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In-stream movement of *Ambystoma altamirani* (Caudata: Ambystomatidae) from the Arroyo los Axolotes, Mexico

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Abstract

In-stream movement of *Ambystoma altamirani* (Caudata: Ambystomatidae) from the Arroyo los Axolotes, Mexico. Knowledge of the movements of amphibians can be useful in developing conservation strategies. We studied the movement of *Ambystoma altamirani,* a Mexican endemic salamander, in a montane stream near Mexico City, Mexico. We obtained movement estimates from 35 recaptured male, female, and juvenile salamanders. The majority of individuals moved during the study. Mean movements were > 250 m, with several individuals having movements > 500 m. Movements in *A. altamirani* did not have an upstream or downstream bias. Movement patterns (i.e., direction, mean distance, mean net displacement) did not differ among males, females, and juveniles. However, there was a tendency for the direction of net displacement to differ among males, females, and juveniles. Individuals that moved did not differ in snout–vent length (SVL) growth rate, initial SVL, or initial body mass (BM) from those that did not move; however, they showed greater BM change than those that did not move. We found that *A. altamirani* moved more than we had predicted. Our results suggest that maintaining aquatic and terrestrial conditions in the Arroyo los Axolotes to allow movements may be crucial in conserving this species.

Keywords: Amphibians, Downstream, Moviment patterns, Salamanders, Upstream.

Resumo

Movimentação de *Ambystoma altamirani* (Caudata: Ambystomatidae) dentro de um riacho de Arroyo los Axolotes, México. O conhecimento dos movimentos dos anfíbios pode ser útil no desenvolvimento de estratégias de conservação. Estudamos a movimentação de *Ambystoma altamirani*, uma salamandra endêmica mexicana, em um riacho montanhoso próximo à Cidade do México, México. Obtivemos estimativas da movimentação de 35 salamandras machos, fêmeas e juvenis recapturados. A maioria dos indivíduos movimentou-se durante o estudo. Os movimentos

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médios foram > 250 m, com vários indivíduos com movimentos > 500 m. Os movimentos de *A. altamirani* não mostraram uma tendência a montante ou a jusante. Os padrões de movimentação (ou seja, direção, distância média, deslocamento médio da rede) não diferiram entre machos, fêmeas e juvenis. No entanto, houve uma tendência de que a direção do deslocamento da rede fosse diferente entre machos, fêmeas e jovens. Os indivíduos que se deslocaram não diferiram em relação à taxa de crescimento do comprimento rostro-cloacal (SVL), SVL inicial ou massa corporal inicial (BM) daqueles que não se deslocaram; no entanto, apresentaram maior mudança na BM do que aqueles que não se deslocaram. Descobrimos que *A. altamirani* movimentou-se mais do que havíamos previsto. Nossos resultados sugerem que a manutenção das condições aquáticas e terrestres no Arroyo los Axolotes que permitem os movimentos pode ser crucial para a conservação dessa espécie.

Palavras-chave: Anfíbios, Jusante, Montante, Padrões de movimentação, Salamandras.

Introduction

Understanding how and why amphibians move and the consequences of these movements can aid in developing conservation strategies (Bailey and Muths 2019). Movement of salamanders in streams is often examined in the context of upstream and downstream movement, with species showing upstream-biased movements (Lowe 2010, Cosentino *et al.* 2009, Campbell Grant *et al.* 2010), downstream-biased movements (Bruce 1986, Schafft *et al.* 2022), or equal movement upstream and downstream (Bendik *et al.* 2016). In addition to the direction of movement, the distance of in-stream movements by salamanders can vary dramatically among species. Many species of stream-dwelling salamanders show relatively short movements, with movements typically < 10 m (e.g., Barthalmus and Bellis 1972, Holomuzki 1991, Cosentino *et al.* 2009). However, some species show longer movements. For example, *Eurycea tonkawae* Chippindale, Price, Wiens, and Hillis, 2000 often made movements of > 15 m in a stream, frequently recolonizing sites that had dried (Bendik *et al.* 2016), and *Gyrinophilus porphyriticus* (Green, 1827) can move up to 565 m along a -km stream (Lowe 2010).

Previous studies of Mexican stream-dwelling *Ambystoma* salamanders suggested that they do not move much along the streams they inhabit, due to low temperatures and poor terrestrial habitat matrix quality (little canopy cover), likely leading to a small degree of subpopulation genetic structure associated with substrates in the streams (Sunny *et al.* 2014). We examined the movement of a Mexican endemic salamander, *Ambystoma altamirani* Dugès, 1895, in the Arroyo los Axolotes, state of Mexico. *Ambystoma altamirani* occurs in streams in the mountains near Mexico City (Lemos-Espinal *et al.* 1999, Woolrich-Piña *et al.* 2017). The ecology and natural history of *A. altamirani* have been extensively studied in the Arroyo los Axolotes (Lemos-Espinal *et al.* 2016, Villarreal Hernández *et al.* 2019, 2020a,b, Gómez-Franco *et al.* 2022, Sánchez-Sánchez *et al.* 2022, Hernández-Luría *et al.* 2023, 2025). This species spends most, if not all, of its life in streams or immediately adjacent to streams (Lemos-Espinal *et al.* 1999). The abundance of *A. altamirani* along a stream appears to be driven more by in-stream factors (e.g., hydroperiod, total dissolved solids, stream width, bank height, water velocity, water temperature, and water depth) than terrestrial factors (e.g., presence of livestock, distance to forest) (Gómez-Franco *et al.* 2022). We specifically studied the distance and the direction (upstream or downstream) moved by individuals. We also determined the relation between distance and direction moved and sex, stage, size, and growth of the individuals.

Materials and Methods

Study Area

Arroyo los Axolotes is a stream located along the southern edge of an extensive 100-ha pasture called the Llano Las Navajas, which is surrounded by a *Pinus hartwegii* Lindl. forest in the municipality of Isidro Fabela, Sierra de las Cruces, State of Mexico (19°32'12.2" N, 99°29'52.7" W, datum WGS84, 3479 m a.s.l.). Between May and November, surface water flows in two main channels; however, between December and April it is limited to a single channel with several shallow pools (about ≤ 3.5 m diameter, ≤ 1 m depth) connected by branches of the main channel that have very slow water flow. Livestock grazing and human recreational activities are concentrated on the northern edge of the pasture (Gómez-Franco *et al.* 2022).

Field Methods

From 25 February 2022 to 13 April 2023, we visited the study area once or twice per month, usually 15 d apart. We searched a 1-km section of the Arroyo los Axolotes for *A. altamirani,* capturing salamanders using dipnets. We recorded each captured individual's location using a mobile global positioning system [GPS] unit (Garmin Etrex Venture GPS, Olathe, Kansas, USA; accuracy to within < 15 m). We measured SVL of each individual to the nearest 1 mm using a transparent plastic ruler and weighed each salamander to the nearest 0.001 g using a portable digital pocket scale (Zencro® 0.001–50 g; Dongguan Zencro Industrial Co., Dongguan, China). Adult males were identified by the presence of a bulge on each side of the tail near the cloaca (i.e., swollen cloacal lips) and adult females by the absence of this bulge (Brandon and Altig 1973). Males with swollen cloacal lips were observed throughout the year, suggesting that this is a reasonable way to sex individuals in this population. Adults of *A. altamirani* at the Arroyo los Axolotes generally lack gills once they complete metamorphosis (Villanueva Camacho *et al.* 2020). Size class was assessed based on SVL (20–34 mm: larvae; 35–64 mm: juveniles, and > 64 mm: adults) (Lemos-Espinal *et al.* 2016, Villanueva-Camacho *et al.* 2020, Gómez-Franco *et al.* 2022). During each survey, we used Visible Implant Elastomer (Northwest Marine Technology, Inc., Anacortes, Washington, USA) to mark any unmarked individuals using individual codes created from VIE color and location on the body, using up to four marks (MacNeil *et al.* 2011). The VIE injector was sterilized between uses to prevent potential contamination among individuals. We did not detect any loss of VIE from the salamanders (i.e., no incomplete marks that would have suggested the loss of VIEs). Previous studies using VIE to mark aquatic salamanders have generally found high retention and readability rates for VIEs (e.g., Phillips and Fries 2009, Moon *et al.* 2022, Knapp *et al.* 2023), and VIEs have been successfully used in *A. altamirani* (Guerrero de la Paz *et al.* 2020). We returned salamanders to their capture location and monitored their activity for a few minutes to ensure they were in good condition.

Data Analysis

We used the distance between the coordinates taken at the time of capture and recapture of an individual to measure displacement, as well as direction (i.e., upstream or downstream) of any movement. Distance moved was calculated by summing the absolute value of all movements made by an individual for all recapture intervals. We calculated net displacement by assigning negative values to upstream movements and positive values to downstream movements. For example, if an individual moved 40 m upstream in one interval and 50 m downstream in the next interval the net displacement was -10 m and total movement was 90 m. We also calculated the median net displacement, skewness, and kurtosis of the distribution of net displacements. We calculated SVL growth rate and BM change by subtracting the final SVL or BM by the initial SVL or BM and dividing by the number of days between captures.

We compared frequencies of movements (upstream, downstream, and not moved) between males and females using a chi-square test or Fisher's exact test. We tested whether mean distance moved and mean net displacement differed among males, females, and juveniles using analyses of variance. We used linear regressions to examine the relationships between distance moved and net displacement with initial SVL. We used a two-way ANOVA to examine if the initial SVL, mean SVL growth rate, and mean BM change differed as a function of movement status (moved or not moved) and sex. Means are given ± 1 SE.

Results

During our surveys we marked a total of 194 individual *A. altamirani* throughout the study section, which provides a minimum density estimate of 0.194 individuals m^{-1}. We recaptured 35 individuals (4 juveniles, 22 females, 9 males) an average of 2.3 ± 0.1 times (median = 2), and the mean number of recaptures did not differ among males, females, and juveniles ($F_{2,32} = 0.19, p = 0.83$).

The distribution of net displacements for all individuals is given in Figure 1. Mean net displacement for all individuals was 41.66 ± 44.89 m (positive = downstream); however, the median was 0. The skewness was -0.12 and kurtosis was 1.16.

Males and females showed similar frequencies of upstream, downstream, and no movements (Table 1; $c^2_2 = 2.34, p = 0.31$) and upstream vs downstream movement (Fisher's exact test, $p = 0.33$). Overall, individuals showed no tendency to move upstream, downstream, or to not move (Table 1; $c^2_2 = 3.5$, $p = 0.17$). Of those individuals that did move, there was no preference to move upstream or downstream for all individuals (Table 1; $c^2_2 = 1.8$, $p = 0.18$), just females (Table 1; $c^2_1 = 0.33, p = 0.56$), or just males (Table 1; Fisher's exact test, $p = 0.28$).

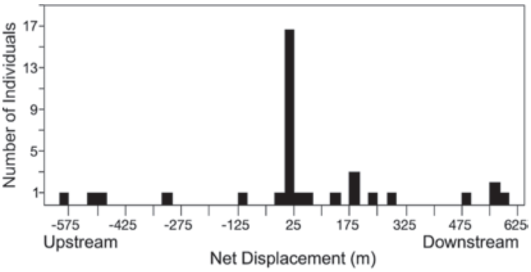

Figure 1. The distribution of net displacements of *Ambystoma altamirani* along the Arroyo los Axolotes.

Mean distance moved did not differ between males, females, and juveniles (Table 1; $F_{2,32} = 0.19, p = 0.83$). Mean net displacement also did not differ between males, females, and juveniles; however, it appears net displacement by juveniles was negative, males positive, and females near 0 (Table 1; $F_{2,32} = 2.09, p = 0.14$).

The distance moved was not related to the initial SVL of the salamander ($N = 35$, $r^2 = 0.024$, $p = 0.38$) nor was the distance moved per day ($N = 35, r^2 = 0.031, p = 0.31$). There was a tendency for net displacement to decrease with the initial SVL of the salamander (Figure 2; $N = 35, r^2 = 0.10, p = 0.065$).

The mean initial SVL of salamanders that moved and did not move did not differ (Figure 3A; $F_{1,27} = 0.30$, $p = 0.59$). Mean initial SVL did not differ between males and females (Figure 3A; $F_{1,27} = 0.09$, $p = 0.76$). The interaction between sex and movement was not significant (Figure 3A; $F_{1,27} = 0.91, p = 0.35$).

The mean initial BM of salamanders that moved and did not move did not differ (Figure 3B; $F_{1,27} = 0.32$, $p = 0.57$). Mean initial BM did not differ between males and females (Figure 3B; $F_{1,27} = 0.03$, $p = 0.87$). The interaction between sex and movement was not significant (Figure 3B; $F_{1,27} = 2.68, p = 0.11$).

Mean SVL growth rate did not differ between males and females (Figure 3C; $F_{1,27} = 0.66$, $p = 0.42$). The mean SVL growth rate of

Table 1. The number of male, female, juvenile, and all *Ambystoma altamirani* individuals that moved upstream, downstream, or did not move over the course of the study in the Arroyo los Axolotes, Mexico. Mean ± SE distance moved (with and without individuals showing no movement) and mean ± SE net displacement (+ = downstream, - = upstream) are also given. *One male moved upstream and downstream to return to its original location.

	Males	Females	Juveniles	All
Upstream	1*	5	1	7*
Downstream	6*	7	0	13*
Not moved	3	10	3	16
Total	9	22	4	35
Mean distance moved (m)	200.4 ± 72.4 (9)	161.2 ± 45.6(22)	125 ± 125 (4)	167.1 ± 36.0 (35)
Mean distance moved (no 0 values) (m)	300.7 ± 81.0 (6)	295.5 ± 60.0 (12)	500	307.9 ± 45.9 m (19)
Mean net displacement (m)	172.4 ± 75.3 (9)	18.4 ± 57.5 (22)	-125 ± 125 (4)	41.7 ± 44.9 (35)

salamanders that moved and did not move did not differ (Figure 3C; $F_{1,27} = 0.65$, $p = 0.43$). The interaction between sex and movement was not significant (Figure 3C; $F_{1,27} = 0.08$, $p = 0.78$).

Mean BM change did not differ between males and females (Figure 3D; $F_{1,27} = 1.47$, $p = 0.24$). Mean BM change of salamanders that moved was greater than that of salamanders that did not move (Figure 3D; $F_{1,27} = 5.14$, $p = 0.032$). The interaction between sex and movement was not significant (Figure 3D; $F_{1,27} = 0.02$, $p = 0.89$).

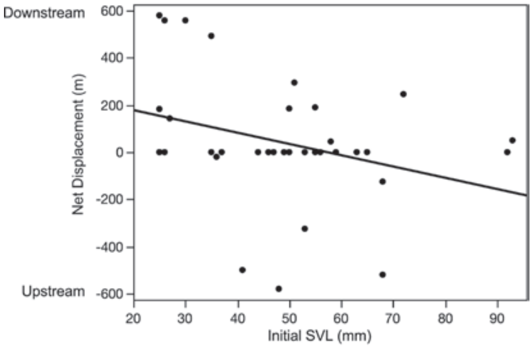

Figure 2. The relationship between initial SVL and net displacement of *Ambystoma altamirani* in the Arroyo los Axolotes.

Discussion

One of our most surprising results is how much *A. altamirani* moved over the course of the study. More than one-half of all individuals moved during the study. In addition, the distances moved were substantial, with mean movements being > 250 m, and several > 500 m. This result contrasts with previous studies on movement of *Ambystoma* in streams. Holomuzki (1991) found evidence for relatively limited dispersal within a stream in *Ambystoma barbouri* Kraus and Petranka, 1989, with 78% of larvae recaptured within 1.5 m of the release point. *Ambystoma leorae* Dugès, 1895 showed a small degree of subpopulation genetic structure associated with substrates in the streams, possibly due to limited mobility of individuals along the stream (Sunny *et al.* 2014).

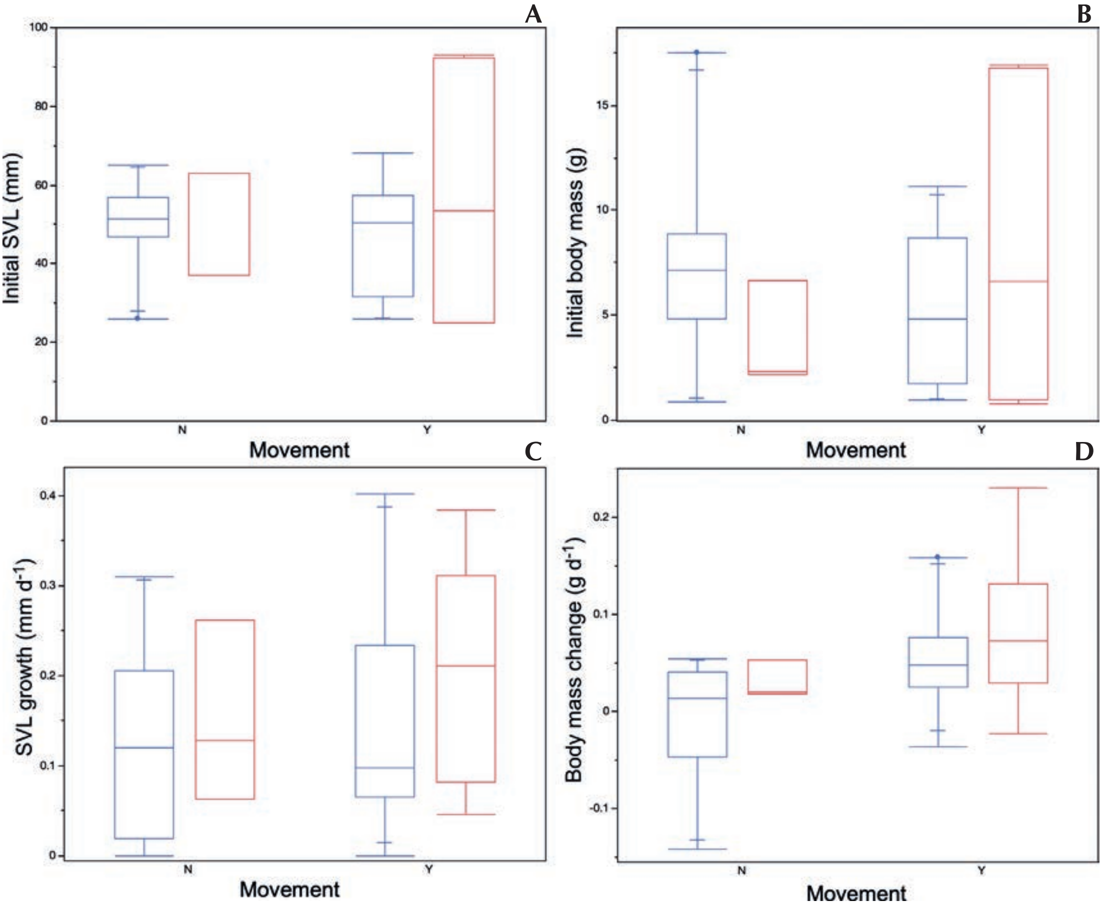

Figure 3. Box and whisker quantile plot of (**A**) initial SVL, (**B**) initial body mass, (**C**) SVL growth rate, and (**D**) BM change of male (blue) and female (red) *Ambystoma altamirani* along the Arroyo los Axolotes that did and did not move over the course of the study.

Ambystoma altamirani in the Arroyo los Axolotes moved both upstream and downstream with no apparent bias. We cannot determine whether these movements took place entirely in the water of if terrestrial movement was involved. For example, movement of the stream-dwelling salamanders, *Desmognathus fuscus* (Green, 1818) and *D. monticola* Dunn, 1916, occurred both in-stream and overland (Campbell Grant *et al.* 2010). For juveniles and gilled individuals, terrestrial movements would seem unlikely. We do not know this for certain, but we have never observed juveniles or gilled individuals on land in this well-studied population. The serpentine nature of the Arroyo los Axolotes is conducive to short overland movements by adults without gills. The distances we report are straight-line distances and would be much longer if movements were strictly aquatic. Using radiotracking could be informative to determine the paths used and whether terrestrial movements are undertaken. Such information could be used to identify whether particular terrestrial habitats might facilitate or hinder overland movements or if all movements are in the stream channel (see Wang *et al.* 2009). Determining this is important to maintain connectivity within populations by ensuring appropriate terrestrial and aquatic habitats.

We did not find statistically significant differences in movement patterns (i.e., direction, mean distance, mean net displacement) between males, females, and juveniles. However, there were tendencies for differences in the direction of the net displacement among males, females, and juveniles. Greater sample sizes, especially of males and juveniles, may permit determination of whether those trends are or are not more strongly supported.

Ambystoma altamirani that moved showed greater BM change than those that did not move; however, they did not differ in SVL growth rate, initial SVL, or initial BM. These results suggest *A. altamirani* that moved may be moving to improve conditions (i.e., find more food, more favorable temperatures) that allow increase in body mass. For example, individuals of *Gyrinophilus porphyriticus* that dispersed farther along a stream had higher survival and growth rates, probably because the ability to settle in a good habitat increased with dispersal distance (Lowe 2010). Alternatively, the individuals who moved were those in better physical condition, and thus increased BM more, were more likely to move. Again, more fine-scale monitoring of movements using radiotelemetry or more frequent observations could help differentiate these options, as well as determine more accurately the total movement of each individual.

In conclusion, our results show that *A. altamirani* does not appear to be sedentary and indeed moves more than we had expected based on prior work on Mexican *Ambystoma* (e.g., Sunny *et al.* 2014). Such movement may permit greater admixture of genes. *Ambystoma leorae* in streams near Mexico City showed some small degree of subpopulation structure associated with substrates in the streams, possibly because individuals do not appear to move very much from specific sites along the stream (Sunny *et al.* 2014). Future studies should investigate habitat use and spatial ecology of the species and the implications of its high mobility (e.g., movement may allow greater admixture of genes, increase genetic diversity and structure), in order to evaluate if and how maintaining particular aquatic and terrestrial conditions in the Arroyo los Axolotes may favor the conservation of *A. altamirani.*

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