Official journal website:
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Amphibian & Reptile Conservation
14(3) [General Section]: 162–168 (e263).

Feeding habits of the threatened aquatic Andean frog *Telmatobius rubigo* (Anura: Telmatobiidae)

***Mauricio Sebastián Akmentins and María Soledad Gastón**

Instituto de Ecorregiones Andinas (INECOA), Universidad Nacional de Jujuy, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Canónigo Gorriti 237, Y4600 San Salvador de Jujuy, ARGENTINA

***Abstract.*—The aquatic Andean frogs of the genus *Telmatobius* have evolved closely with the aquatic ecosystems of the Andes of South America. The Laguna de Los Pozuelos' Rusted Frog (*Telmatobius rubigo*) is a Threatened and endemic species of the Central Andean Puna ecoregion in Argentina. This species has a specialized feeding mechanism which relies on the inertial suction of prey, but our knowledge about its natural history is still incomplete. This study examined the feeding habits of *T. rubigo* by the stomach flushing technique. The relevance of the registered prey items was assessed using the dietary importance value index, and the relationship between frog body size and prey volume was determined. In total, 189 prey items were identified in 29 stomach content samples, reaching a representative number of diet samples for this species. *Telmatobius rubigo* had a fully aquatic diet, with a clear predominance of adult aquatic coleopterans, immature stages of benthic insects, and crustaceans; and a high incidence of non-nutritive elements (sand and vegetation debris) was also found in the stomach contents. The results indicate that the species exhibits generalist feeding habits, and the volume of consumed prey items is positively related to the body size of the frogs. We suggest that the species develops mainly an active search mode of their benthic prey. This study represents one of the most complete dietary records for a *Telmatobius* species, and helps us to understand the ecology of this species in the extreme desert environment of the high Andes Puna. These results can contribute to the conservation efforts being made for *Telmatobius* species.**

Keywords. Aquatic prey, diet, Puna, stomach flushing, suction feeding, trophic niche

Citation: Akmentins MS, Gastón MS. 2020. Feeding habits of the threatened aquatic Andean frog *Telmatobius rubigo* (Anura: Telmatobiidae). *Amphibian & Reptile Conservation* 14(3) [General Section]: 162–168 (e263).

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Accepted: 27 September 2020; **Published:** 1 Novmber 2020

Introduction

Telmatobius is a genus of anuran amphibians that has closely evolved with the aquatic ecosystems of the Andes of South America; and unlike other amphibian taxa, these aquatic Andean frogs are actually more diverse at high altitudes (Barrionuevo 2017). The aquatic life habit in such demanding high-altitude environments poses a series of biological and physiological challenges for these frogs (Lavilla and De la Riva 2005). In this regard, there is only fragmentary knowledge about the feeding habits of the aquatic Andean frogs; and what little is known is mostly based on occasional observations made on a limited number of individuals (Garman 1876; Allen 1922; Barrionuevo 2015, 2016; Cuevas and Formas 2002; Formas et al. 1999; Wiens 1993). Few studies have assessed the trophic ecology of *Telmatobius* species with a representative number of individuals that is sufficient to show the predominance of invertebrate aquatic prey in their diets (Lavilla 1984; Lobos et al. 2016; Valencia et al. 1982; Watson et al. 2017).

In Argentina, the species of genus *Telmatobius* are significantly threatened, with the main causes of decline being habitat alteration, the introduction of exotic predatory fishes, chytrid fungus infection, and the indirect consequences of extreme climate events (Barrionuevo and Mangione 2006; Barrionuevo and Ponssa 2008; IUCN 2020; Vaira et al. 2012). Despite the increasing level of concern regarding the conservation of the aquatic Andean frogs, there is very little information about the natural history of the 15 species registered in the country (Duré et al. 2018; Vaira et al. 2012).

The Laguna de Los Pozuelos' Rusted Frog (*Telmatobius rubigo* Barrionuevo and Baldo, 2009) is the most recently described species of genus *Telmatobius* in Argentina. This species is endemic to the Central Andean Puna ecoregion of Jujuy province in Argentina, particularly in the arreic river systems of the Laguna

Correspondence. **msakmentins@conicet.gov.ar*

Fig. 1. Adult male of *Telmatobius rubigo* in its natural habitat in the locality of Santa Catalina, Jujuy province, Argentina. *Photo by Mauricio Sebastián Akmentins.*

de Los Pozuelos basin (Barrionuevo and Abdala 2018; Barrionuevo and Baldo 2009). This fully aquatic frog has a unique feeding behavior among anurans, using a specialized feeding mechanism of inertial suction to capture their prey (Barrionuevo 2016). Beyond this singular prey capture mechanism, the knowledge about the trophic ecology of this species remains incomplete.

This study analyzed the feeding habits of the Laguna de Los Pozuelos' Rusted Frog in the desert Puna environment of Jujuy province, Argentina. Due to the combination of a strictly aquatic life habit and the inertial suction feeding mechanism, we expected a predominance of aquatic items in the diet of this species. Determining the composition of prey can provide valuable biological information to better understand the ecology of this threatened aquatic Andean frog.

Materials and Methods

The study was conducted in three localities of occurrence of *Telmatobius rubigo* in Jujuy province, Argentina (Barrionuevo and Abdala 2018): Queta, in the southern distributional range (22°43'7.88"S, 65°58'19.71"W; 3,548 m asl); Casa Colorada, in the western distributional range (22°22'8.9"S, 66°13'29.7"W; 4,333 m asl); and Santa Catalina, in the northern distributional range, near the type locality of the species (21°56'58.2"S, 66°02'21.6"W; 3,802 m asl). These localities are in the Central Andean Puna ecoregion (Dinerstein et al. 1995). The climate is typical of high-altitude desert, being cold and dry with large daily thermal fluctuations. Precipitation events are scarce, occurring as snow and hail in the winter and rain in summer (Barrionuevo and Baldo 2008).

The frogs were located in the rivers through an active search by visual encounter (Crump and Scott 1994), during January and March 2020 (Fig. 1). The frogs were captured manually, and the stomach contents were obtained *in situ* by the modified technique of stomach flushing (Legler and Sullivan 1979; Solé et al. 2005), which avoids mortality of the frogs. The stomach contents were individually preserved with 70% ethanol in 1.5 ml polypropylene tubes for subsequent analysis. For each frog, the sex was recorded based on secondary sexual characters, such as nuptial pads and keratinized spicules on the chest (Barrionuevo and Baldo 2009). The size of each frog was measured as the Snout-Vent Length (SVL) with a digital dial caliper to the nearest 0.1 mm (Mitutoyo Absolute Digimatic, Kawasaki, Japan) and each frog was weighed with a portable digital scale to the nearest 0.1 g (OHAUS, Parsippany, New Jersey, USA). After diet samples and measurements were taken, the frogs were released at the capture site.

The stomach contents were analyzed under a stereomicroscope, and prey were identified to the level of subclass for Annelida, and to the level of order or family for Arthropoda. For each item (prey category), the number (N), volume (V), and occurrences (F) were calculated as both absolute and percentage values. The volume for intact prey items was estimated according to the formula used by Dunham (1983) for a prolate spheroid: $V = 4/3\ \pi \times (\text{prey length}/2) \times (\text{prey width}/2)^2$.

The representativeness of the diet sample was evaluated by constructing a coverage-based (species richness) rarefaction curve for incidence data (Chao and Jost 2012), using iNEXT package, version 2.0.5 (Chao et al. 2016) in the program R (R Core Team 2017).

The dietary importance value index for pooled stomach samples was calculated to determine the importance of each prey item according to the formula described by Biavati et al. (2004): $Ip = (N\% + V\% + F\%)/3$, where N% is numeric percentage, V% is volumetric percentage, and F% is occurrence percentage. Intraspecific differences in diet composition were explored by calculating the *Ip* values for pooled stomach samples classified by sex (females and males).

The trophic niche breadth, for the species and by sex, were calculated using Levin's standardized index (Krebs 1989):

$$B = \frac{1}{(n-1)}\left[\frac{1}{(\sum_i^n P_i^2)} - 1\right]$$

where n is the total number of prey items, and P_i is the proportion of prey item i in the stomach contents. Breadth niche values range from 0 to 1, and were arbitrarily set here as high (> 0.6), intermediate (0.4 to 0.6), or low (<0.4), according to Novakowski et al. (2008).

The degree of diet overlap between females and males was calculated using the Morisita-Horn Index (Horn 1966):

$$\hat{C}\lambda = \frac{2\sum_i^n P_{ij}P_{ik}}{\sum_i^n P_{ij}^2 + \sum_i^n P_{ik}^2}$$

where n is the total number of prey items, P_{ij} is the proportion of the prey item i consumed by females, and P_{ik} is the proportion of the prey item i consumed by males. Values greater than 0.60 were considered to represent a significant diet overlap (Zaret and Rand 1971).

The biometric measures of females and males were compared using a two-sample t-test to compare the SVL (normal distribution), and a Mann–Whitney U-test to compare weight (non-normal distribution). A linear regression analysis was used to test the relationship between the frog size (SVL) and the log-transformed mean volume of the consumed prey (Hodgkison and Hero 2003). For all analyses, $p < 0.05$ was considered to represent a statistically significant difference.

Results

Thirty-one diet samples were obtained from 12 females, 18 males, and one indeterminate individual. Females had a body size of 51.9 ± 6.5 mm (mean SVL ± SD) and weight of 12.2 ± 5.3 g (mean ± SD). Males had a body size of 48.4 ± 6.7 mm (mean SVL ± SD) and weighed 10.8 ± 4.4 g (mean ± SD). For the individual of undetermined sex, the SVL was 40 mm and the body mass was 5.8 g. No significant differences were found between the sexes in the SVL ($t = 1.44$; $p = 0.16$) or the body mass (Mann-Whitney: $U = 95$; $p = 0.539$).

A total of 189 prey items were identified in 29 of the 31 stomach content samples, with a mean number of prey items per stomach of 6.5 ± 6.4 (mean ± SD).

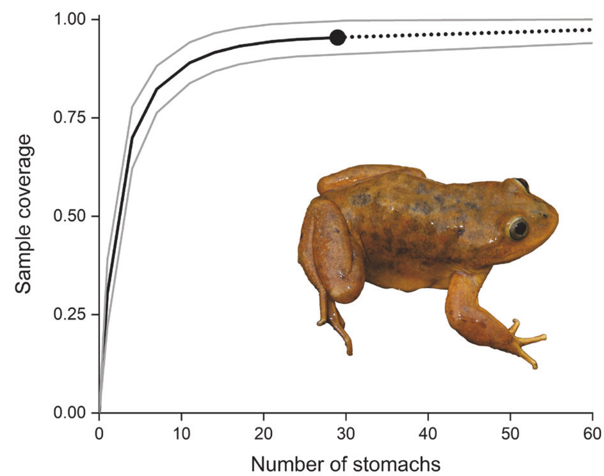

Fig. 2. Coverage-based rarefaction (solid line) and extrapolation (dotted line) curves for prey sample completeness (Hill numbers of order q = 0) of the analyzed stomachs of *Telmatobius rubigo*. The 95% confidence interval boundaries (gray lines) were calculated based on 200 bootstrap replicates.

The coverage-based rarefaction curve showed that the sampling effort was appropriate and reached 95.4% of completeness for prey richness (Fig. 2).

The trophic niche of *T. rubigo* was found to be based on invertebrates, with prey representing a wide range of taxa and a greater diversity of insects. The most important prey were adults of aquatic coleopteran families Dytiscidae and Elmidae, and the remainder of the diet was mainly composed of slow-moving benthic prey with a clear predominance of larvae of Coleoptera and Diptera. Crustaceans also were a relevant food item, dominated by *Hyalella* sp. shrimps and diminutive ostracods. The only relevant allochthonous prey items found in the diet of *T. rubigo* were earthworms. Vegetal debris and/or sand were registered in more than half of the stomach contents analyzed. *Telmatobius rubigo* has an intermediate niche

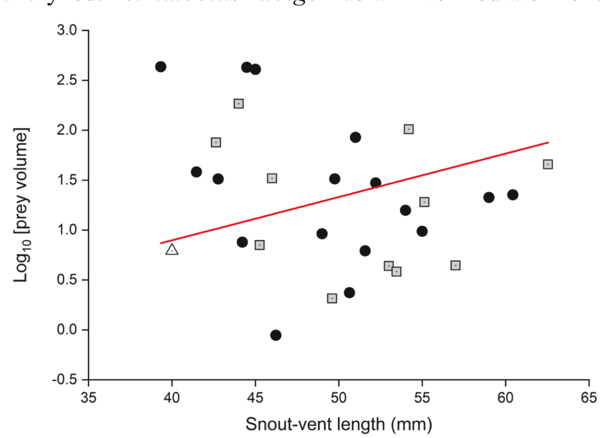

Fig. 3. Relationship between Snout-Vent Length (SVL) of *Telmatobius rubigo* and log-transformed mean volume of the consumed prey. The white triangle represents the indeterminate individual, grey squares represent female individuals, and black circles represent male individuals. The red line represents the linear fit estimated by the regression analysis considering all individuals.

Table 1. Summary of the identified prey items, with the absolute values and percentages of number (N), volume (V, in mm^3), frequency of occurrence (F), and dietary importance value index (*Ip*) of the principal prey items consumed by *Telmatobius rubigo*. The development stages of the insect prey items are specified in parentheses. Categories with *Ip*-values above 10% are in bold. In the last row, Levin's standardized index of trophic niche breadth is given for *T. rubigo*.

Prey taxa	N (%)	V (%)	F (%)	*Ip*
ANNELIDA				
Hirudinea	1 (0.5)	10.6 (0.3)	1 (3.4)	1.4
Oligochaeta*	8 (4.2)	1339.5 (36.7)	4 (13.8)	**18.2**
ARTHROPODA				
Crustacea				
Amphipoda	30 (15.9)	265.7 (7.3)	13 (44.8)	**22.7**
Hyalellidae				
Ostracoda	20 (10.6)	10.9 (0.3)	6 (20.7)	**10.5**
Isopoda*	6 (3.2)	75.4 (2.1)	1 (3.4)	2.9
Hexapoda				
Coleoptera (larvae)	25 (13.2)	157 (4.3)	13 (44.8)	**20.8**
Elmidae				
Dytiscidae				
Coleoptera (adult)	45 (23.8)	663.9 (18.2)	15 (51.7)	**31.2**
Elmidae				
Dytiscidae				
Diptera (larvae)	25 (13.2)	44.5 (1.2)	10 (34.5)	**16.3**
Chironomidae				
Muscidae				
Tabanidae				
Syrphidae				
Diptera (adult)	4 (2.1)	8.5 (0.2)	4 (13.8)	5.4
Ephemeroptera (nymph)	9 (4.8)	62.7 (1.7)	6 (20.7)	9.1
Hemiptera (adult)	7 (3.7)	118.1 (3.2)	3 (10.3)	5.8
Notonectidae				
Hymenoptera (adult)*	5 (2.6)	18 (0.5)	5 (17.2)	6.8
Formicidae				
Lepidoptera (larvae)*	1 (0.5)	147.3 (4.0)	1 (3.4)	2.7
Odonata (nymph)	2 (1.1)	617.0 (16.9)	2 (6.9)	8.3
Odonata (adult)*	1 (0.5)	110.4 (3.0)	1 (3.4)	2.3
Vegetal debris**			19 (65.5)	
Sand**			17 (58.6)	
Levin's standardized index	0.45			

*Allochthonous prey items; **only considering the frequency of occurrence in the stomach contents.

breadth, and Table 1 shows a summary of the quantitative analysis of the diet for the species.

Analyzing the prey consumption data by sex revealed differences in the prey importance between females and males, with females showing a wider trophic niche than males. There was a significant diet overlap among sexes. Table 2 shows a summary of the quantitative analysis of diet for each sex. A significant positive relationship ($R^2 = 0.382$, $p < 0.05$) was found between the body size of the frogs and the log-transformed mean volume of consumed prey (Fig. 3).

Discussion

The registered prey items in the stomach contents of the Laguna de Los Pozuelos' Rusted Frog showed a clear predominance of small slow-moving and gregarious benthic prey, confirming the hypothesis of a fully aquatic diet which coincides with the strictly aquatic life habits of this species.

As found here in the diet of *Telmatobius rubigo,* a predominance of adult insects also was observed in *T. hauthali* (Lavilla 1984). In addition, several studies have

Table 2. Dietary importance value index (*Ip*) of the prey items consumed by females and males of *Telmatobius rubigo*. The development stages of the insect prey item are specified in parentheses. Categories with *Ip*-values above 10% are in bold. The two last rows show Levin's standardized index of trophic niche breadth for each sex of *T. rubigo*, and the Morisita-Horn index of dietary overlap between the sexes.

Prey taxa	*Ip* females	*Ip* males
Hirudinea	—	0.4
Oligochaeta*	3.6	**20.6**
Amphipoda	**16.5**	8.2
Ostracoda	7.1	5.1
Isopoda*	—	2.7
Coleoptera (larva)	**12.2**	7.6
Coleoptera (adult)	**19.3**	**12.3**
Diptera (larva)	3.6	6.0
Diptera (adult)	**10.7**	0.3
Ephemeroptera (nymph)	**12.2**	1.5
Hemiptera (adult)	**13.8**	—
Hymenoptera (adult)*	**10.7**	0.7
Lepidoptera (larva)*	3.6	—
Odonata (nymph)	3.6	0.3
Odonata (adult)*	—	1.9
Levin's standardized index	0.66	0.51
Morisita-Horn index	0.71	

*Allochthonous prey items.

shown that the immature stages of benthic insects are the most common items in the trophic niche of other aquatic Andean frogs (Lavilla 1984; Lobos et al. 2016; Valencia 1982; Watson et al. 2017). The amphipod shrimps also are a representative prey in the diet of various *Telmatobius* frogs (Allen 1922; Lobos et al. 2016; Valencia 1982; Watson et al. 2017), and other species of strictly aquatic anurans of Argentina (Cuello et al. 2006; Velasco et al. 2019). The presence of allochthonous prey, such as earthworms, indicates that they were most likely consumed underwater when they accidentally fell from the riverbanks.

The common presence of non-nutritive elements, mainly vegetal debris and sand, in the stomachs of *T. rubigo* is evidence of the strategy of foraging in the benthos of rivers and is related to the suction force of the feeding mechanism used by these frogs for capturing their prey (Barrionuevo 2016). A similar high incidence of non-nutritive items in the stomach contents was also reported in Chilean species of the *Telmatobius marmoratus* group (Valencia 1982), suggesting a shared foraging tactic in this species group (Barrionuevo 2017).

Overall, these results show that *T. rubigo* exhibits generalist and opportunistic feeding habits, as has been noted in other species of *Telmatobius* (Lavilla 1984; Valencia 1982). We suggest that *T. rubigo* performs a mainly active search of their prey. Despite the differences in the importance of consumed prey and the width of the trophic niche between females and males of *T. rubigo*, we suggest there is no trophic niche segregation due to the absence of sexual dimorphism in biometric measures and the high diet overlap between the sexes.

Telmatobius rubigo was found in high densities in some parts of the surveyed river systems, occurring in sympatry with two other anuran species, *Pleurodema cinereum* and *Rhinella spinulosa*. We did not register any cases of cannibalism or anurophagy in *T. rubigo,* as has been reported in some other *Telmatobius* species (Allen 1922; Barrionuevo 2015; Valencia et al. 1982; Wiens 1993). The insight of trophic niche segregation in *T. rubigo* indicated here, due to the relationship between the mean volume of consumed prey with the frog size, may be a mechanism to avoid competition and cannibalism. However, a more in-depth analysis including seasonal changes in the diet and prey availability/prey selection will be necessary to fully understand the trophic ecology of Laguna de Los Pozuelos' Rusted Frog.

Conclusions

The results of this study have direct contributions for understanding the ecology of Laguna de Los Pozuelos' Rusted Frog (*Telmatobius rubigo*), as well as for its conservation. *Telmatobius rubigo* is threatened by direct and indirect consequences of human activities (IUCN 2020; Vaira et al. 2012). Among the direct threats that we observed during our fieldwork are the poor water management for human and animal consumption, the introduction of exotic predatory fishes (salmonids), inappropriate management of solid waste, liquid effluents from human settlements, and mining leachate pollution. All these threats affect not only the aquatic Andean frogs but also the populations of their aquatic invertebrate prey (Valdovinos et al. 2007; Van Damme et al. 2008; Vimos et al. 2015).

As far as we know, this study represents one of the most complete dietary records for an aquatic Andean frog of the genus *Telmatobius*, due to the numbers of surveyed localities and sampled individuals. The results obtained in this study can be used as a guide for the *ex situ* conservation efforts being made for *Telmatobius* species, particularly for improving the food provided to these frogs in captive breeding programs.

***Acknowledgments*.—**We thank Laura C. Pereyra for helping with the statistical analyses of data. This research was partially supported by PUE INECOA 22920170100027CO. Permits for fieldwork were provided by Ministerio de Ambiente, Dirección Provincial de Biodiversidad de Jujuy, Argentina (171/2015 DPB).

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Mauricio Sebastián Akmentins is an Assistant Researcher at the Consejo Nacional de Investigaciones Cientificas y Tecnicas (CONICET) of Argentina. Mauricio received a Doctorate degree in Biological Sciences from the Universidad Nacional de Córdoba (Argentina). His main areas of interest are in the bioacoustics, ecology, and conservation of anuran amphibians of the Andean ecoregions of northwestern Argentina.

María Soledad Gastón is an Assistant Researcher at the Consejo Nacional de Investigaciones Cientificas y Tecnicas (CONICET) of Argentina. María received a Doctorate degree in Biological Sciences from the Universidad Nacional de Córdoba (Argentina). Her main areas of interest are the ecophysiology, behavior, and conservation of amphibians.