

DIET OF DIRECT-DEVELOPING FROGS (ANURA: CRAUGASTORIDAE: *Pristimantis*) FROM THE ANDES OF WESTERN COLOMBIA

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ABSTRACT

We studied the diet of 15 montane frog species of the genus *Pristimantis* (Craugastoridae) from the Andes of Western Colombia to determine the diet range, breadth of niche and overlap among species. We identified 499 prey items from stomach and intestinal contents of 154 specimens. Prey items were included in 74 different categories. The most common 15 prey categories accounted for 65 % of all frogs' diet. The invertebrate families Isotomidae, Chironomidae, Formicidae, and Tipulidae were the most abundant categories and accounted for 32 % of the frogs' diet. Ten of the 15 frog species were found with at least one item of Araneae. Coleoptera and Tipulidae were found in nine frog species, and Acari and Carabidae in eight frog species. In general, beetles were found in gastrointestinal tracts of all species examined, except for *P. quantus*, but interpretation needs caution because only one individual of this species was caught. *Pristimantis hectus* showed a specialized diet, consuming mainly dipterans of the family Chironomidae, while the remaining species showed a generalist diet. *Pristimantis palmeri* showed niche overlap with *P. erythropleura* ($\Phi_{jk} = 0.69$), *P. myops* ($\Phi_{jk} = 0.64$), and *P. orpacobates* ($\Phi_{jk} = 0.64$). Our results suggest that most of the frogs species studied are generalist, foraging opportunistically on dipterans, arachnids, collembolans, coleopterans, and hymenopterans. Here, we report the diet of montane *Pristimantis* species and discuss the results in comparison with data on related species in montane and lowland regions.

Keywords: Colombia, diet, niche breadth, niche overlap, *Pristimantis*, Western Cordillera.

INTRODUCTION

Understanding resource partitioning within and between species is important to determine the mechanism underlying the composition of ecological assemblages (Cody and Diamond, 1975). Ecological traits of coexisting species have provided explanations to the history and evolution of species diversity and the conformation and stability of communities (Cody and Diamond, 1975; Colston *et al.*, 2010). Diet has been the main niche axis of interest to ecologists because competition for food can potentially shape community attributes such as number of coexisting species and their niche breadth and overlap (Diamond, 1975; Case, 1983; Toft, 1985).

Studies of prey type in anurans have been useful for determining the patterns of assemblage composition, ecological niches and organization of the species in their respective communities (Woolbright and Stewart, 1987; Ovaska, 1991; Alonso *et al.*, 2001; Gutiérrez-L, 2003; Ortega *et al.*, 2005). Moreover, anuran diets can help us to understand life history, patterns of behaviour, and the phylogenetic relationships between populations and clades (Wells, 1978; Lima and Magnusson, 1998; Sanabria *et al.*, 2005; Juncá and Eterovick, 2007). This information is also important to predict the effects of decreasing populations in threatened worldwide anuran species and informing conservation plans for frog communities (Diamond, 1975; Young *et al.*, 2001; Moritz, 2002; Vignoli and Luiselli, 2012).

Colombia hosts the highest species diversity of direct-developing frogs (Anura: Terrarana) in the world and the genus *Pristimantis* (family Craugastoridae) represents at least 27 % of the total anuran diversity in the country (AmphibiaWeb, 2014). A sizable number of *Pristimantis* is found in the Western Cordillera of the Andes, where it is the most common anuran group (Lynch, 1998a). The mountains of southwestern Colombia present unique anuran assemblages composed of more than 150 species above 1000 m a.s.l (Bernal and Lynch, 2008), but little is known about the diet of these species.

This study examined the diet composition of 15 montane frog's species of the genus *Pristimantis* in five localities of the Western Cordillera. Here, we used this data to analyse niche characteristics (food) and ecological correlations of niche preferences among species of local assemblages to answer the following questions: 1) What is the food composition of montane *Pristimantis* species in southwestern Colombia?, 2) Does diet composition vary among species?, and 3) How large are niche breadth and niche overlap of montane *Pristimantis* species in the Western Cordillera?

MATERIALS AND METHODS

Study area

This study was conducted in Colombia at 1) Serranía de Los Paraguas (4°50'N, 76°15'W), municipality El Cairo, 2000–2200 m a.s.l., between the Departments of Valle del Cauca and Chocó, 2) Loma Alta (3°30'N, 76°39'W), municipality Dagua, 1750–2100 m a.s.l., Department of Valle del Cauca, 3) Chicoral (3°35'N, 76°36'W), municipality La Cumbre, 1800–1900 m a.s.l., Department of Valle del Cauca, 4) Peñas Blancas, Farallones de Cali National Park (3°25'N, 76°39'), 1900–2200 m a.s.l., municipality Cali, Department of Valle del Cauca, and 5) La Romelia, Munchique National Park (2°38', 76°54'), 2400–2800 m a.s.l., municipality El Tambo, Department of Cauca (Fig. 1).



FIGURE 1. Map of western Colombia showing the five sampling localities in the departments of Cauca and Valle del Cauca.

Sampling

Samples were collected on straight-line transects set up at each locality between 0.2 to 2.0 kilometres (km). Frog specimens were hand-collected using Visual Encounters Survey (Crump and Scott, 1994) from 19:00 h to 24:00 h. Euthanasia of frogs was performed with chloretone within a maximum of eight hours after capture. This study was carried out in strict accordance with evaluation of environmental, social, and educational impacts established at the Universidad del Valle (Convocatoria Interna number CI-746). Permit for sampling of specimens was obtained from Ministerio de Medio Ambiente, Vivienda y Desarrollo Territorial de Colombia (Resolución 573 del 10 de abril/08). Specimens were deposited at the herpetological collection – Universidad del Valle (Voucher numbers: UVC15812–915, UVC15917, UVC15919–24, UVC15927–52, UVC15955–71, UVC15975–79, UVC15982).

Gastrointestinal tracts (from stomach to cloaca) of each species were removed and fixed in 75 % ethanol. Prey items were sorted in a Petri dish, and later separated and categorized using a Nikon SMZ-645 stereoscope. Identification of prey items, depending on preservation of the prey, was held to the lowest possible taxonomic level using the dichotomous key by Triplehorn and Johnson (2005).

Diet composition

The quantitative importance of each prey group in the diet of *Pristimantis* was estimated using the index of relative importance (IRI) of Pinkas *et al.*, (1971). The IRI provides a summary of dietary composition using the frequency of occurrence (% O) and percentage by number (% N) as follows:

$$\%O = n / N * 100 \quad (1)$$

$$\%N = Nn / Nt * 100 \quad (2)$$

Where n = number of gastrointestinal tracts that have the prey i , N = total number of analyzed gastrointestinal tracts, Nn = number of prey items of prey group n observed, and Nt = total number of prey items of all prey groups. The volume and length of the prey were not used because they were found disarticulated and highly digested.

Analysis of niche breadth was performed on species with $n \geq 5$ individuals. Niche breadth of diet was calculated using Levins' index (1968) from the absolute frequencies (p_i) of the number of prey categories (n):

$$B = \frac{1}{\sum p_i^2} \quad (3)$$

We standardized the scale from 0 to 1 to compare the rates of niche breadth among species of *Pristimantis*, where 0 correspond to specialist species and 1 generalist species (Pereira *et al.*, 2004). We used the formula of Levins' standardized index (Krebs, 1989) from the value calculated above (3) and the number of prey categories (n):

$$B_s = \frac{B-1}{n-1} \quad (4)$$

Niche overlap was performed on *Pristimantis* species with $n \geq 5$ individuals focusing on species with sympatric distributions according to Lynch (1998b), and constructing a numerical abundance dietary matrix of prey items using Pianka index (Pianka, 1974):

$$\Phi_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}} \quad (5)$$

Where Φ_{jk} = niche overlap between species j and k , P_{ij} and P_{ik} = proportions of predator j and k with prey i in their stomachs or digestive tracts. Diet overlap increases as the Pianka index increases and overlap is generally considered to be significantly when greater than 0.60 (Zaret and Rand, 1971; Calderón-Arguedas and Troyo, 2007).

RESULTS Diet composition

We examined 154 gastrointestinal tracts from 15 species of *Pristimantis* ([Supplementary Table S1](#)), of which only 13 gastrointestinal tracts were found empty. A total of 499 prey items were identified and placed into 74 categories ([Table S1](#)): two classes, 14 orders, four suborders, 53 families, and one category named "other arthropods" (OA) when identification was not possible. Occasionally, plant materials were found such as leaves, branches or seeds. Overall, for the species studied, between one (*P. quantus* and *P. w-nigrum*) and 38 (*P. palmeri*) prey categories were found. Sample sizes of *P. calcaratus*, *P. achatinus*, *P. juanchoi*, and *P. w-nigrum* were small (1 – 3 individuals) and a few prey items were found (1 – 7 items; [Table S1](#)). Araneae was the most frequent category found in gastrointestinal tracts. Ten of the 15 frog species had at least one item of Araneae, followed by Coleoptera and Tipulidae (nine frog species), and Acari and Carabidae (eigth frog species).

The prey items with the highest frequency of occurrence (% O) were found within the families Isotomidae (35.1 %), Chironomidae (26 %), and Formicidae (20.8 %). These items were mainly found in *Pristimantis* sp., *P. acatallelus*, *P. hectus* and *P. palmeri*. However, Formicidae was the most abundant item in *P. myops* (25 %), *P. erythropleura* (15.6 %), and *P. orpacobates* (15.6 %). Dipterans were the most abundant arthropods (25.7 %) followed by arachnids (16.6 %), coleopterans (13.4 %), and hymenopterans (11 %). Species with high amount of dipterans in their diet were *P. hectus* (32 items), *P. acatallelus* (23 items), *P. brevifrons* (16 items), *P. palmeri* (16 items), *P. jubatus* (13 items) and *P. angustilineatus* (10 items). *Pristimantis palmeri* and *P. jubatus* contained the greatest amount of coleopterans (22 and eight items, respectively) and hymenopterans (15 and 11 items, respectively), while *P. jubatus* and *P. acatallelus* contained most of the prey items in Araneae (10 and nine items, respectively). Beetles were observed in gastrointestinal tracts for all species with the exception of *P. quantus*, but only one specimen was collected for this species.

Intermediate and high values of niche breadth standardized index were found for most of the *Pristimantis* species evaluated, indicating a generalist diet ([Table 1](#)). However, *P. hectus* showed a specialized diet, consuming mainly dipterans of the family Chironomidae; almost half of the items (28 of 57 items) found in *P. hectus* were identified as belonging to this family. Furthermore, eight species showed exclusive consumption for some prey categories ([Table S1](#)). For example, Anapidae, Silvanidae, Neelidae, Forficullidae, Dipsocoridae, and Diplopoda were only consumed by *P. acatallelus*; Scarabeidae, Anobiidae, and Otitidae were only found in *P. brevifrons*; Tenebrionidae, Elateridae, Membracidae, Chalcididae, and Apocrita were exclusively found within *P. jubatus* individuals, while Bostrichidae, Miridae, Meinertellidae, Opiliones, and Homoptera were found in *P. palmeri*.

TABLE 1. Diet breadth of *Pristimantis* from the Western Cordillera. *n* – total number of prey categories found in each species; B – Levins' index of niche breadth; Ba – Levins' standardized index of niche breadth.

Species	n	B	Ba
<i>P. acatallelus</i>	26	12.24	0.45
<i>P. angustilineatus</i>	12	5.76	0.43
<i>P. brevifrons</i>	26	17.92	0.68
<i>P. erythropleura</i>	20	13.84	0.68
<i>P. hectus</i>	18	3.81	0.17
<i>P. jubatus</i>	32	22	0.68
<i>P. myops</i>	12	8	0.64
<i>P. orpacobates</i>	20	13.47	0.66
<i>P. palmeri</i>	38	20.15	0.52

Three niche overlaps were discovered among species evaluated (Table 2): *P. palmeri* vs *P. erythropleura* ($\Phi_{jk} = 0.69$), *P. palmeri* vs *P. myops* ($\Phi_{jk} = 0.64$), and *P. palmeri* vs *P. orpacobates* ($\Phi_{jk} = 0.64$). *Pristimantis palmeri* shared with *P. erythropleura*, *P. myops* and *P. orpacobates* a large amount of food items in the categories Formicidae, Acari, Araneae, Coleoptera, and Tipulidae.

TABLE 2. Niche overlap of *Pristimantis* species examined from southwestern Colombia. * – Significant diet overlap according to Pianka's index (> 0.6). Values in shaded cells correspond to non-sympatric species following Lynch (1998b).

	A	B	C	D	E	F	G	H	I
<i>P. acatallelus</i> (A)	1.00	0.27	0.40	0.33	0.38	0.22	0.28	0.23	0.016
<i>P. hectus</i> (B)		1.00	0.17	0.086	0.20	0.10	0.097	0.12	0.37
<i>P. jubatus</i> (C)			1.00	0.33	0.55	0.4	0.41	0.30	0.40
<i>P. angustilineatus</i> (D)				1.00	0.55	0.14	0.46	0.25	0.27
<i>P. brevifrons</i> (E)					1.00	0.44	0.49	0.35	0.56
<i>P. erythropleura</i> (F)						1.00	0.53	0.53	0.69*
<i>P. myops</i> (G)							1.00	0.58	0.64*
<i>P. orpacobates</i> (H)								1.00	0.64*
<i>P. palmeri</i> (I)									1.00

DISCUSSION

The diet of *Pristimantis* is composed of a variety of arthropods but mostly dipterans (128 total items), arachnids (83 total items), collembolans (70 total items), coleopterans (67 total items), and hymenopterans (55 total items) which are abundant in leaf litter (especially collembolans, spiders and beetles of the family Carabidae) and low vegetation (Johnson and Catley, 2005). While most species in our study were generalists, *P. hectus* has a specialist diet consuming mainly dipterans, which are an abundant food resource in tropical rainforests (Didham, 1997). *Pristimantis hectus* has a diurnal foraging activity in low vegetation below 50 cm (Lynch and Duellman, 1997; García-R *et al.*, 2005; García-R and Lynch, 2006). These characteristics, diurnal activity and foraging in low strata, may offer an opportunity for niche partitioning and prevent food competition with species that are nocturnal.

Dietary overlaps of *P. palmeri* among *P. erythropleura*, *P. myops* and *P. orpacobates* suggest that these species may compete for food. However, this competitive pressure might be reduced if there are differences in prey size in relation to body size within and between species, as it is common in other vertebrates (Ashmole, 1968; Dickman, 1988; Weise *et al.*, 2010), and if each frog species use different microhabitat strata. For instance, *P. myops* is a minute frog with a snout-vent length in males of 10 – 13 mm and females of 14 – 17 mm (Lynch, 1998b), while males of *P. palmeri* are approximately 20 mm and females 28 mm (Bolívar-G *et al.*, 2011). A

difference of twice the size may suggest that *P. palmeri* can eat larger prey items than *P. myops* and thereby avoid direct competition. In addition, ants are the main prey among these species, a source readily available, since they live in colonies and are slow and therefore easy to catch. Likewise, ants have a low nutrient content (Parmelee, 1999) and their chitinous body make them difficult to digest (Toft, 1985), which is probably the reason of large quantities consumed.

Terrarana frogs in South America (Table 3) have shown a wide spectrum of prey types with predominance of coleopterans and hymenopterans in their diets, including previous studies of *Pristimantis* in the Eastern Cordillera from the Andes of Colombia (Piñero and Durant, 1993; Parmelee, 1999; Menendez-Guerrero, 2001; Guayasamin *et al.*, 2004; Arroyo *et al.*, 2008; Dietl *et al.*, 2009; Castro and Gutiérrez, 2011). Montane frogs are mainly insectivore generalists that choose their prey depending on microhabitat preferences and food availability (Ortega *et al.*, 2005; Arroyo *et al.*, 2008). However, the presence and abundance of prey items may vary by elevation and dominant vegetation type at each site. For example, according to Parmelee (1999), ants are an important component of the diet of several species of *Pristimantis* in lowland Amazonia. In contrast, ants provided a small contribution to the diet of the montane *Pristimantis* species studied here and did not contribute much to the diet of other species studied at high elevations (Table 3). The small contribution of ants in frog's diet at high altitudes is better explained by low ant density in montane forests compared to sub-montane and lowlands forests. Lower temperatures may affect ants' larvae development and food acquisition because of the low availability of food resources (Basset, 2001). Alternatively, it is also possible that the trophic opportunism for ants is more gradated within ecologically complex *Pristimantis* assemblages in relatively highland habitats.

TABLE 3. Diet composition of Terrarana frogs in South America. Type of forest refers to the habitat in the geographical range of the species studied. First, second and third prey categories refer to contribution in each species.

Species	Type of forest	1st prey	2nd prey	3th prey	Source
<i>Pristimantis douglasi</i>	Montane forest	Isopoda	Araneae	Coleoptera	Arroyo <i>et al.</i> , (2008)
<i>P. merostictus</i>	Montane forest	Coleoptera	Araneae	Isopoda	Arroyo <i>et al.</i> , (2008)
<i>P. mijatai</i>	Montane forest	Collembola	Coleoptera	Isopoda	Arroyo <i>et al.</i> , (2008)
<i>P. vanadise</i>	Montane forest	Coleoptera	Diptera		Piñero and Durant (1993)
<i>P. eugeniae</i>	Montane forest	Coleoptera	Araneae	Hemiptera	Guayasamin <i>et al.</i> , (2004)
<i>P. factiosus</i>	Montane forest	Araneae	Hymenoptera		Castro and Gutiérrez (2011)
<i>P. viejas</i>	Montane forest	Hymenoptera	Araneae		Castro and Gutiérrez (2011)
<i>P. imitatrix</i>	Lowland forest	Coleoptera	Orthoptera		Parmelee (1999)
<i>P. toftae</i>	Lowland forest	Orthoptera	Coleoptera	Hymenoptera	Parmelee (1999)
<i>P. peruvianus</i>	Lowland forest	Orthoptera			Parmelee (1999)
<i>P. fenestratus</i>	Lowland forest	Orthoptera	Blattodea		Parmelee (1999)
<i>P. ockendeni</i>	Lowland forest	Orthoptera	Hemiptera	Coleoptera	Menéndez-Guerrero (2001)
<i>Ischnocnema henselii</i>	Lowland forest	Araneae	Hymenoptera	Orthoptera	Dietl <i>et al.</i> , (2009)

CONCLUSION

Species of *Pristimantis* distributed in the montane regions of southwestern Colombia present a wide range of items consumed without strong differences in diet composition. The similarity of diets, however, did not indicate a marked competition because the high availability of food resources, suggesting an important factor for coexistence.

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