H = 42.7$, $df = 10$, $P < 0.001$; Table 3). It is also clear from looking at the mean number of individuals observed at each site along the stream per month that some sites were occupied by more salamanders than other sites (Table

TABLE 1. Results of Akaike Information Criterion (AIC) model selection procedures for different occupancy models. Symbols are Ψ = occupancy, γ = colonization, ϵ = extinction, and p = detectability.

| Model | AIC | Δ AIC | AICc Weights | # Parameters |
|--|---------|--------------|--------------|--------------|
| $\Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\cdot)$ | 1544.77 | 0 | 0.45 | 4 |
| $\Psi(\cdot), \gamma(\cdot), \epsilon(\cdot), p(\text{month}, \text{precip})$ | 1548.14 | 3.37 | 0.08 | 14 |
| $\Psi(\text{month}), \gamma(\text{month}), \epsilon(\text{month}), p(\text{month})$ | 1554.74 | 9.97 | 0.003 | 32 |
| $\Psi(\text{month}), \gamma(\text{month}), p(\text{month})$ | 1554.75 | 9.98 | 0.003 | 32 |
| $\Psi(\text{month}), \epsilon(\text{month}), p(\text{month})$ | 1554.91 | 10.14 | 0.003 | 32 |
| $\Psi(\text{month}), \gamma(\cdot), \epsilon(= 1-\gamma), p(\text{month})$ | 1564.62 | 19.85 | 0 | 22 |
| $\Psi(\text{precip}), \gamma(\text{precip}), \epsilon(\text{precip}), p(\text{precip})$ | 1580.63 | 35.86 | 0 | 4 |
| $\Psi(\text{month}, \text{precip}), \gamma(\cdot), \epsilon(\cdot), p(\cdot, \text{precip})$ | 1597.85 | 53.08 | 0 | 12 |

TABLE 2. Summary of mean number of the Mountain Stream Siredon (*Ambystoma altamirani*) observed in a specific site along the Arroyo los Axolotes, State of México, Mexico, during a given month from February 2018 to December 2018. The number of visits to each site in a month is in parentheses. A superscript of D indicates the site was dry for at least one of the visits in a month.

| Site | February (5) | March (10) | April (8) | May (7) | June (9) | July (9) | August (6) | September (10) | October (8) | November (8) | December (5) |
|------|-----------------|---------------|--------------|-------------------|-------------------|----------------|-------------------|-------------------|----------------|-----------------|-----------------|
| 1 | 0 | 0 | 0 | 0 ^D | 0 ^D | 0 | 0.17 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 ^D | 0 ^D | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 ^D | 0 ^D | 0.91 | 1 | 1 | 1 | 1 | 0.2 |
| 4 | 0 | 0 | 0 | 0 ^D | 0 ^D | 0 ^D | 0 | 0 | 0 | 0 | 0 |
| 5 | 0 | 0 | 0 | 0.33 ^D | 0 ^D | 0.11 | 0 | 0 | 0 | 0 | 0 |
| 6 | 0 | 0 | 0 | 0.6 ^D | 0 ^D | 0.54 | 0.56 | 0.1 | 0.33 | 0.12 | 0.33 |
| 7 | 0 | 0 | 0.12 | 0.33 ^D | 0 ^D | 0.11 | 0.17 | 0 | 0.12 | 0.12 | 0.4 |
| 8 | 0 | 0 | 0.44 | 0.43 | 0.69 | 0.3 | 0.17 | 0.18 | 0 | 0.62 | 0.43 |
| 9 | 0.2 | 0.36 | 0.67 | 0.82 | 0.5 | 0.92 | 0.28 | 0.53 | 0.4 | 0.67 | 0 |
| 10 | 0 | 0.1 | 0.86 | 0.8 | 0 | 0.44 | 0 | 0 ^D | 0.25 | 0 | 0.2 |
| 11 | 0.67 | 0.86 | 0.96 | 0 | 0.11 | 0.3 | 0 | 0 ^D | 0 | 0 | 0 |
| 12 | 0 | 0 | 0.5 | 0.28 | 0 | 0.54 | 0 ^D | 0.18 ^D | 0 | 0 | 0.4 |
| 13 | 0 | 0.1 | 0.25 | 0.58 | 0.56 | 0.3 | 0 ^D | 0.1 ^D | 0.3 | 0 | 0 |
| 14 | 0 | 0 | 0.12 | 0.5 | 0.78 | 0.89 | 0.43 ^D | 0.1 ^D | 0.33 | 0.25 | 0.5 |
| 15 | 0 | 0.33 | 0.68 | 0.68 | 0 | 1.73 | 0 ^D | 0 ^D | 0 | 0 | 0 |
| 16 | 0 | 0 | 0.25 | 0.33 | 0 | 0 | 0 ^D | 0.1 ^D | 0 | 0 | 0 |
| 17 | 0 | 0 | 0 | 0 | 0.57 | 0 | 0 | 0.27 ^D | 0 | 0 | 0 |
| 18 | 0 | 0.1 | 0 | 0.88 | 1.23 | 0.33 | 0.5 | 0.1 | 0.125 | 0.125 | 0.33 |
| 19 | 0.2 | 0 | 0.42 | 0.94 | 0.85 | 2.16 | 0.75 | 0.1 | 0.6 | 0.96 | 1.33 |
| 20 | 0 | 0 | 0 | 0.82 | 0 | 0.11 | 0 | 0.1 | 0 | 0 | 0 |
| 21 | 0 | 0 | 0.54 | 0.67 | 0 | 0.11 | 0 | 0.1 | 0 | 0 | 0 |
| 22 | 0 | 0 | 0.36 | 0 | 0.36 ^D | 1.41 | 0.7 | 0.45 | 0.78 | 0.91 | 0 |
| 23 | 0 | 0 | 0.61 | 0 ^D | 0 ^D | 0 | 0 | 0.67 | 0 | 0 | 2.17 |
| 24 | 0 | 0 | 0.46 | 0 ^D | 0 ^D | 0 | 0 | 0 | 0.22 | 0.12 | 0 ^D |
| 25 | 0 | 0 | 0 | 0 ^D | 0 ^D | 0.2 | 0 | 0 | 0.25 | 0 | 0 |

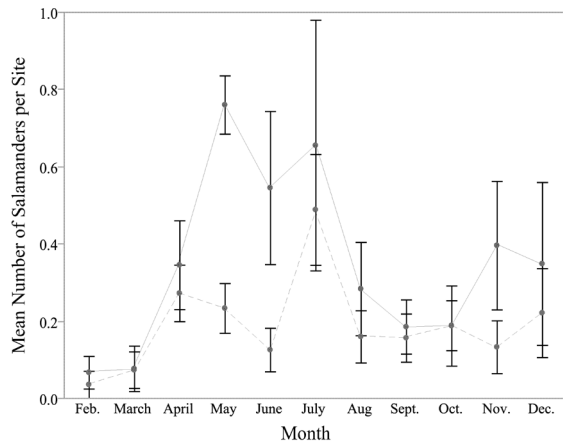


FIGURE 3. Mean (\pm one standard error) number of the Mountain Stream Siredon (*Ambystoma altamirani*) per site for each month for sites from Arroyo Los Axolotes, State of Mexico, Mexico, that dried (red dots) and that did not dry (blue dots) during the study period (February 2018 to December 2018).

2). Sites that dried at some time during the study had a lower mean number of observed salamanders per month than those that did not dry ($F_{1,23} = 6.67, P = 0.017$; Fig. 3). We found no effect of month on salamander abundance (time: $F_{10,14} = 0.54, P = 0.836$). There was also no significant time by drying condition interaction ($F_{10,14} = 1.99, P = 0.116$; Fig. 3).

Mean SVL varied significantly among months, with a much higher mean in February than all other months ($F_{10,111} = 2.14, P = 0.027$; Table 3). The size structure of the population of *A. altamirani* along the Arroyo los Axolotes, however, was relatively constant throughout the year, with the only exception being the appearance of small larvae (< 25 mm SVL) in May, June, and July (Fig.

TABLE 3. Mean (\pm one standard error) number of individuals observed per visit, snout-vent length (SVL), and proportion of individuals with gills of the Mountain Stream Siredon (*Ambystoma altamirani*) from February 2018 to December 2018 from the Arroyo los Axolotes, State of México, Mexico. The number of site visits each month is given in parentheses.

| Month | Number of individuals | SVL (mm) | Proportion with gills |
|----------------|-----------------------|----------------|-----------------------|
| February (5) | 1.2 \pm 0.2 | 77.0 \pm 5.1 | 0.30 \pm 0.20 |
| March (10) | 3.0 \pm 0.6 | 57.4 \pm 5.0 | 0.88 \pm 0.10 |
| April (8) | 13.4 \pm 4.3 | 60.5 \pm 3.3 | 0.64 \pm 0.12 |
| May (7) | 22.8 \pm 5.3 | 58.5 \pm 0.7 | 0.84 \pm 0.03 |
| June (8) | 11.4 \pm 2.8 | 57.2 \pm 5.7 | 0.41 \pm 0.12 |
| July (9) | 21.1 \pm 5.8 | 58.9 \pm 2.2 | 0.21 \pm 0.05 |
| August (6) | 12.2 \pm 1.6 | 59.5 \pm 1.1 | 0.08 \pm 0.04 |
| September (10) | 9.5 \pm 1.2 | 64.3 \pm 2.8 | 0 |
| October (8) | 9.1 \pm 0.6 | 60.1 \pm 1.9 | 0.08 \pm 0.03 |
| November (8) | 9.6 \pm 1.5 | 60.0 \pm 1.5 | 0.22 \pm 0.10 |
| December (5) | 9.2 \pm 4.7 | 56.9 \pm 2.9 | 0.17 \pm 0.10 |

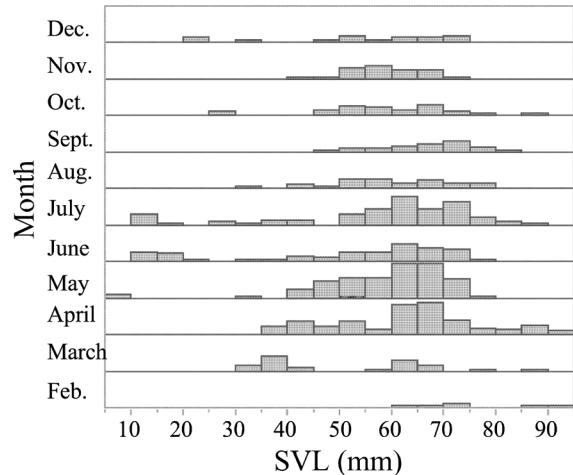


FIGURE 4. Size structure of the Mountain Stream Siredon (*Ambystoma altamirani*) along the Arroyo los Axolotes, State of Mexico, Mexico, in each month of the study (February 2018 to December 2018).

4). The proportion of gilled individuals (larvae) in the Arroyo los Axolotes varied from month to month, peaking from March to May with very few or none from August to October ($H = 45.99, df = 10, P < 0.001$; Table 3).

We found most salamander on muddy substrates (40.4%), followed by sand with gravel or rocks (22.1%), and mud with gravel or rocks (13.4%; Table 4). Substrates including mud constituted 71.4% of the observations (Table 4), suggesting mud may be an important substrate for these salamanders. Rock related substrates, such as bedrock and gravel or rock dominated substrates, had relatively few observations (Table 4). In addition, mud substrates were used throughout the study period, but most of the substrates were only used in fewer months (Table 4).

DISCUSSION

The abundance of *A. altamirani* along the Arroyo los Axolotes peaked in July with lows in February, March, and August through December. A previous study of *A. altamirani* in the Arroyo los Axolotes found a similar peak abundance from June to August (Lemos-Espinal et al. 2016). *Ambystoma leorae* abundances also peak from May to July in streams in the mountains surrounding Mexico City (Sunny et al. 2014; Lemos-Espinal et al. 2017). These peaks in abundance coincide with the peak precipitation for the area.

We observed fewer *A. altamirani* in reaches that dried at least once during the study period compared to reaches that never dried. Our results are consistent with other studies on the effect of drying on *Ambystoma* abundances, with drying habitats having lower abundances than non-drying habitats (e.g., Semlitsch 1983), and drought negatively affecting occupancy

TABLE 4. The substrate types used by the Mountain Stream Siredon (*Ambystoma altamirani*) each month in the Arroyo los Axolotes, State of México, Mexico, from February 2018 to December 2018. The number of site visits each month is given in parentheses. The months that are abbreviated are Feb. = February, Aug. = August, Sept. = September, Oct. = October, Nov. = November, and Dec. = December.

| Substrate | Feb. (5) | March (10) | April (8) | May (7) | June (9) | July (9) | Aug. (6) | Sept. (10) | Oct. (8) | Nov. (8) | Dec. (5) | Total |
|-------------------------------|-------------|---------------|--------------|------------|-------------|-------------|-------------|---------------|-------------|-------------|-------------|-------|
| Bedrock | 0 | 0 | 0 | 5 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 7 |
| Bedrock - clay | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Bedrock - clay/ rocks | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| Bedrock - mud/ rocks | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| Bedrock - rock or gravel | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 6 |
| Clay | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 4 |
| Clay - sand/ mud | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Gravel or rocks | 0 | 0 | 13 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 15 |
| Gravel or rocks/ clay | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 5 |
| Gravel or rocks/ clay and mud | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Gravel or rocks – sand/ mud | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Mud | 5 | 29 | 67 | 42 | 30 | 59 | 15 | 28 | 27 | 24 | 15 | 341 |
| Mud - sand | 0 | 0 | 0 | 16 | 3 | 7 | 1 | 9 | 4 | 6 | 3 | 49 |
| Mud - clay | 0 | 1 | 0 | 2 | 2 | 13 | 6 | 0 | 1 | 2 | 0 | 27 |
| Mud - clay/ gravel or rocks | 0 | 0 | 0 | 2 | 0 | 8 | 4 | 0 | 0 | 0 | 0 | 14 |
| Mud - clay/ sand | 0 | 0 | 0 | 0 | 3 | 6 | 0 | 0 | 0 | 0 | 0 | 9 |
| Mud - gravel or rocks | 0 | 0 | 20 | 32 | 27 | 8 | 1 | 2 | 3 | 18 | 4 | 115 |
| Mud - sand/ gravel or rocks | 0 | 0 | 0 | 33 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 36 |
| Mud - grass | 0 | 0 | 0 | 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 |
| Sand | 0 | 0 | 1 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| Sand - gravel or rocks | 1 | 0 | 2 | 0 | 8 | 28 | 42 | 54 | 36 | 19 | 1 | 191 |

(Walls et al. 2013; Anderson et al. 2015; Davis et al. 2017). This result is consistent with the observation of a previous study of *A. altamirani* along the Arroyo los Axolotes that the sites where *A. altamirani* were found were deeper and wider than sites without *A. altamirani*, suggesting they may choose sites for their water retaining potential (Lemos-Espinal et al. 2016).

One limitation of our study is that we did not consider the surrounding terrestrial habitat along the Arroyo los Axolotes as a factor in the distribution of *A. altamirani* along the stream. We are currently exploring this issue with additional fieldwork that is specifically quantifying the terrestrial habitat and its relationship to the abundance of salamanders in the Arroyo los Axolotes. Other *Ambystoma* are known to be affected by loss of forest along streams (Niemiller et al. 2006; Perkins and Hunter 2006; Maigret et al. 2014) or by terrestrial habitat bordering wetlands (Gorman et al. 2009; Anderson et al. 2015; Crawford et al. 2017). Indeed, Sunny et al. (2014) found that two of the three most important microhabitat descriptors for *A. leora* (Leora's Stream Siredon) populations in streams near Mexico City were concerned with the vegetation around the stream. In the future, examination of the terrestrial

habitats neighboring the Arroyo los Axolotes are needed. In particular, such information is needed to understand how the potential impacts of human activities on the terrestrial habitats might have on the salamanders in the stream.

Mean SVL of *A. altamirani* peaked in February; however, the size structure of the population of *A. altamirani* along the Arroyo los Axolotes does not vary much during the year, but small larvae (< 25 mm SVL) appear from May to July. The observation of larvae in these months is consistent with previous observations of egg laying in June in *A. altamirani* in the Arroyo los Axolotes (Lemos-Espinal et al. 2016). The constant presence of individuals ranging from 40–90 mm SVL suggests the presence of both unmetamorphosed and metamorphosed individuals throughout the year because transformation in this population occurs between 62 and 70 mm SVL (Lemos-Espinal et al. 2016). The proportion of gilled individuals (larvae) in the Arroyo los Axolotes, however, peaks from March to May with very few or no larvae from August to October, suggesting metamorphosis might coincide with the period just prior to the likely low point in stream depth (i.e., period following several months with lower precipitation).

Mud substrates were often where we found *A. altimirani* along the Arroyo los Axolotes but we rarely found them in rock related substrates. Our observations and those of Lemos-Espinal et al. (2016) suggest that mud is an important substrate for *A. altimirani*, as it appears to be for *A. leorae* (Lemos-Espinal et al. 2017) and *A. rivulare* (Toluca Stream Siredon; Bille 2009). Our observations and those of Lemos-Espinal et al. (2016) also suggest *A. altimirani* avoid using gravel or bedrock substrates. Because we did not quantify the availability of each substrate type at a relevant scale, however, these conclusions need to be confirmed with comparison of salamander use to the availability of the substrates in the stream.

Our study of the population of *A. altimirani* in the Arroyo los Axolotes in the Sierra de las Cruces has demonstrated that there is a substantial portion of their ecology that varies throughout the year, namely abundance, distribution, proportion of gilled individuals, and substrate use, with less variation in size structure except for the appearance of larvae in June and July. Some of this variation among months, at least for abundance and distribution and perhaps the proportion of gilled individuals, appears to be linked to whether a particular site along the stream dries or not. Our observations, along with those of Lemos-Espinal et al. (2016) and Estrella Zamora et al. (2018), suggest that some stream characteristics may be critical for persistence of *A. altimirani* in streams: sites that do not dry during the year (i.e., deeper and wider sites), presence of mud substrates, and the absence of fish. Conservation and management plans for streams inhabited by *A. altimirani* should include efforts to maintain these particular stream characteristics.

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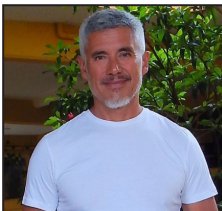
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