Trophic Ecology of *Pristimantis labiosus* (Anura: Craugastoridae) from South-Western Colombia

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Abstract. To date, the diet of the frog *Pristimantis labiosus* is not known. We analysed the feeding habits of adults and juveniles of this species and evaluated whether dietary shift was related to variation in body and/or mouth size. Diet was analysed in terms of number, volume and frequency of occurrence of items. Both length and volume of prey were correlated with snout-vent length, and mouth width to identify if there was ontogenetic shift in prey size consumption with the increase in body and head size. The diet was composed of 18 taxa of arthropods and gastropods distributed in 217 items. Adult frogs consumed a greater number of food items (N = 139) than juveniles (N = 78), and the two age-classes consumed a similar array of prey taxa. The most frequent prey in adults was Formicidae (60%), whereas in juveniles the most frequent prey taxa were Diptera and Hemiptera (13% each). Adults had a broader trophic niche (0.57) than juveniles (0.08) with a relatively low trophic overlap among them (0.39). Although we found differences in body size and in mouth width between the two age-classes, we did not observe a corresponding ontogenetic shift in prey size consumption with the increase of morphological variables. Based on these results, *P. labiosus* is considered opportunistic widely-foraging predator, consuming any type of prey available in the environment.

Keywords: diet, feeding habits, trophic niche breadth, stomach flushing, morphology, ontogeny.

Introduction

Ontogenetic dietary shifts are probably common in amphibians and reptiles but are not well studied although it is known that potential ontogenetic shifts in diet can be related to the morphological variation among age groups (Vitt & Caldwell 2014). The ontogenetic variation of the body and/or mouth size, has been demonstrated to be related with intrapopulation differences in the use of food resources (e.g. Maglia 1996, Hirai & Matsui 1999, Hodgkison & Hero 2003, Biavati et al. 2004, Schriever & Williams 2013, Del Río-García et al. 2014). In most studies, amphibians generally change their diet from eating small prey when they are juveniles to large prey when they are large, but with a considerable dietary overlap in the prey taxa. Some studies, however, have shown a different behaviour, where prey size was not related to individual body size (Maglia 1996, Miranda et al. 2006, Quiroga et al. 2009). Such results could be explained under the scenario that in species with broad diets and ontogenetic changes in head size, there are no variations in prey sizes

consumed by the distinct age classes because the juveniles as suggested by Maglia (1996) for salamanders. Testing this scenario in frogs require more examples providing details of prey resource use between juveniles and adults in relation to the variation in body and/or mouth size.

Several qualitative and quantitative studies on feeding habits of Colombian anurans have been published in the last 16 years (e.g., Daza-Vaca & Castro-Herrera 1999, Muñoz-Guerrero et al. 2007, Valderrama-Vernaza et al. 2009, Hoyos-Hoyos et al. 2012, Gutiérrez-Cárdenas et al. 2013, Méndez-Narváez et al. 2014, Agudelo et al. 2015, Blanco-Torres et al. 2015). However, there still are many gaps in ecological information species-specific and/or population-specific, which need to be covered with additional research efforts. Studies on intrapopulation variation in the use of food resources, such as García-R. et al. (2012) and Moreno-Barbosa & Hoyos-Hoyos (2014), are a way to fill those gaps. Despite the abundance of species of *Pristimantis* frogs in Colombia (> 200 species; Frost 2014), qualitative and quantitative data about trophic ecology of these frogs are available only for

16 Colombian species occurring in the three Andean ranges (Arroyo et al. 2008, Garcia-R. et al. 2012, 2015, Hoyos-Hoyos et al. 2012, Moreno-Barbosa & Hoyos-Hoyos 2014).

Pristimantis labiosus (Lynch, Ruíz-Carranza & Ardila-Robayo 1994) occurs along the western flank of the Cordillera Occidental in Colombia (from south of Buenaventura municipality), south to north-western Ecuador, inhabiting tropical forests at elevations of 150–1500 m, with humid tropical and subtropical regimes (Lynch & Duellman 1997). Natural history information of this species is limited to anecdotal notes on the micro-habitats where the individuals perch at night (Lynch & Duellman 1997, Mueses-Cisneros & Moreno-Quintero 2011, Arteaga et al. 2013).

In this study, we provide both qualitative and quantitative information on the dietary habits of a population of *P. labiosus* from a premontane rain forest in south-western Colombia. More specifically, we asked: (1) what are the dietary habits of *P. labiosus*?; (2) are there differences in the diet between adults and juveniles?; (3) is there an ontogenetic shift in prey size as the body and/or mouth size increases?

Material and methods

We conducted this study in the Reserva Natural Río Ñambí (hereafter RNRÑ; latitude 1.286280, longitude -78.074540, datum WGS84; 1100-1900 m above sea level), Barbacoas, Department of Nariño, south-western Colombia, along the road #10 between Pasto and Tumaco municipalities (Fig. 1). The reserve is a premontane rain forest (following Holdridge 1996), with annual rainfall above 8500 mm, mean annual temperature of 19.3 ± 1.6 °C (range 16.3-23.8 °C), and relative humidity between 65% and 88% (Salaman 2001).

We studied the population of *P. labiosus* from January to February 2013, with searches over 6-9 consecutive nights in each month, between 18:00 h and 00:00 h. We conducted visual encounter surveys (Crump & Scott 1994) in 38 different transects in RNRÑ to search for frogs in time constrained transects (1 hour), totalling a sampling effort of 76 h/person. We captured frogs manually and transferred to the field station within a maximum of two hours after capture. We measured all captured individuals for snout-vent length (SVL), and mouth width (MW), with digital calliper (to the nearest 0.1 mm). In order to test for ontogenetic variation in prey use, we grouped the captured frogs as adult according to size ranges reported by Lynch et al. (1994): SVL ≥ 35 mm; all individuals with body size below this value were considered as juveniles.

We flushed each frog´s stomach following the methodology described by Solé et al. (2005). All frogs were re-
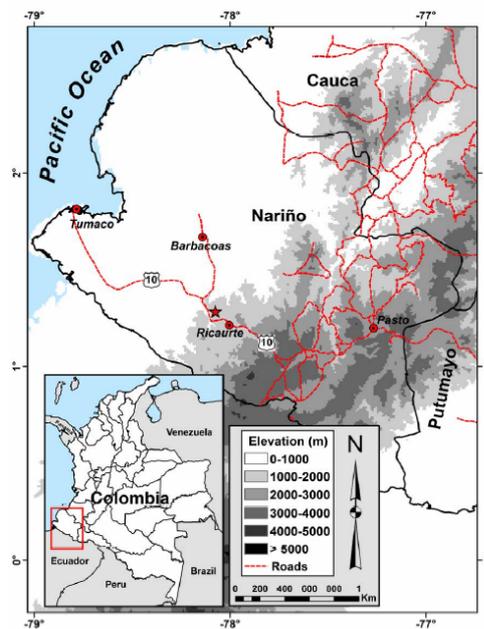

Figure 1. Map of Department of Nariño (Colombia) showing the localization of the Reserva Natural Río Ñambí (star), and the municipalities of Tumaco, Barbacoas and Pasto.

leased at the original capture site in the next morning after having been captured. Stomach contents were transferred into small labelled vials with 70% ethanol, and posteriorly identified under a stereomicroscope in the Universidad de Nariño (Pasto, Colombia). We identified prey items to the order level, except for Hymenoptera, which were classified as Formicidae and non-Formicidae, and snails and millipedes which were classified as classes Gastropoda and Diplopoda, respectively. We measured prey items for length (L) and width (W) using a digital calliper (to the nearest 0.1 mm). With these measures we calculated its volume (in mm³) using the formula for a prolate spheroid $[V = 4/3\pi \ (L/2) \ (W/2)^2]$ (Dunham 1983). Diets of both adults and juveniles were quantified as the number (N_i), the volume (V_i), and the frequency of occurrence (O_i; number of stomachs that contained that prey taxon) of each prey taxon (i). We also recorded empty stomachs. Because any of the measures used alone is biased towards large-sized or sporadically abundant prey (Pinkas et al. 1971, Manicom & Schwarzkopf 2011), we compared the relative proportion of each prey category using the index of relative importance (IRI) introduced by Pinkas et al. (1971) and suggested by Solé & Rödder (2009) for dietary assessments of amphibians: %IRI = ($\%O_i$)($\%N_i$+$\%V_i$), where $\%O_i$, $\%N_i$ and $\%V_i$ are the prey occurrence, numeric, and volumetric percentages, respectively.

We estimated trophic niche breadth for adults and for juveniles based only on the number of food items consumed (because we could not calculate the volume to all

prey categories), to evaluate to what extent the two age classes differ in the use of prey types. We used the half the Gini-Simpson index: $B_D = 1/2(1-\Sigma p_i^2)$, where p_i is the relative resource use of prey i by a species based on total numbers of its prey use records (N). We used this index assuming that the resources used are completely distinct and $p_i = f_i$ (p = relative resource use; f = relative resource preference), when resource availability data are not available or are not taken into account (De Cáceres et al. 2011). This index ranges from 0 (use of only one prey category) to 1 (all prey types used equally). We estimated the similarity in diet among age classes using a variation of the Pianka's (1974) overlap index: $Ø_D = (\Sigma p_{i1}p_{i2})/(\sqrt{[\Sigma p_{i1}^2][\Sigma p_{i2}^2]})$, where p_{i1} and p_{i2} represent the proportions of the ith resource used by the 1 and 2 species. The analysis was done with retained niche breadth and reshuffled zero states (RA3 randomization algorithm) in the software EcoSim professional v1.2d (Entsminger 2012). The expected value of niche overlap (or similarity in their diets) was given by the mean value of 1000 simulations. The resulting values can vary between 0 which indicates no overlap to 1 suggesting complete overlap.

We used Analysis of Covariance (ANCOVA) with frog SVL as the covariate to test for differences in MW between adults and juveniles (Zar 2010) and Spearman Rank Correlation for analyses the relationship between the SVL and MW. We tested for differences in the number of prey taxa, the number of prey items and both the length and the volume of the largest prey per stomach for each age class using the Kolmogorov-Smirnov test. Finally, we used Spearman Rank Correlation to test the relationship between both the log-transformed length and the log-transformed volume of the largest prey consumed by frogs in each age class and to each of the frog log-transformed morphological variables. All tests used above were made after we tested for the normality of the data distribution. Statistical data are given as mean ± 1 SD.

Results

Morphological analysis

Of the 58 individuals of *P. labiosus* sampled, mean SVL of adults was 53.10 ± 7.90 mm (N = 28; range = 38.70–70.44) and that of juveniles was 25.46 ± 5.70 mm (N = 30; range = 15.91–34.94). Adult frogs had significantly wider mouths than that of sub adult frogs (ANCOVA: $F_{1,55} = 364.24$, $p < 0.001$; Fig. 2A). The MW was significantly and positively correlated with frog SVL ($r_s = 0.98$, $p < 0.001$), and it increased slightly more strongly with SVL in juveniles than in adults (Fig. 2B).

Feeding habits

We flushed 58 individuals (28 adults, 30 juveniles) of *P. labiosus*, of which 22 adults (78.57%; SVL = 52.34 ± 8.59 mm, range 38.69–70.44 mm) and 23
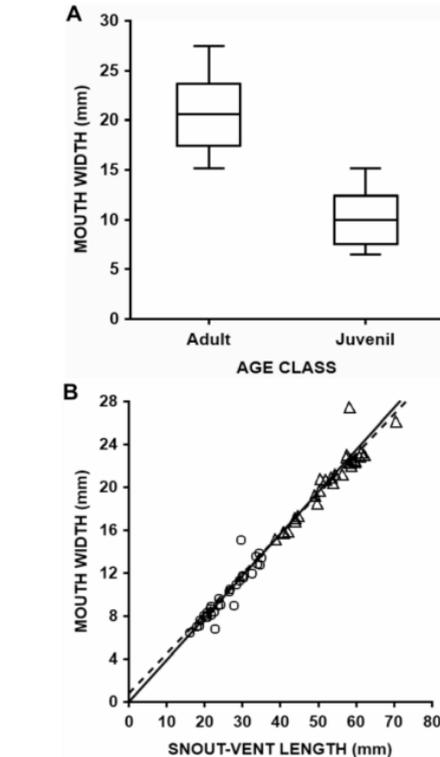

Figure 2. (A) Box plot of mouth width (in mm) and **(B)** relationship (with lines represent total adjustment) and between snout-vent length and mouth width (in mm) of adults (triangles; dashed line) and juveniles (circles; solid line) of *Pristimantis labiosus* (28 adults and 30 juveniles) from Reserva Natural Río Ñambí (Nariño, Colombia). In (A), lines within the boxes represent median values, upper and lower boundaries of boxes are ± 1 standard deviation, and whiskers are minimum and maximum values.

juveniles (76.67%; SVL = 25.38 ± 5.65 mm, range 15.91–34.94 mm) had at least one taxon of prey in their stomachs. We did not obtain prey during flushing from eight adults and five juveniles, suggesting they had empty stomachs. We found 179 prey items distributed across 17 taxa of arthropods (mainly insects, of which three prey were unidentified larvae) and one Gastropoda (three prey); 15 preys were unidentified arthropods and three frogs contained mosses (Bryophyta) in their stomachs (Table 1). Based on 43 individuals having prey (not included two adults which had only mosses in their stomachs), Formicidae was the most abundant (41.47%) prey taxon, followed by Coleoptera (7.37%), Diptera (5.99%), Orthoptera (5.07%) and Hemiptera (4.61%) (Table 1).

Table 1. Prey composition of the diet of juveniles and adults of *Pristimantis labiosus* from the Reserva Natural Río Ñambí (Nariño, Colombia). Abbreviations: N: number of prey; V: prey volume (in mm³); O: frequency of occurrence; and IRI: index of relative importance (only for prey taxa in which it was possible to calculate the volume).

Prey taxa	Adults (N = 22)				Juveniles (N = 23)			
	N (%)	V (%)	O (%)	IRI	N (%)	V (%)	O (%)	IRI
ARTHROPODA								
Arachnida								
Acari	2 (1.44)	0.18 (0.03)	1 (4.55)	6.69	2 (2.56)	0.14 (0.02)	2 (8.70)	22.49
Araneae	2 (1.44)	-	1 (4.55)	-	3 (3.85)	7.98 (1.25)	3 (13.04)	66.42
Opiliones	1 (0.72)	17.26 (3.20)	1 (4.55)	17.83	1 (1.28)	35.81 (5.59)	1 (4.35)	29.89
Scorpiones	3 (2.16)	-	3 (13.64)	-	-	-	-	-
Diplopoda	2 (1.44)	-	2 (9.09)	-	2 (2.56)	-	2 (8.70)	-
Insecta								
Blattodea	1 (0.72)	-	1 (4.55)	-	2 (2.56)	55.96 (8.74)	2 (8.70)	98.29
Coleoptera	7 (5.04)	162.94 (30.24)	4 (18.18)	641.29	9 (11.54)	19.61 (3.06)	6 (26.09)	380.89
Collembola	-	-	-	-	2 (2.56)	-	2 (8.70)	-
Dermaptera	2 (1.44)	58.21 (10.80)	2 (9.09)	111.27	3 (3.85)	11.07 (1.73)	3 (13.04)	72.71
Diptera	3 (2.16)	0.02 (0.004)	3 (13.64)	29.48	10 (12.82)	1.59 (0.25)	8 (34.78)	454.57
Hemiptera	-	-	-	-	10 (12.82)	61.20 (9.56)	8 (34.78)	778.37
Hymenoptera (non-Formicidae)	3 (2.16)	-	3 (13.64)	-	-	-	-	-
Hymenoptera (Formicidae)	84 (60.43)	175.08 (32.49)	2 (9.09)	844.72	6 (7.69)	1.17 (0.18)	3 (13.04)	102.71
Lepidoptera	1 (0.72)	117.31 (21.77)	1 (4.55)	102.22	2 (2.56)	144.48 (22.56)	2 (8.70)	218.50
Orthoptera	5 (3.60)	-	5 (22.73)	-	6 (7.69)	6.47 (1.01)	4 (17.39)	151.35
Phasmatodea	-	-	-	-	1 (1.28)	289.36 (45.19)	1 (4.35)	202.05
Trichoptera	1 (0.72)	-	1 (4.55)	-	-	-	-	-
Larvae	1 (0.72)	-	1 (4.55)	-	2 (2.56)	1.49 (0.23)	2 (8.70)	24.32
Unidentified arthropods	20 (14.39)	-	13 (59.09)	-	15 (19.23)	-	9 (39.13)	-
MOLLUSCA								
Gastropoda	1 (0.72)	7.91 (1.47)	1 (4.55)	9.94	2 (2.56)	4.01 (0.63)	2 (8.70)	27.74
Plant remains (Bryophyta)	-	-	3 (13.64)	-	-	-	-	-
TOTAL	139	538.92	22		78	640.3	23	

Volumetrically, Phasmatodea (V = 24.54%) and Lepidoptera (V = 22.20%) were the dominant prey taxa (Table 1). The number of consumed prey taxa as well as the diet composition, varied among the two age classes of frogs (Table 1). Most prey taxa (N = 13) found in the diet were consumed by both juveniles and adults, whereas Hymenoptera (non-Formicidae), Scorpiones, Trichoptera were consumed only by adults and Collembola, Hemiptera and Phasmatodea were consumed only by juveniles (Table 1). We did not find significant differences between adults and juveniles in mean number of prey taxa consumed (Kolmogorov-Smirnov Z = 0.47, N = 44, *p* = 0.98; Fig. 3A).

Among adults, Formicidae was the most important prey taxon both numerically and volumetrically, although this taxon was found only in two individuals (one adult individual with 80 ants). Because of the high number of ants present in stomachs of adults, Formicidae was also the taxon with the highest IRI (Table 1). Coleoptera was the second most important prey taxon in number of prey, in terms of volume and in IRI (Table 1). Or-thoptera was the most common prey taxon in stomachs of adult frogs, present in 22.73% of individuals. Among juveniles, Diptera, Hemiptera and Coleoptera were the dominant prey taxa by number, followed by Formicidae and Orthoptera (Table 1), and Phasmatodea was the most important prey taxon by volume. Hemiptera and Diptera were the taxa with the higher IRIs and the most common prey (occurring in 35% of sub adult frogs). The other prey taxa were rare among juveniles, being present only between 4% and 26% of sub adult frogs (Table 1). Overall, we found that adults consumed a greater number of prey than juveniles (Fig. 3B), but these values did not differ significantly among the two age classes (Kolmogorov-Smirnov Z = 0.33, N = 44, *p* = 1.0).

We found that adults consumed longer and more voluminous prey than juveniles (Fig. 3C-D), but each of these values did not differ significantly among the two age classes (Kolmogorov-Smirnov, Length: Z = 0.68, N = 20, *p* = 0.74; Volume: Z = 0.83, N = 20, *p* = 0.50). We did not find relationship between the log-transformed length and the log-
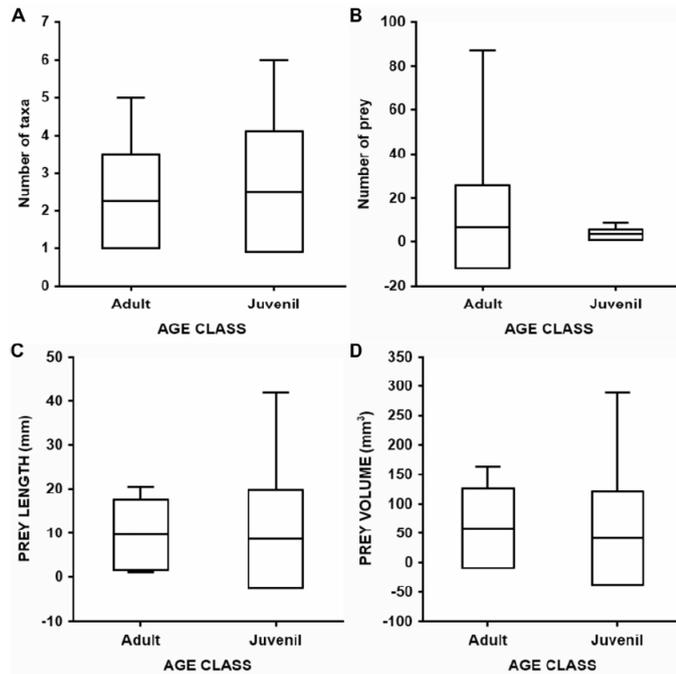
Figure 3. Box plot of number of taxa (A), number of prey (B), length (C) and volume (D) of the largest prey ingested by adults and juveniles of *Pristimantis labiosus* from Reserva Natural Río Ñambí (Nariño, Colombia). Lines within the boxes represent median values, upper and lower boundaries of boxes are ± 1 standard deviation, and whiskers are minimum and maximum values. For figures A-B, N adults = 28 and N juveniles = 30; for C-D, N adults = 6 and N juveniles = 14.
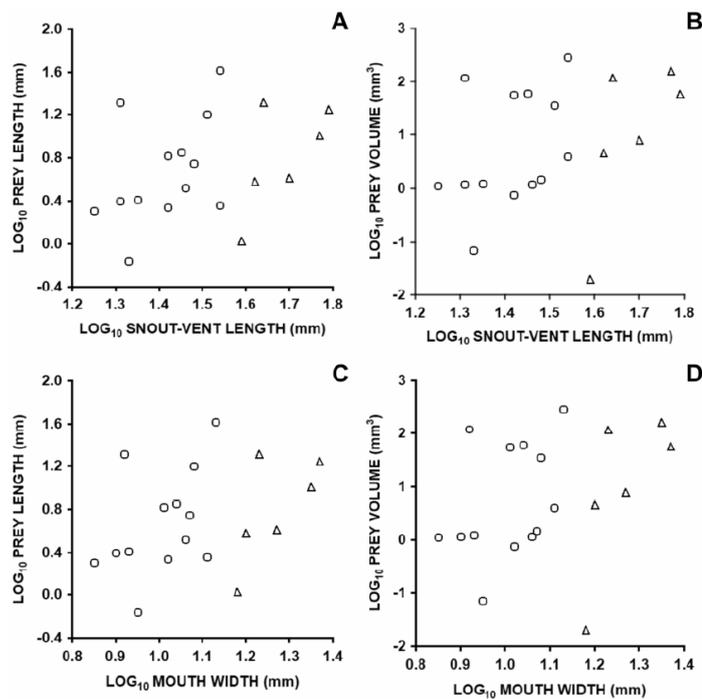

Figure 4. Relationship between length (in mm) and volume (in mm^3) of the largest prey and **(A-B)** snout-vent length (in mm) and **(C-D)** mouth width (in mm) for individual adults (triangles; $N = 6$) and juveniles (circles; $N = 13$) of *Pristimantis labiosus* from Reserva Natural Río Ñambí (Nariño, Colombia). In either case, no significant relationship (Spearman) was revealed ($0.35 \le r_s \le 0.38$; $0.11 \le p \le 0.14$, N = 19). All variables were log-transformed.

transformed volume of prey consumed with both log-transformed SVL and log-transformed MW (Fig. 4). Foraging niche was broader for juveniles ($B_D = 0.449$) than for ($B_D = 0.247$). We found a small overlap between the two age classes ($O_D = 0.387$), but when was removed from the analysis

the adult individual with 80 ants in its stomach, the trophic overlapping was above 74%.

Discussion

Apart from the difference found in body size between adult and sub adult individuals, our results showed also that mouth width varied also in a similar way between the two age classes. Such differences and the positive relationship observed between MW and body size are expected due to the increase directly proportional between that linear cephalic dimension and body length (Wyckmans et al. 2007). Based on this, our results are in agreement with the fact that frogs maintain a similar shape over a wide size range (Emerson 1978). In general, the positive allometric growth as observed in our dataset has been related with ontogenetic shifts in diets in some studies (Maglia 1996, Ivanović et al. 2007, Wyckmans et al. 2007, Richardson et al. 2011).

We found that *P. labiosus* consumed a relatively wide array of prey types (19 prey types), predominantly arthropods, with Formicidae, Coleoptera, Hemiptera and Diptera being the more important prey in the sampled population. Except for Formicidae, these prey taxa are also commonly found in the diet of other *Pristimantis* species (e.g. Toft 1980, Parmelee 1999, Guayasamin et al. 2004, Duellman 2005, Arroyo et al. 2008, Hoyos-Hoyos et al. 2012). Because of this, *Pristimantis* species are considered as both generalist and opportunistic feeders, preying on different prey in relation to their availability in the environment (Lynch & Duellman 1997). In addition, because these frogs consumed few ants (e.g. Duellman 2005, Guayasamin et al. 2004, García-R. et al. 2012, 2015) they cannot be considered ant specialists. The high number of ants found in the diet of our sampled individuals of *P. labiosus* could be considered an atypical value, which was maximized by the contribution of 88.9% of the ants by a single individual, whereas the other numerical important prey were found in two or more individuals. Therefore, we can consider *P. labiosus* as an opportunistic feeder and the outlier observed can be related with the fact that some individuals may take advantage of prey often clumped like the ants (Quiroga et al. 2009). Although we found plant remains in the sampled frogs, we considered that in *P. labiosus* plants are not part of its diet due to the small amount of plant remains found and were present in less than 7% of stomachs of analysed frogs; therefore we assumed that these plants were likely ingested incidentally during the process of prey capture (Hirai & Matsui 1999, Cooper and Vitt 2002, Quiroga et al. 2009, Brito et al. 2012).

The adults consumed more and larger prey than juveniles, but we did not find evidence of ontogenetic shift in prey size with an increase in SVL or MW. Such results suggest that larger individuals do not necessarily consume larger prey. A positive correlation between body size (and MW) and prey size has been demonstrated in several anuran species (Toft 1981, 1985, Parmelee 1999, Lima & Magnusson 2000), but this fact appear not be applicable to frogs that are food generalists/opportunists such *Pristimantis* frogs (Arroyo et al. 2008, Moreno-Barbosa & Hoyos-Hoyos 2014, García-R. et al. 2015) or ranids (Hirai & Matsui 1999), which tend to forage on prey of all sizes available in the environment opportunistically depending on encounter rates with prey (Lynch & Duellman 1997, Hirai & Matsui 1999).

The trophic niche breadth estimated suggests that sub adult individuals have a more generalist foraging behaviour than adults. A greater number of prey taxa was also found in the diet of juveniles of *P. achatinus* and *P. jubatus* (García-R. et al. 2012, Moreno-Barbosa & Hoyos-Hoyos 2014). We found a low trophic overlap between the two age classes analysed, but this result can be influenced by the high number of ants consumed by a single individual. The trophic overlap above 74% found is more realistic considering the observed opportunistic foraging behaviour of *P. labiosus* and the absence of an ontogenetic shift in the prey size as the body and/or mouth size increase.

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