Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil

L. W. Cavalheiro, C. B. Fialho

Cavalheiro, L. W., Fialho, C. B., 2019. Ontogeny of feeding by *Astyanax paris* in streams of the Uruguay River Basin, Brazil. *Animal Biodiversity and Conservation*, 42.1: 9–18.

Abstract
Ontogeny of feeding by Astyanax paris *in streams of the Uruguay River Basin, Brazil.* We studied the ontogeny of feeding by *Astyanax paris*, an insectivorous characid fish from streams of the Uruguay River Basin in southern Brazil. Size–based differences in diet composition were evaluated using permutational multivariate analysis of variance (PERMANOVA). Six streams surveyed over twelve months yielded twenty specimens for analysis of stomach contents. Smaller individuals (SL ≤ 25 mm) consumed mainly aquatic insects. As body size increased, there was a gradual shift to a diet dominated by terrestrial insects. Ontogeny of feeding habitats thus changes the species' position in stream food webs.

Key words: Characiformes, Diet, Insectivorous, Freshwater fish

Resumen
Ontogenia de la alimentación de Astyanax paris *en los arroyos de la cuenca fluvial del río Uruguay, en Brasil.* Estudiamos la ontogenia de la alimentación de *Astyanax paris*, un pez carácido insectívoro de los arroyos de la cuenca del río Uruguay, en el sureste de Brasil. Las diferencias de la composición de la dieta en función del tamaño se analizaron mediante el análisis de varianza multivariante con permutaciones (PERMANOVA). Se muestrearon seis arroyos durante 12 meses y se obtuvieron 20 especímenes para analizar el contenido del estómago. Los individuos más pequeños (longitud estándar ≤ 25 mm) consumieron principalmente insectos acuáticos. A medida que aumentaba el tamaño corporal, se pasaba gradualmente a una dieta compuesta principalmente por insectos terrestres. En consecuencia, la ontogenia de los hábitats de alimentación cambia la posición de las especies en las redes tróficas de los arroyos.

Palabras clave: Caraciformes, Dieta, Insectívoro, Peces de agua dulce

Received: 18 XII 17; Conditional acceptance: 05 III 18; Final acceptance: 10 IV 18

Laísa Wociechoski Cavalheiro, Clarice Bernhardt Fialho, Dept. de Zoologia, Universidde Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, Prédio 43435, CEP 91501–970, Porto Alegre, RS, Brazil.

Corresponding author: Laísa Wociechoski Cavalheiro. E–mail: isa_woci@hotmail.com

ISSN: 1578–665 X
eISSN: 2014–928 X

Introduction

Fish are important components of stream food webs and have been shown to influence ecosystem dynamics (Vanni, 2010; Rodríguez–Lozano et al., 2016). Studies of fish feeding habits have shown how trophic strategies can affect intraspecific and interspecific interactions and energy flux through ecosystems (Pompanon et al., 2012; Pendleton et al., 2014).

The differential use of food resources is a well–known intraspecific strategy to avoid trophic niche overlap between juveniles and adults in several freshwater fish species (Bonato and Fialho, 2014; Cavalheiro and Fialho, 2016; Dala–Corte et al., 2016). Some species may therefore concentrate on different food resources at different stages of their development (Rudolf and Lafferty, 2011). The shift from soft–bodied, small prey to large and difficult–to–swallow prey is a common pattern among fish and reduces intraspecific competition for food resources (Russo et al., 2014).

Ontogenetic niche shifts are the key to the functional variation among the life history stages in a population (Rudolf and Rasmussen, 2013). In practice, a species' taxonomic identity alone is not sufficient to *a priori* predict its ecological interactions. Additional information on its biology should also be collected because fish are known for their high phenotypic plasticity in life–history traits, including body shape and trophic morphology in response to different food types (Kerschbaumer et al., 2011; Rudolf et al., 2014; Karjalainen et al., 2016). In this context, studies of diet variation in relation to modifications in body size are essential not only to characterize species as generalists or specialists, but also to identify their trophic strategies. According to Rudolf and Lafferty (2011), major challenges in studying trophic nets lie in determining the different functional roles within species and integrating such information into their trophic identity. Studies addressing the ecological relationships below the species level are therefore necessary to better understand natural communities.

Ontogenetic development in fish affects morphological structures associated with feeding, thus allowing different sized individuals to consume different sized prey. Larger individuals often consume larger prey to maximize energy consumption (Keppeler et al., 2014). The trophic strategy of shifting diet composition according to ontogenetic changes allows smaller, less competitive fish to explore several food resources until they reach a size where they can compete with larger individuals of the same, or other, species (Russo et al., 2014).

The genus *Astyanax*, the most speciose of the family Characidae, currently contains 158 valid species distributed in rivers from southern USA to Argentina, including the Uruguay River basin (Lima et al., 2003; Eschmeyer et al., 2016). In the Uruguay River basin, there are 13 valid species of the genus *Astyanax*, including *A. paris* Azpelicueta, Almirón and Casciotta, 2002 (Lucena et al., 2013b). This species was originally described from Fortaleza and Yabotí–Miní streams, both tributaries of the Yabotí–Guazú River, Upper Uruguay River in Misiones province, Argentina (Azpelicueta et al., 2002). *Astyanax paris* was considered endemic to locality (Lima et al., 2003; López et al., 2003; Liotta, 2005) until it was recorded in Upper Uruguay in the Brazilian state of Santa Catarina (Bertaco et al., 2016).

The taxonomy and distribution of *Astyanax* species have been relatively well studied in the Uruguay River basin (Azpelicueta and Garcia, 2000; Bertaco and Malabarba, 2001; Azpelicueta et al., 2002; Casciotta et al., 2003; Bertaco and Lucena, 2010; Lucena et al., 2013a, 2013b; Bertaco et al., 2016). However, no information on the diet or any ecological data of *A. paris* isavailable in the literature so far. This paper thus increases understanding of the species' biology and ecology in relation to how different age classes consume different food resources. Other species of *Astyanax* are considered generalists, such as *A.* aff. *fasciatus* (Cuvier, 1819), *A. eigenmanniorum* (Cope, 1894), *A. lacustris* (Lütken, 1875) and *A. intermedius* Eigenmann, 1908 in Tibagi River basin, Brazil (Bennemann et al., 2005) and *A. lacustris* in Maquiné River, Brazil (Vilella et al., 2002). Omnivory has been reported for *A. bifasciatus* Garavello and Sampaio, 2010, *A. dissimilis* Garavello and Sampaio, 2010 (Neves et al., 2015), and *A. lacustri* in Iguaçú River basin, Brazil (Cassemiro et al., 2002). *Astyanax eigenmanniorum* has been considered herbivorous in Lago del Fuerte Dam, Argentina (Grosman, 1999).

This study aimed to investigate the feeding habits of *A. paris* from streams of the Ijuí River sub–basin in the state of Rio Grande do Sul. Hypothesis tested: *A. paris* follows the pattern of other freshwater neotropical fishes, modifying prey according to the sequences of life cycle states (ontogeny).

Material and methods

Study area

The Uruguay River drains an area of about 365,000 km² and extends 1,838 km from the Serra Geral in southern Brazil to La Plata River estuary in Uruguay/Argentina (Di Persia and Neiff, 1986; Cappato and Yanosky, 2009; Bertaco et al., 2016). The basin can be divided into upper, middle, and lower courses (Bertaco et al., 2016). The river's main tributaries are the Negro (Uruguay/Brazil), Quaraí (Uruguay/Brazil), Ibicuí (Brazil), and Ijuí (Brazil) Rivers (Carvalho and Reis, 2009). The Ijuí River is a tributary of the upper portion of the Uruguay River basin in the north–northwestern state of Rio Grande do Sul. It has a drainage area of 10,649.13 km² extending over 20 municipalities. Surveys were carried out at six streams along Ijuí River, from near its headwaters to near its confluence with the Uruguay River (Três Negrinhos: 28.432277778 ºS, 53.970805556 ºW; Nock: 28.316222222 ºS, 53.904972222 ºW; Santa Bárbara: 28.201722222 ºS, 54.218583333 ºW; Ibicuá: 28.394861111 ºS, 54.451638889 ºW; Araçá: 28.228 ºS, 54.956888889 ºW; Lajeado Grande: 28.170416667 ºS, 55.065944444 ºW).

Surveys

We carried out surveys at each point bimonthly over one year, from July 2015 to May 2016. Fish were captured by the electric fishing technique along a 100 m stretch in each stream, with a sampling effort of one hour per site. In the field, individuals were anaesthetized and euthanized with 10 % eugenol (Chair et al., 2014) and fixed with 10 % formalin. In the laboratory, specimens were identified according to taxonomic literature (Azpelicueta et al., 2002; Lucena et al., 2013b).

Specimens were measured (Standard length, SL in mm) and dissected for diet examination. Voucher specimens were deposited in the fish collection of the Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil (vouchers: UFRGS 21927, 21928, 21929). Fieldwork and sampling were carried out under a scientific collection permit (Permit Number 48291–1) issued by the Instituto Chico Mendes de Conservação da Biodiversidade, Ministério do Meio Ambiente, Brasília–Federal District, Brazil.

Stomach contents were analyzed under a dissecting microscope and identified according to the standard taxonomic references (McCafferty, 1998; Mugnai et al., 2010; Segura et al., 2011). Food items were quantified by the volumetric method (VO %) (Hynes, 1950), associated with the frequency of occurrence (FO %) (Hyslop, 1980).

Data analysis

Changes in the diet according to the sampling site and intraspecific ontogenetic influences on the diet composition of *A. paris* were tested with permutational multivariate analysis of variance (permanova; $\alpha < 0.05$) (Anderson, 2001), based on a Bray–Curtis dissimilarity matrix (Borcard et al., 2011). The Bray–Curtis index was used to construct the dissimilarity matrix as it considers data both of presence/absence and of abundance (Borcard et al., 2011). To assess possible ontogenetic variations, specimens were arbitrarily divided into three body size categories: small (SL ≤ 25 mm; n = 10), medium (SL 25 to 51.5 mm; n = 4), and large (SL ≥ 51.5 mm; n = 6). These three categories were determined according to the grouping in small, medium and large fish, of standard length classes defined by the Sturges' rule using the equation:

$$h = (X - x) / (1 + 3.222 * \log(n))$$

where: h = class interval; X = maximum standard length; x = minimum standard length; n = number of individuals (Sturges, 1926). A canonical analysis of principal coordinates (CAP) was used to compare diet composition in relation to standard length size classes (Legendre and Anderson, 1999). This method of ordering was chosen because of the possibility to apply a distance matrix between objects (the Bray–Curtis metrics), because this enables assessment of the relationships between the principal coordinates (dietary data) and variables (size categories) by redundancy analysis (RDA), and because it performs a permutation test that does not depend on the usual assumptions of data normality (Legendre and Anderson, 1999). The analysis of variance (ANOVA) with permutation tests was used to test the significance of the ordering analysis and its respective axis and terms ($\alpha < 0.05$) (Legendre and Anderson, 1999).

The indicator value index (IndVal) with randomization (Borcard et al., 2011) was used to determine whether any food items were associated with particular body size categories of *A. paris.* IndVal compares abundances and relative frequencies of food items in the diet of the studied groups (Cardoso et al., 2013). The statistical significance of such associations of food items and body size categories is confirmed by a permutation test (De Caceres, 2013). The higher the IndVal (Stat), the higher the association between a given food item and a specific group (De Caceres, 2013). Components A (comp A) and B (comp B) in the test vary from 0–1, and respectively indicate the probability of a food item being restricted to a given group and the probability of all sampled stomachs of a given group containing that food item (De Caceres, 2013).

Statistical tests were carried out using R Project for Statistical Computing software, version 3.4.1. PERMANOVA, CAP, and ANOVA analyses were implemented in the statistical package Vegan, version 2.4–5 (Oksanen et al., 2017), whereas IndVal test was conducted done in the package Indicspecies, version 1.7.6 (De Caceres and Legendre, 2009).

Results

Twenty specimens of *A. paris* were collected (13 at Lajeado Grande and seven at Ibicuá). They measured between 21.9 and 80.5 mm in standard length. The diet was composed of 20 food items, classified according to their characteristics, origins, and relevance (table 1). The species presented an insectivorous feeding habit with insects making up 94 % of the volume of items consumed. This pattern did not vary between the two sampled streams (PERMANOVA; $F = 0.97$, $R^2 = 0.04$, $p = 0.51$).

This study reports the first occurrence of *A. paris* in Rio Grande do Sul, thus extending its geographical distribution to the Medium Uruguay River Basin (fig. 1). The species was captured at two of the six sampled streams, namely, Ibicuá (28.394861111 ºS, 54.451638889 ºW municipality of Vitória das Missões) and Lajeado Grande (28.170416667 ºS, 55.065944444 ºW municipality of Dezesseis de Novembro; fig. 2). Both these streams are 1–1.5 m deep and have strong currents. Ibicuá stream is narrower, with muddy dark water and small stones on bottom (fig. 2A). Lajeado Grande stream is the widest. It has clear water and a rocky bottom with flat slippery stones (fig. 2B).

The diet of *A. paris* is affected by ontogeny (PERMANOVA; $F = 3.68$, $R^2 = 0.30$, $p = 0.0007$). There is a marked shift in the species' diet as it grows. The stomach contents of small specimens (SL ≤ 25 mm) consisted of 69.78 % (VO) aquatic insects and 28.97 %

Table 1. Indicator values (IndVal) of food items consumed by standard length size classes (SL) of *Astyanax paris*. Small: SL ≤ 25 mm; medium: SL 25 to 51.5 mm; large: SL ≥ 51.5 mm. The components A (Comp A) and B (Comp B) in the test vary from 0–1, and respectively indicate the probability of a food item being restricted to a given group and the probability of all sampled stomachs of a given group containing that food item. The Stat (test statistic) is the association between a given food item and a specific group. * α < 0.05.

*Tabla 1. Valores del indicador (IndVal) de los alimentos consumidos por clase de longitud estándar (LE) de Astyanax paris. Pequeña: LE ≤ 25 mm; mediana: LE 25 a 51,5 mm; y grande: LE ≥ 51,5 mm. Los componentes A (Comp A) y B (Comp B) de la prueba se sitúan entre 0 y 1, e indican, respectivamente, la probabilidad de que un alimento esté limitado a un grupo determinado y la probabilidad de que dicho alimento se encuentre en todos los estómagos analizados. La Stat (prueba estadística) es la asociación entre un alimento determinado y un grupo específico. * α < 0,05.*

Food item	Comp A	Comp B	Stat	*p*–value
Small				
Aquatic Diptera	1.00	0.10	0.32	1.00
Medium				
Aquatic Plecoptera	0.64	0.75	0.69	0.10
Plant fragments	0.81	0.50	0.64	0.07
Fragments of terrestrial insects	0.73	0.50	0.61	0.19
Aquatic Acarina	1.00	0.25	0.50	0.20
Large				
Terrestrial Hymenoptera	0.98	1.00	0.99	0.0001*
Terrestrial Coleoptera	0.93	0.33	0.56	0.14
Terrestrial Araneae	1.00	0.17	0.41	0.49
Terrestrial Lepidoptera larvae	1.00	0.17	0.41	0.49
Aquatic Odonata	1.00	0.17	0.41	0.49
Terrestrial Odonata	1.00	0.17	0.41	0.49
Terrestrial Orthoptera	1.00	0.17	0.41	0.49
Small and medium				
Aquatic Ephemeroptera	1.00	0.71	0.85	0.02*
Aquatic Diptera	1.00	0.36	0.60	0.33
Fragments of aquatic insects	1.00	0.36	0.60	0.46
Seeds	1.00	0.14	0.38	0.84
Small and large				
Terrestrial Hemiptera	1.00	0.25	0.50	0.75
Terrestrial Coleoptera	1.00	0.13	0.35	1.00
Medium and large				
Aquatic Trichoptera	1.00	0.30	0.55	0.29
Fish scales	1.00	0.20	0.45	0.47

(VO) of terrestrial insects. Medium–size specimens consumed 46.56 % (VO) of aquatic and 42.11 % (VO) of terrestrial insects. Large specimens mainly consumed (VO = 91.81 %) terrestrial insects, with aquatic insects representing only 2.7 % (VO) of the stomach contents.

Other prey items were consumed only occasionally or in low numbers. Aquatic ticks (Acarina) were found in the stomach of a medium–size specimen only, corresponding to 0.4 % (VO) of prey consumed by fish in this group size. Similarly, terrestrial spiders (Araneae) were found in the stomach of only one large specimen. Plant items (fragments and seeds) were found in the stomach of one small specimen (VO = 1.25 %), in the stomach of two medium–size specimens

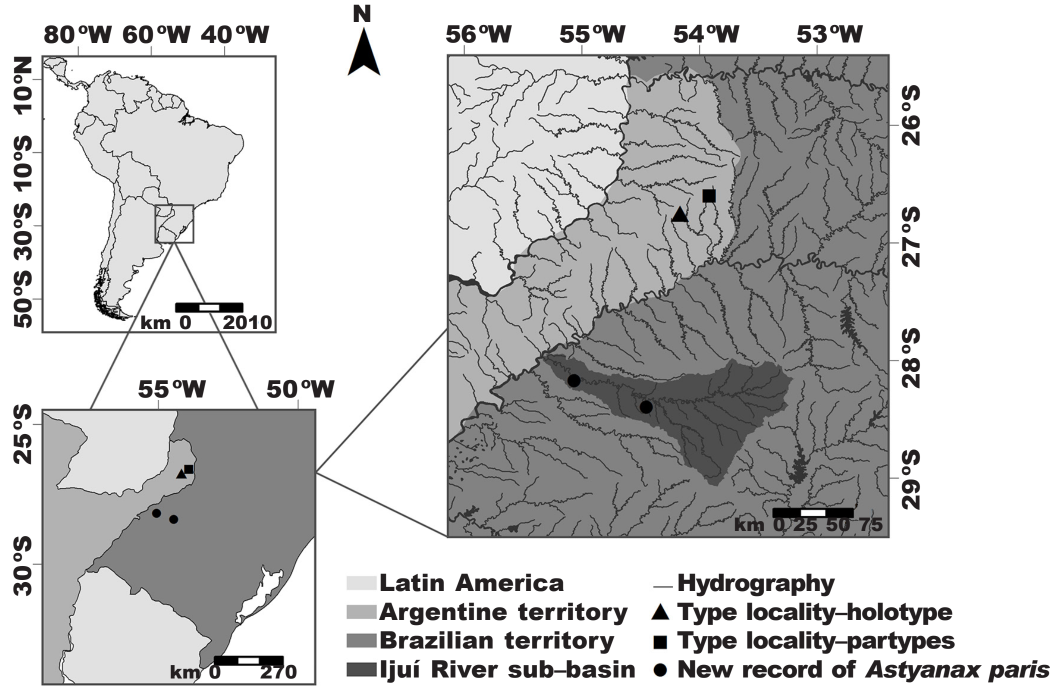

Fig. 1. Records of *Astyanax paris* in Argentinean and Brazilian regions, with indication of the species' type locality (Azpelicueta et al., 2002) and new records from Ijuí River sub–basin, Rio Grande do Sul.

Fig. 1. Registros de Astyanax paris en las regiones de Argentina y Brasil, con indicación de la localidad tipo de la especie (Azpelicueta et al., 2002) y nuevos registros de la subcuenca del río Ijuí, en Rio Grande do Sul.

Fig. 2. Localities of collection of *Astyanax paris* in Ijuí River sub–basin, Rio Grande do Sul, Brazil. Ibicuá stream, municipality of Vitória das Missões (A), Lajeado Grande stream, municipality of Dezesseis de Novembro (B).

Fig. 2. Localidades de recogida de Astyanax paris *en la subcuenca del río Ijuí, en Rio Grande do Sul, Brasil. Arroyo Ibicuá, municipio de Vitória das Missões (A), arroyo Lajeado Grande, municipio de Dezesseis de Novembro (B).*

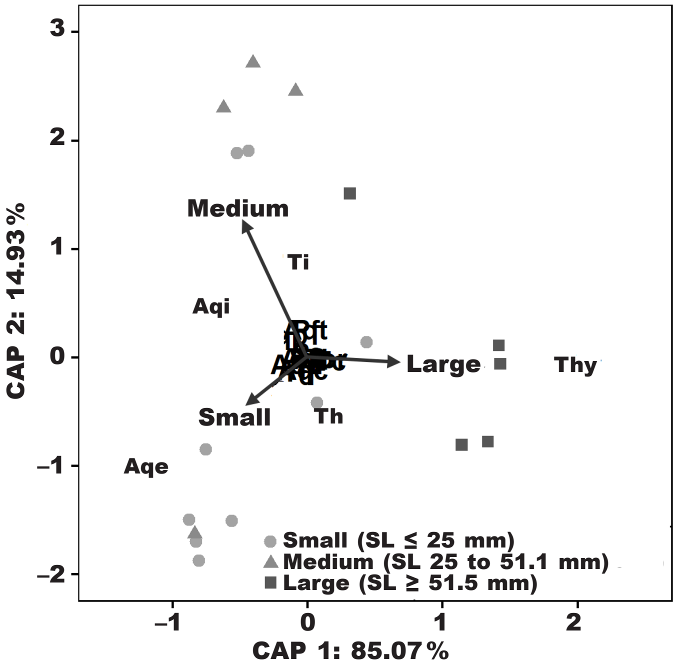

Fig. 3. Canonical analysis of principal coordinates (CAP) of food composition of *Astyanax paris* from Ijuí River sub–basin, Rio Grande do Sul, Brazil: Ac, aquatic Acarina; Ar, terrestrial Araneae; Aqc, aquatic Coleoptera; Tc, terrestrial Coleoptera; Aqd, aquatic Diptera; Td, terrestrial Diptera; Aqe, aquatic Ephemeroptera; Th, terrestrial Hemiptera; Thy, terrestrial Hymenoptera; Tll, terrestrial Lepidoptera larvae; Aqo, aquatic Odonata; To, terrestrial Odonata; Tor, terrestrial Orthoptera; Aqp, aquatic Plecoptera; Aqt, aquatic Trichoptera; Aqi, fragments of aquatic insects; Ti, fragments of terrestrial insects; Sc, scales; Pf, plant fragments; Se, seeds.

Fig. 3. Análisis canónico de las coordinadas principales (CAP) de la composición de la dieta de Astyanax paris *de la subcuenca del río Ijuí, en Rio Grande do Sul, Brasil: Ac, ácaros acuáticos; Ar, individuos del orden Araneae terrestres; Aqc, coleópteros acuáticos; Tc, coleópteros terrestres; Aqd, dípteros acuáticos; Td, dípteros terrestres; Aqe, efemerópteros acuáticos; Th, hemípteros terrestres; Thy, himenópteros terrestres; Tll, larvas terrestres de lepidópteros; Aqo, odonatos acuáticos; To, odonatos terrestres; Tor, ortópteros terrestres; Aqp, plecópteros acuáticos; Aqt, tricópteros acuáticos; Aqi, fragmentos de insectos acuáticos; Ti, fragmentos de insectos terrestres; Sc, escamas; Pf, fragmentos vegetales; Se, semillas.*

(VO = 9.31 %), and in that of one large specimen (VO = 3.60 %). Fish scales were found in the stomach of one medium–size specimen (VO = 2.02 %) and in one large (VO = 1.17 %) specimen.

The Canonical Analysis of Principal coordinates (F = 3.58, p = 0.0009) showed a standard length segregation of populations, especially in relation to the first axis (F = 6.12, p = 0.0001). This is further evidence of the shift in species diet from aquatic to terrestrial insects, mainly Ephemeroptera and Hymenoptera (fig. 3). These prey items are indicators of the species diet, as shown by IndVal within the 20 food items identified in this study (table 1).

Aquatic Ephemeroptera is an indicator of small and medium–size specimens (Stat = 0.84, p = 0.02). This prey item has both a probability to occur in most stomachs of (comp B from IndVal = 0.71), and was restricted to (comp A from IndVal = 1.00) small and medium–size specimens. Large specimens did not consume Aquatic Ephemeroptera. In contrast, terrestrial Hymenoptera is a strong indicator of large specimens (Stat = 0.99, p = 0.0001). Hymenoptera was restricted to large size class and was also predated by all analyzed individuals (comp B from IndVal = 1.00) (table 1).

Discussion

The fact the of *A. paris* was caught in two capture events and occurred in two streams, despite a year of intense sampling, suggests it has a low population size throughout the Ijuí River sub–basin and that it is naturally rare or extremely difficult to capture. This hypothesis is supported by the lack of previous records of *A. paris* in Rio Grande do Sul even though the ichthyofauna from Brazil's portion of the Uruguay River Basin has been well studied (Bertaco et al., 2016).

The original description of the species was based on a few specimens (one holotype and 15 paratypes), currently in the Museo De La Plata (MLP) and Muséum National d'Histoire Naturelle (MHNG) (vouchers MLP 9584, 9585 e 9586 e MHNG 2623.65) (Azpelicueta et al., 2002). The other records of *A. paris* from scientific collections also consist of few specimens. The Pontifícia Universidade Católica do Rio Grande do Sul (MCP) has six specimens collected in the state of Santa Catarina (voucher MCP 40063), two from São Domingos River in the municipality of Cunha Porã (26.8891658783 ºS, 53.180557251 ºW) and three from Uruguay River in São Joaquim (26.8891658783 ºS, 53.180557251 ºW) (Bertaco et al., 2016). The collection of the Núcleo de Pesquisa em Limnologia Ictiologia e Aquicultura (Nupélia) da Universidade Estadual de Maringá (UEM) has six other specimens from the same state (vouchers NUP 16279 e 16282), all collected in Rio das Contas, municipality of Bom Jardim da Serra (28.4933333 ºS, 49.7825 ºW). UEM also has five specimens labeled as '*A.* aff. *paris*' (voucher NUP 16279) from Ijuí in Rio Grande do Sul (28.3016667 ºS, 53.8927778 ºW); however, their identification should be confirmed.

The lack of changes in the feeding behavior of *A. paris* according to the sampling site, despite the marked environmental characteristics in the two streams where it was collected, indicates the species is a probable insectivorous specialist feeder. Insectivorous fish influence both aquatic and terrestrial environments and play an important ecological role in regulating populations of their prey (Knight et al., 2005; Wesner, 2012; Xiang et al., 2016).

This research confirms the hypothesis that *A. paris* presents ontogenetic variation in the diet with specific prey items for each life cycle stage. The variation of food items according to the standard length shows that different age classes play different functional roles in the trophic dynamics of the species habitat. Trophic webs are often studied through a traditional approach wherein species are assigned to guilds or trophic groups, without considering ontogeny (Rudolf et al., 2014). This practice has often been adopted in the existing research on *Astyanax* species (Bennemann et al., 2005; Silva et al., 2014). However, ontogenetic niche shifts are known from 80 % of animal taxa (Werner, 1988; Hertz et al., 2016); furthermore, the main source of intraspecific diversity in ecosystems is the variation across ontogenetic stages and size of individuals (Rudolf and Rasmussen, 2013). These aspects may lead to intraspecific functional differences in the role of individuals within ecosystems and affect the structural dynamics of communities (Hertz et al., 2016).

Astyanax paris moves from a diet of aquatic to terrestrial insects as it ages. Ontogenetic shifts in the diet are often correlated with ontogenetic shifts in micro–habitat use, or preference for prey of different sizes (Rudolf and Rasmussen, 2013). Small individuals of *A. paris* feed mainly on aquatic Ephemeroptera, which are smaller than terrestrial Hymenoptera, Hemiptera, Coleoptera, and Orthoptera. These four items, in respective order of importance, made up most of the diet in terms of volume of large fish, although only Hymenoptera was found to be an indicator of this size category. The shifting from soft to hard and larger prey, which aremore difficult to catch, was observed in *A. paris*. Mobility and higher competition capacity have often been cited as the aspects of larger fish prey selectivity (Russo et al., 2014). From this perspective, the ontogenetic shifts in the diet of *A. paris* can be viewed as a trophic strategy to reduce intraspecific competition, as seen in other Neotropical freshwater fish (Bonato and Fialho, 2014; Cavalheiro and Fialho, 2016; Dala–Corte et al., 2016).

Species that change their diet during growth and show 'specialist phases'" may well appear generalists at species level if size is not taken in account in the study of their diets. Furthermore, these species may behave as sequential specialists as they change their tropic niche during development and are hypersensitive to food resource loss and habitat degradation (Rudolf and Lafferty, 2011). Studies investigating the ontogenetic influences on diet of species inhabiting areas vulnerable to impacts are essential. Ibicuá and Lajeado Grande streams show poorly conserved riparian vegetation. This may affect *A. paris*, which relies on terrestrial food resources.

Astyanax paris relies on varied food resources (terrestrial and aquatic) across its life–stages. Protection of its habitats should consider not only the environmental quality of the streams, but also the integrity of adjacent riparian vegetation. The importance of riparian vegetation to fish diet is well recognized and documented for the allochthonous feeder *Astyanax* species (Gomiero and Braga, 2003; Borba et al., 2008; Ferreira et al., 2012; Souza and Lima–Junior, 2013; Silva et al., 2014; Leite et al., 2015). Conserving the streams is also important for those autochthonous feeders (Cavalheiro and Fialho, 2016).

In conclusion, *A. paris* has an insectivorous tendency and plays different roles in the stream trophic web during its life–history. It shows marked ontogenetic shifts in diet, changing its food source from aquatic to terrestrial insects as it grows.

Acknowledgements

The authors would like to thank Gilmar Nunes Cavalheiro, Maria Ivone Wociechoski Cavalheiro, Amanda A. S. Santos, Dario F. Fuster, José Vanderlei da Silva, Juliano Ferrer, Júnior A. Chuctaya, Laura M. Donin, Leomar B. Medeiros and Rafael Angrizani for help and companionship in fieldwork, and Priscilla C. Silva for help with species identification. The first author received a PhD scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

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