Diet of Ambystoma ordinarium (Caudata: Ambystomatidae) in undisturbed and disturbed segments of a mountain stream in the trans-Mexican Volcanic Belt

Laura Ruiz-Martínez¹, Javier Alvarado-Díaz¹, Ireri Suazo-Ortuño¹ & Ricardo Pérez-Munguía²

 ¹⁾ Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo, Av. San Juanito Itzicuaro s/n, Col. Nueva Esperanza, Morelia, Michoacán 58337, México
²⁾ Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, CU, Morelia, Michoacán 58000, México

Corresponding author: JAVIER ALVARADO-DÍAZ, e-mail: jvr.alvarado@gmail.com

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Abstract. We collected field information on the diet of *Ambystoma ordinarium* in a mountain stream in the trans-Mexican Volcanic Belt. Additionally, we examined the influence of habitat disturbance on the diet of this species by comparing stomach contents and prey availability between undisturbed and disturbed stream segments. The diet of the population consisted of 57 prey types. Prey items contributing the most to the diet were arthropods representing the families Chironomidae, Baetidae, Daphniidae and Simuliidae, and the order Ostracoda. About 50% of the 47 types of prey evaluated for electivity (found in both environments and stomachs) were taken in relation to their availability in the environment. However, 14 (29.8%) types of prey presented high values of electivity. Salamanders from undisturbed and disturbed segments presented differences in stomach contents, sharing only 42.1% of the prey types. Additionally, dominant prey types presented different ranks and volumes in salamanders from the two habitat conditions. The most abundant potential prey types in the environment were Chironomidae, Physidae, Simuliidae, Hydroptilidae and Heptageniidae. Although these prey types were present in both undisturbed and disturbed segments, the abundance of each type of prey was significantly higher in undisturbed segments. Salamanders from undisturbed segments were more abundant (N = 181) and presented higher indices of body condition (IBC = 0.23) than salamanders from disturbed segments (N = 101; IBC = 0.18). Our results suggest that differences in diet composition and availability of prey account for the higher abundance and higher values of body condition found in salamanders from undisturbed segments.

Key words. México, Michoacán, ecology, paedomorphic salamanders.

Introduction

The loss and modification of natural habitats represent a major threat to the conservation of global biodiversity (VITOUSEK et al. 1997), and in synergism with other factors, is resulting in the extinction and decline of amphibian populations across the globe (LIPS et al. 2005). Anthropogenic habitat disturbance plays a critical role in shaping streams and their associated communities (CAIRES et al. 2010), including changes in the diversity and abundance of prey consumed by amphibians (SUAZO-ORTUÑO et al. 2007, SUAZO-ORTUÑO et al. 2008). Availability of critical resources such as food is frequently associated with the condition of habitats and persistence of animal populations (CONROY 1999). In amphibians, it has been reported that diet breadth might be related to species vulnerability to habitat modifications, since dietary specialists are at a higher risk of demographic collapse if disturbance factors affect the availability of their preferred prey (RODRÍGUEZ-ROBLES 2002, SWIHART et al. 2002). Therefore, information on diet composition and diet diversity relative to prey availability is a critical component in the planning of conservation strategies for animal species. Data available on the biology of Ambystoma ordinarium are restricted to its species description (TAYLOR 1940), distribution (SHAFFER 1989, ANDERSON & WORTHINGTON 2001), preliminary data on diet composition (ALVARADO-DÍAZ et al. 2003), and phylogeny (WEISROCK et al. 2006). Here we report on the dietary habits of this species. Additionally, we evaluated dietary differences amongst individuals occupying undisturbed and disturbed segments of a mountain stream in the highlands of the trans-Mexican Volcanic Belt.

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Material and methods

Ambystoma ordinarium is a facultatively paedomorphic ambystomatid species that inhabits mountain streams in pine and fir forests in the central part of the trans-Mexican Volcanic Belt. All known localities are located between the vicinity of Lake Patzcuaro in the north-central part of Michoacán state and Tianguistenco in the eastern part of the state of México.

Study area

We analysed stomach contents of paedomorphic individuals of A. ordinarium collected in a mountain stream located in Morelia Municipality, state of Michoacán in the central part of the trans-Mexican Volcanic Belt. The studied stream has its source in the mountains south of the city of Morelia (state of Michoacán) at Agua Zarca (19°36'33" N, 101°07'02" W, 2,220 m) and drains into the Rio Grande, a tributary of Lake Cuitzeo. We sampled from the stream headwaters to a distance of 13.7 km downstream. Along this stretch, stream banks were dominated by riparian vegetation (Agnus acuminata, Fraxinus uhdei, Ilex tolucana and Salix bonpladiana). The vegetation of adjacent upslope areas consisted of pine, oak and pine-oak forests. Anthropogenic disturbances inflicted on the stream and adjacent areas included bank erosion from trampling by cattle and people, selective logging of riparian vegetation, and conversion of upslope vegetation to suit agricultural activities.

Habitat condition

The habitat conditions of 15 segments of the stream (each 100 m in length and separated by a distance of at least 200 m) were evaluated by Rapid Bioassessment Protocols (RBPS) (BARBOUR et al. 1999). Since relocation movement in A. ordinarium is very limited (mean = 0.22 m, range = 0.0-1.36 m) (MONTES-CALDERÓN et al. 2011), 200 m gaps between sampled segments were considered adequate to ensure sampling independence. Rapid Bioassessment Protocols use variables such as streambank vegetative protection, type and embeddedness of substrate, channel flow status, patterns of velocity and depth, sediment deposition, riffle frequency, and human alterations to assess habitat quality. This method assesses the condition of an aquatic habitat in relation to what is expected of the same type of habitat in pristine condition. Values obtained thus range from o, indicating an extremely disturbed condition, to 200, indicating a pristine habitat (BARBOUR et al. 1999). Of the 15 evaluated segments, we selected the three with the highest RBPS values (range = 168-177) as the undisturbed habitat segments and the three with the lowest values (range = 65-114) as the disturbed habitat segments.

Diet composition

We sampled the six selected segments at the end of the dry season (May and June) of 2008. A crew of four people surveyed each segment using time-constrained (1 h) visual searches of the stream bottom and cavities under rocks and logs. Salamanders were captured with hand-held nets, measured (snout-vent length, SVL), and weighed. Stomach contents were sampled from salamanders > 30 mm SVL using a flushing technique (LEGLER & SULLIVAN 1979) within 15 min following their capture, and the yields were preserved in 70% ethanol. To avoid capturing the same individuals more than once, they were held in buckets filled with stream water. Once the search for specimens and procurement of their stomach contents were completed, the salamanders were released at their sites of original capture. The period between sampling of undisturbed and disturbed segments was no more than 10 days (mean = 4 days). Prey types were later identified to family or order, counted and measured volumetrically. We calculated the relative abundance by number (% N), relative abundance by volume (% V), and relative number of stomachs that contained the respective food item as frequency of occurrence (% F). Using these values, we calculated an Index of Relative Importance: $IRI = (\% N + \% V) \times (\% F)$ (Pinkas et al. 1971). This index ranges from 0.0 through 20,000, with higher values representing food types of greater importance. To test for variation in the diet composition between salamanders from undisturbed and disturbed segments, we used Mann-Whitney U-tests to compare the volumes of main prey items (IRI \geq 1,000). We used the Shannon-Weiner Index (H') to quantify the dietary diversity (using abundance data) of salamanders from undisturbed and disturbed stream segments. Values of this index usually fall between 1.5 and 3.5, rarely exceeding 4.5 (MAGURRAN 1988). Dietary niche overlap between salamanders from undisturbed and disturbed segments were quantified as the Morisita Index as produced by the software EstimateS (COLWELL 2005). The value of this index ranges from 0 (no similarity) to 1 (perfect similarity) (KREBS 1999).

Prey in the environment

ALVARADO-DÍAZ et al. (2003) observed paedomorphic *A. ordinarium* foraging at the bottom of streams. Therefore, we quantified prey availability in the environment by collecting benthic macro-invertebrates with a D-frame dip net (BARBOUR et al. 1999). Sampling units were 0.5 square metres at the bottoms of both pools and riffles. These habitats are typical of the sampled stream. Collected invertebrates were preserved in 70% ethanol, counted and identified to family or order. Invertebrate sampling was carried out within three days of the sampling of the stomach contents of the salamanders. We compared the observed prey abundance in the environment to the expected abundance in either of the habitat conditions, contrasting obtained values against a null hypothesis of equal abundance using a 2×2 chi-square (X^2) contingency table analysis.

We used Shannon-Weiner's Index (H') to quantify prey diversity in the two habitat conditions. Similarity between potential prey types in the two habitat conditions was assessed with Morisita's Index.

Prey selectivity

To quantify prey selectivity we used Ivlev's Selection Index (E) (STRAUSS 1979): E = (ri - pi)/(ri + pi); where ri is the proportion of the *i*-taxon found in stomachs and p*i* the proportion of the *i*-taxon present in the environment. This index presents values ranging from -1 (total rejection) to +1 (total preference). Only prey types found both in stomach contents and benthic samples were considered for electivity analysis. Prey types with E = +0.50 to +0.69 were considered to be moderately preferred, and prey types with E = -0.50 to -0.69 were considered to be moderately rejected. Prev types with $E \ge +0.70$ were considered to be markedly preferred, and prey types with $E \ge -0.70$ were considered to be markedly rejected. Prey types with E < +0.50 or < -0.50were considered to be taken at approximately the same proportion as their availability in the environment. These electivity value ranges were arbitrarily selected.

Body condition

We calculated the physical conditions of salamanders using the Index of Body Condition (IBC; ANGILLETA et al. 2001): IBC = w/SVL, wherein w = weight and SVL = snout-vent length. We used *t*-tests to evaluate differences in body condition amongst salamanders inhabiting undisturbed and disturbed segments. An alpha level of 0.05 was used in all statistical tests. Means are given as ± 1 *SE*.

Results

Diet composition

We collected a total of 187 salamanders (mean = 62.3 ± 14.9 ; range = 41-91) in undisturbed segments and 101 salamanders (mean = 33.6 ± 11.8 ; range = 19-57) in disturbed segments. This difference in abundance was significant (X^2 = 25.6; df = 1, P < 0.05). We flushed the stomaches of 80 salamanders and prey was obtained from 72 individuals (46 from undisturbed and 26 from disturbed segments). Of the 57 different prey types registered when pooling stomach contents of salamanders from undisturbed and disturbed segments, 87.75% were arthropods, 7.0% molluscs, 3.5% annelids, and 1.75% were frog larvae (Tab. 1). We found 46 prey types in the stomachs of salamanders from undisturbed segments, and 35 prey types in those from disturbed segments. The contribution to the diet shared by salamanders from undisturbed and disturbed segments was dominated by a small group of aquatic arthropods. Values of IRI were highest for chironomid larvae (Chironomidae, IRI = 3,272), followed by seed shrimps (Ostracoda, IRI = 1,648), mayfly larvae (Baetidae, IRI = 990), daphnia (Daphniidae, IRI = 682), and black fly larvae (Simuliidae, IRI = 233) (Tab. 1). The rest of the prey types presented IRI values well below the former groups of prey (range = 0.08-89) (Tab. 1). The only vertebrate prey recorded was a frog larva (Ranidae).

Diet in salamanders from undisturbed and disturbed segments

The importance of the main prey types in salamanders from undisturbed and disturbed segments presented some differences. Although Chironomidae produced the highest IRI in both habitat conditions (Tab. 1), their contribution by volume was significantly higher in salamanders from undisturbed segments (mean = 0.020±0.023 mm, range = 0.001-0.05, versus mean = 0.016 ± 0.045 mm, range = 0.001-0.2 for salamanders from disturbed segments) (Mann-Whitney U = 1, P < 0.05). Ostracoda showed the second highest IRI in salamanders from undisturbed segments and Bateidae in salamanders from disturbed segments (Tab. 1). Considering all prey types, regardless of their ranking in contribution to diet, 24 (42.1%) of the 57 prey types were shared by salamanders of the two habitat conditions. Twenty-one (36.8%) prey types were only found in salamanders from undisturbed segments, and 12 (21.5%) were only found in salamanders from disturbed segments. This was reflected in a moderate degree of diet similarity in salamanders from the two habitats (Morisita Index = 0.61). For all salamanders combined (undisturbed and disturbed segments), the diet breadth value (H') was 2.04. Salamander diet breadth was similar in undisturbed (H'= 1.6) and disturbed (H'= 1.7) segments.

Prey selectivity

The electivity values of prey types with the highest IRI (Chironomidae, Ostracoda, Baetidae, Daphniidae and Simuliidae) indicated that only Ostracoda was markedly preferred (E = +0.77). The rest of the main prey types were moderately rejected (Simuliidae, E = -0.64) or taken at approximately the same proportion as their availability in the environment (Daphniidae, E = +0.006; Baetidae, E = +0.43; Chironomidae, E = -0.11) (Tab. 1). Of the 47 prey types evaluated for electivity, 23 (49%) were taken at approximately the same proportion as their availability in the environment (E < +0.50 or E < -0.50) (Tab. 1).

Index of Body Condition

Salamanders from undisturbed segments showed significantly higher values of the IBC (mean = 0.23 ± 0.01 ; range = 0.02-0.57; N = 65) than salamanders from disturbed segments (mean = 0.18 ± 0.01 ; range = 0.05-0.51; N = 80) (*t* = 1.34, df = 96, P < 0.05).

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Table 1. Stomach contents of Ambystoma ordinarium in undisturbed and disturbed stream segments. The top line of each entry is
presented as follows: percent in numbers / percent in volume (mm ³) / percent of frequency of occurrence. The number in the second
line of each entry corresponds to the Index of Relative Importance (IRI). Electivity is given as Ivlev Index values.

Prey items	Undisturbed segments	Disturbed segments	Pooled	Electivity
Molluscs Physidae	0.36/1.73/10.87 22.72	1.09/9.00/11.54 116.48	0.36/1.52/9.72 18.27	-0.91
Ancylidae	0.20/0.02/6.52 1.47			-0.17
Planorbidae	0.08/0.01/4.35 0.4			-0.39
Sphaeriidae	0.56/0.75/10.87 14.28	1.21/2.31/23.08 81.25	0.73/1.04/15.28 26.96	-0.17
Annelids Lumbriculidae	0.08/6.04/4.35	0.12/0.29/3.85	0.09/5.14/4.17	-0.52
Hirudinidae	20.01	0.12/1.44/3.85 6.02	0.03/0.25/1.39 0.39	0.41
Arthropods Hydrachnidae	0.08/0.01/4.35 0.4			-0.33
Bothriuridae		0.12/0.29/1.33 1.58		0.005
Daphniidae	23.46/1.02/52.17 1277.4	1.33/0.06/7.69 10.7	18.02/0.87/36.11 682.4	0.006
Ostracoda	29.94/7.15/60.87 2257.84	18.55/3.92/26.92 604.97	27.20/6.71/48.61 1648.16	0.77
Copepoda	0.56/0.04/15.22 9.17	0.24/0.03/3.85 1.04	0.48/0.04/11.11 5.82	0.83
Isopoda	0.04/0.09/2.17 0.28			0.007
Asellidae	0.04/0.24/2.17 0.61			
Baetidae	4.60/2.85/56.52 421.02	21.09/21.79/84.62 3628.33	8.63/6.23/66.67 990.64	0.43
Heptageniidae	0.60/0.33/19.57 18.12	1.82/3.52/19.23 102.68	0.91/0.89/19.44 34.98	-0.64
Neoephemeridae	3.64/2.77/34.78 223.16	0.97/1.21/11.54 25.17	2.99/2.55/26.39 146.09	0.78
Caenidae		10.18/7.99/50 908.8		0.98
Leptophlebiidae	0.68/0.66/19.57 26.29	0.60/1.73/11.54 26.97	0.66/0.86/16.67 25.45	0.39
Limnephilidae	0.02/0.41/8.70 5.3			0.41
Gomphidae	0.04/0.30/2.17 0.74			
Calopterygidae	0.04/0.18/2.17 0.48	0.12/0.29/3.85 1.58	0.06/0.20/2.78 0.73	-0.28
Lestidae	0.60/6.30/21.74 149.99	0.12/0.58/3.85 2.69	0.48/5.40/15.28 89.95	0.66
Coenagrionidae	0.52/5.79/17.39 109.69	0.36/6.67/11.53 81.12	0.48/6.04/15.28 99.72	0.93
Perlidae	0.08/0.08/4.35 4.02	0.12/0.58/3.84 2.69	0.09/0.81/4.17 3.76	0.76
Veliidae		0.36/0.75/7.69 8.57		-0.94
Gerridae	0.04/0.15/2.17 0.41			
Corixidae	0.28/0.17/10.87 4.88	1.94/6.49/34.62 291.91	0.70/1.28/19.44 38.47	0.14

Diet of Ambystoma ordinarium

Prey items	Undisturbed segments	Disturbed segments	Pooled	Electivity
Notonectidae	0.16/0.22/6.52	0.36/3.46/7.69 29.44	0.21/0.79/6.94	0.38
Hebridae	2.10	0.12/0.14/3.85 1.02	0.27	0.66
Cycadellidae	0.04/0.06/2.17 0.22	0.12/0.58/3.85 2.69	0.06/0.15/2.78 0.59	0.008
Belostomatidae		0.12/0.58/3.85 2.69		0.09
Corydalidae	0.08/4.22/4.35 18.69			0.81
Trichoptera	0.08/0.07/4.35 0.64			0.009
Plycentropodidae	1.12/2.00/28.26 87.89	0.36/1.44/11.54 20.85	0.94/1.93/22.22 63.65	0.96
Hydropsychidae	0.08/0.02/4.25 0.43			0.81
Glossossomatidae	0.08/0.02/4.35 0.45			-0.35
Hydroptilidae	0.08/0.07/2.17 0.32			-0.97
Brachycentridae	0.20/1.00/8.7 10.44			0.85
Calamoceratidae	0.08/0.79/4.35			-0.02
Leptoceridae	0.68/0.42/13.04	1.7/6.93/34.62 298.5	0.94/1.57/20.83	0.51
Noctuidae		0.12/0.87/3.85	-2.10	0.01
Pyralidae	0.08/0.12/4.35	210		
Dytiscidae	0.04/0.12/2.17	0.12/0.03/3.85	0.06/0.11/2.78	0.81
Staphylinidae	0.00	0.24/0.06/7.69	0.10	0.52
Languriidae	0.04/0.12/2.17 0.35	2.01		0.007
Psephenidae	0.04/0.90/2.17			
Elmidae	0.36/0.09/8.70			0.57
Curculionidae	0.12/0.07/4.35			
Diptera	0.04/0.06/2.17	0.36/0.32/7.69	0.12/0.11/4.17	
Chironomidae	25.38/5.45/97.83 3015 64	31.39/11.98/96.15 4170 27	26.95/6.69/97.22 3271 12	-0.11
Dixidae	5015.01	0.36/0.09/7.69	527 1.12	0.76
Simuliidae	3.96/1.02/58.70 292.77	1.94/0.46/42.31	3.48/0.94/52.78	-0.64
Empididae	272.17	0.36/0.35/11.54	253.02	
Tabanidae	0.32/0.35/17.39	1.45/2.91/15.38 67.22	0.60/0.81/16.67	0.96
Tipulidae	0.16/16.03/8.70	07.22	23.31	0.9
Pupae	140.02	0.36/0.87/3.85		
Vertebrates Ranidae	0.04/28.93/2.17	4. <i>1 J</i>		

Prey in the environment

Potential prey amongst the benthic samples represented two orders and 54 families. Of the 56 different prey types registered when pooling the potential prey items recorded from undisturbed and disturbed segments, 87.5% were arthropods, 8.9% molluscs, and 3.6% annelids. We recorded 43 prey types from undisturbed and 39 from disturbed segments. Contribution to prey assemblage of shared prey types, i.e., those found in both habitat conditions, was dominated by a small group of aquatic invertebrates. The highest abundance values were reached by chironomids (Chironomidae) (5,314), followed by black flies (Simuliidae) (2,525), bladder snails (Physidae) (1,271), caddis flies (Hydroptilidae) (670), and mayflies (Heptageniidae) (650). The rest of the prey types presented abundance values well below these (range = 1-562). Significantly higher numbers of the main types of potential prey were found in undisturbed segments than in disturbed segments: Chironomidae (4,230 versus 1,084; $X^2 = 1,862$, df = 1, P < 0.001), Simuliidae (2,116 versus 373; *X*² = 1,220, df = 1, P < 0.001), Physidae (1,193 versus 78; $X^2 = 978$, df = 1, P < 0.001), Hydroptilidae (644 versus 26; $X^2 = 570$, df = 1, P < 0.05), Heptageniidae (443 versus 207; $X^2 = 84$, df = 1, P < 0.001). Considering all prey types, regardless of the ranking in contribution to potential prey assemblage, 26 (37.1%) were shared by undisturbed and disturbed segments. Seventeen (24%) prey types were found only in undisturbed segments and 13 (18.6%) only in disturbed segments. According to the Morisita Index, the similarity of prey assemblages between undisturbed and disturbed segments was 0.77. The diversity value (H') of prey types, including both habitat conditions, was 2.12. In undisturbed segments, diversity values were lower (H'= 1.9) than in perturbed sites (H' = 2.16).

Discussion

The 57 different types of prey recorded from the stomach contents of A. ordinarium greatly increased the number of prev types previously reported for this species. ALVARA-DO-DÍAZ et al. (2003) reported 14 types of prey (invertebrate families) for this species, and of the main prey types found in our study, only Chironomidae was reported earlier. The number of stomachs sampled by ALVARADO-DÍAZ et al. (2003) was 14 (versus 72 with contents in our study) and their sampling was restricted to only one site in the studied stream (versus six in our study). This is a likely explanation for the differences in diet composition and diversity reported by the two studies. Stream-dwelling salamanders tend to be generalist predators of small invertebrates (see Wells 2007 for a review), and considering the number of prey types consumed, A. ordinarium appears to fit this pattern. However, diet diversity was relatively low (H' = 2.04). JAEGER (1981) listed Shannon Diversity Indices as a measure of diet breadth for 21 aquatic salamanders, including three Ambystoma species, with H' ranging from 0.82 in A. tigrinum to 2.13 in A. macrodactylum. Considering that JAEGER's indices were based on higher taxonomic categories (orders) than those we used (families), the H' we found for A. ordinarium may be considered moderately low. Regarding the high number of prey taxa consumed by A. ordinarium, the best explanation for the relatively low index of dietary diversity found in our study is the dominance of a few prey types in the environment. The consumption of a frog larva reported in our study indicates that A. ordinarium also preys upon other aquatic vertebrates. Other studies have found that by feeding on other amphibians, some stream salamanders (e.g., Desmognathus quadramaculatus) may affect local guild dynamics (CAMP 1997). However, the contribution to the diet of A. ordinarium by other amphibians is so low that the effect of A. ordinarium predation on the population dynamics of other amphibian species is likely minimal. Contrastingly, the high contribution of detritivores such as chironomids to the diet of A. ordinarium supports the suggestion by DAVIC & WELSH (2004) that larval stream salamanders might play an indirect role in detritus decomposition and nutrient cycling within aquatic systems.

The diet composition of A. ordinarium was dominated by a small group of aquatic arthropods (Chironomidae, Ostracoda, Baetidae, Daphniidae, and Simuliidae). These main prey items (with the exception of Ostracoda that was markedly preferred), and about 50% of the rest of the prey types evaluated for electivity were taken in proportion to their availability in the environment. These findings strengthen the suggestion that this salamander is a generalist predator. However, the high electivity values presented by 13 prey types suggest that considering A. ordinarium, a generalist predator, is an over-simplification and it may be more accurately described as a predator with a diverse diet that shows a predilection for some prey items. The diets of salamanders from undisturbed and disturbed segments presented differences. The number of prey types was higher in salamanders from undisturbed segments (46 versus 35 in salamanders from disturbed segments). This can be partially explained by the greater availability of prey types in the environment of undisturbed segments (43 versus 39 in disturbed segments). Although the prey composition in the diet of individuals from different habitats was dominated by the same prey items, there were differences in the rankings of these prey types, and only 42% of them were shared.

The prey assemblage in the environment was dominated by a few invertebrate groups. The abundance of these groups was significantly higher in undisturbed segments. Decline of macro-invertebrate abundance has been associated to disturbances in stream systems. (McCABE & Go-TELLI 2000) and GRIMM & FISHER (1989) proposed that these declines were caused by food quality limitation. Considering all prey types, regardless of their rankings in the contribution to the prey assemblage, only 37.1% were shared by undisturbed and disturbed segments. Seventeen (24.3%) prey types were found only in undisturbed segments and 13 (18.6%) only in disturbed segments. Despite some similarities in the diet compositions of salamanders from undisturbed and disturbed segments and some similarity in the prev assemblage composition between the two habitats, we hypothesize that the differences we found in the diet (perhaps due, at least partially, to differences in prey availability) were reflected in higher abundances and higher values of the Body Condition Index in salamanders from undisturbed segments. Various studies indicate that salamanders in better physical condition have increased foraging success and therefore experience greater survivorship and reproductive success than individuals in poor physical condition (see BREANNA et al. 2012 for a review). We conclude that by influencing prey composition and availability, habitat disturbances affect the fitness of A. ordinarium individuals, and therefore imperil the long-term persistence of populations.

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