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Trophic and spatial ecology of *Pristimantis relictus* (Anura: Strabomantidae) in Atlantic Forest remnants of northeastern Brazil

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Abstract

Trophic and spatial ecology of *Pristimantis relictus* (Anura: Strabomantidae) in Atlantic Forest remnants of northeastern Brazil. Natural history studies offer insights into the behavior and interactions of species in various environments, which are crucial for conservation and preservation. *Pristimantis relictus* is a newly described Robber Frog endemic to the isolated mountains of Ceará state, northeast Brazil. Limited information on its ecology is currently available. Herein we describe the feeding habits and microhabitat use of this species from three mountains in Ceará state. We also performed a literature review of the prey items consumed by other species in the genus *Pristimantis* in the Americas. In general, *P. relictus* is a generalist in terms of microhabitat use, foraging in herbaceous plants, on the ground, trees, and shrubs, and for diet, consuming a wide range of prey groups, with beetles and larvae the most common prey. This plasticity of dietary and microhabitat use may be crucial for the persistence and geographic distribution of this species, including their response to environmental changes. The large variety of prey categories utilized by species of *Pristimantis* suggests a generalist diet that may reflect prey diversity in the environment.

Keywords: Amphibians, Diet composition, Food network, Microhabitat use.

Resumo

Ecologia trófica e espacial de *Pristimantis relictus* (Anura: Strabomantidae) em remanescentes de Mata Atlântica do nordeste do Brasil. Estudos de história natural oferecem informações sobre o comportamento e as interações de espécies em vários ambientes, que são cruciais para a conservação

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e preservação. *Pristimantis relictus* é uma perereca recém-descrita, endêmica das montanhas isoladas do estado do Ceará, nordeste do Brasil. Informações limitadas sobre sua ecologia estão disponíveis atualmente. Aqui, descrevemos os hábitos alimentares e o uso de micro-hábitats dessa espécie em três montanhas no estado do Ceará. Também realizamos uma revisão da literatura sobre as presas consumidas por outras espécies do gênero *Pristimantis* nas Américas. De modo geral, *P. relictus* é generalista em termos de uso de microhabitat, forrageando em plantas herbáceas, no solo, árvores e arbustos, e em termos de dieta, consumindo uma ampla gama de grupos de presas, com besouros e larvas sendo as presas mais comuns. Essa plasticidade do uso dietético e de microhabitat pode ser crucial para a persistência e a distribuição geográfica dessa espécie, incluindo sua resposta a mudanças ambientais. A grande variedade de categorias de presas utilizadas pelas espécies de *Pristimantis* sugere uma dieta generalista que pode refletir a diversidade de presas no ambiente.

Palavras-chave: Anfíbios, Composição da dieta, Rede alimentar, Uso de micro-hábitats.

Introduction

Amphibians are one of the most diverse groups of vertebrates, inhabiting a wide range of microhabitats around the world (Frost 2024). Despite their high diversity, some areas of the world remain poorly explored. Amphibians are at a greater risk of extinction than any other vertebrate group (Wake and Koo 2018), mainly due to human impacts (Sodhi *et al.* 2008). Natural history studies provide a good tool to understand how these frogs interact with others and with the environment and provide a starting point for studies aiming at conservation and preservation (Solé and Rödder 2010, Michaels *et al.* 2014), although relatively little is known about the natural history of most anurans.

Feeding habits form a significant aspect of the natural history of a species (Duellman and Trueb 1994). In amphibian populations, diet composition varies considerably, depending on the species, habitat, and environmental conditions, among other variables (Toft 1981, Duellman and Trueb 1994, Blanco-Torres *et al.* 2020). Some species, such as *Elachistocleis bicolor* (Guérin-Méneville, 1838), are ant specialists (López *et al.* 2007), and others feed on fruits, flowers, and nectar, such as *Xenohyla truncata* (Izecksohn, 1959) (Silva and Britto-Pereira 2006, Oliveira-Nogueira *et al.* 2023), but most anurans are carnivores, generalists, and opportunistic predators (Toft 1981). These animals are components of different food webs, sometimes as predators (Ceron *et al.* 2019) and sometimes as prey (Brown and Shine 2002).

The genus *Pristimantis* Jiménez de la Espada, 1870, comprised of 612 species, is one of the most diverse groups of terrestrial frogs. They occur from Honduras eastward through Central America to Colombia and Ecuador to Peru, Bolivia, northern Argentina, the Amazonian and Atlantic Forests of Brazil, and the Guianas; Trinidad and Tobago; and Grenada, Lesser Antilles (Frost 2024). In addition, some populations of these direct-developing frogs also occur in rainforest enclaves in the Caatinga biome (Roberto *et al.* 2022). Despite this high species diversity and some natural history studies (e.g., Arroyo *et al.* 2008, Hutter *et al.* 2016, Alves-dos-Santos *et al.* 2021), there is a lack of information concerning the ecological characteristics of some species of *Pristimantis.*

Species of *Pristimantis* are diet generalists and feed opportunistically on dipterans, arachnids, collembolans, coleopterans, and hymenopterans, among other invertebrates (García-R *et al.* 2015, Arroyo *et al.* 2008). In Brazil, *P. paulodutrai* (Bokermann, 1975) (Alves-dos-Santos *et al.* 2021) and *P. ramagii* (Boulenger, 1888) (Leite-Filho *et al.* 2017, Caldas *et al.* 2019) were generalists with an opportunistic diet. Relatively little is known about other species, including the newly described *Pristimantis relictus* Roberto, Loebmann, Lyra, Haddad, and Ávila, 2022. Herein we describe its microhabitat and diet composition and test the hypothesis that larger frogs tend to eat larger prey items. We also provide a literature review of the most frequently consumed prey items by species of *Pristimantis* in the Americas.

Materials and Methods

Study Area

Our study area included three mountains located in the state of Ceará (Figure 1), northeastern Brazil: Baturité (-4.20547° S, -38.96047° W; datum WGS84; elevation: 900 m), Maranguape (-3.90464° S, -38.72051° W; datum WGS84; elevation: 920 m), and Meruoca (3.54769° S, -40.4486° W; datum WGS84; elevation: 800 m). These mountain chains have rainforest enclaves called "Brejos de altitude" in the midst of the xerophytic vegetation of the Caatinga (Andrade-Lima 1982). They receive high and evenly distributed rainfall (Medeiros and Cestaro 2019) and support three main vegetation types: humid forests found at high elevations, dry forests at mid-elevations, and caatinga in the lowlands (Moro *et al.* 2015).

Anuran Sampling

We manually collected adult individuals of *P. relictus* (Figure 2) using visual and auditory searches (Heyer *et al.* 1994) at night (17:30 to 00:00 h) from February to May 2019.We collected for 15 days in each mountain, totaling 45 days of sampling. For each anuran, we recorded the substrate on which it was found (herbaceous plants, on the ground, trees, and shrubs). All collected individuals were euthanized (Permit: ICMBio 72384, process: 29613) following resolution No. 37 (CONCEA 2018), fixed in 10% formalin, and preserved in 70% alcohol. Voucher specimens are held at the Núcleo Regional de Ofiologia of the Universidade Federal do Ceará, Fortaleza, Brazil (CHUFC

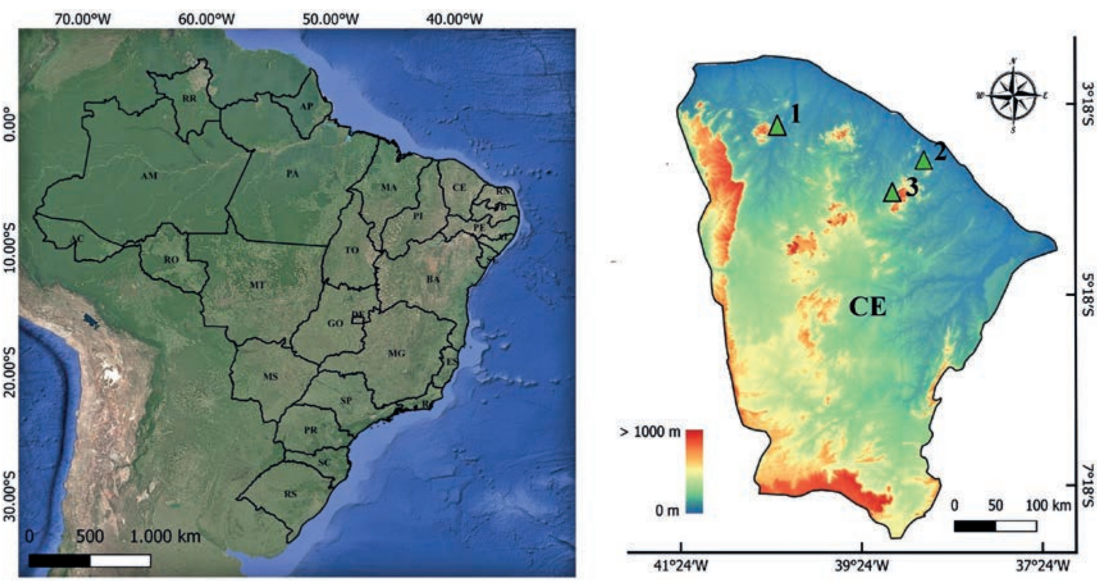

Figure 1. Schematic map of the mountains of Meruoca (1), Maranguape (2), and Baturité (3), where individuals of *Pristimantis relictus* were collected. Green triangles represent the sampled mountains in Ceará state (CE), northeast Brazil.

11726–11732, 12025, 12026, 12029–12033, 12035, 12039–12042, 12049, 12051, 12052, 12833, 12838, 12840, 12843, 12844, 12847, 12851, 12852, 12854, 12856, 12858, 12859, 12862, and 12864).

Data Analyses

In the laboratory, we measured snout–vent length (SVL) and mouth width with a digital caliper (0.01 mm precision) for each specimen. Using a central incision, we removed and identified stomach contents. Prey items were identified to the lowest taxonomic level using the most recent literature in Brazil (Rafael *et al.* 2024). We measured the length and width of each prey item with a digital caliper (accuracy 0.01 mm) and used the ellipsoid formula $V = (4/3)\ \pi\ (L/2)\ (W/2)^2$, where V = volume, L = length, and W width (Dunham 1983) to calculate prey volume. To investigate the relative contribution of each prey category, we used the Index of Relative Importance [IRI = (*F*% + *N*% + V%)/3], where *F*% is the percentage of occurrence, *N*% is the numeric percentage, and V% is the volumetric percentage of each prey item (Powell *et al.* 1990).

We used the Kruskal–Wallis H test to investigate whether the microhabitats used (herbaceous, trees, soil, and shrubs) by *P. relictus* differed between the three mountains studied and used bar plots to show these differences. Regarding diet composition, we used sample-based accumulation curves with 1000 randomizations from an incidence matrix (Gotelli and Colwell 2001) to evaluate whether our sampling methods were satisfactory to estimate the prey composition. The estimators Jackknife 1 and Chao 1 were used to investigate the expected prey richness. Non-parametric Kernel regression test examined how the volume of each prey ingested related to SVL and mouth width.

To compile the most frequently consumed prey items by species of *Pristimantis* in the Americas, we performed literature searches in scientific publications available from seven electronic databases (Google, Google Scholar, PubMed, Scielo, Science Direct, Scopus, and Web of Science) using the following keywords in English and Portuguese: America, Brazil, Craugastoridae, diet composition, *Eleutherodactylus,* feeding habits, Pristimantinae, *Pristimantis,* South America, and Strabomantidae. We constructed a matrix of presence and absence data of prey categories for 29 species of *Pristimantis* distributed in five countries (Brazil, Colombia, Ecuador, Peru, and Venezuela) in South America, and we used a network graph to explore this prey diversity. Statistical analyses were done using the R packages bipartite (Dormann *et al.* 2009), igraph (Csardi and Nepusz 2006) and vegan (Oksanen *et al.* 2016).

Figure 2. Adult male of *Pristimantis relictus* in Mt. Maranguape, Ceará state, northeastern Brazil.

Results

We observed 89 individuals of *P. relictus,* with 34 foraging on herbaceous plants, 33 on the ground, 13 in trees, and nine in shrubs. We did

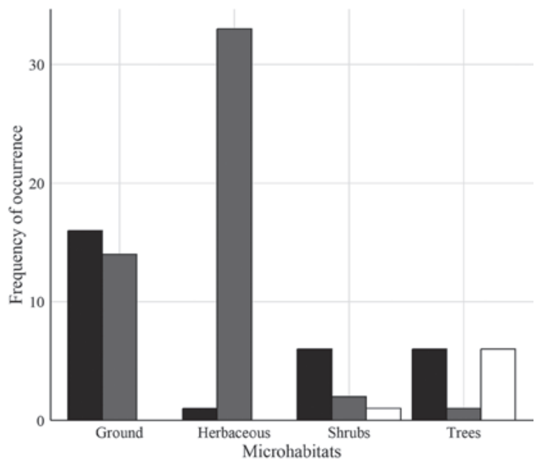

Figure 3. Microhabitats used by *Pristimantis relictus* in rainforest enclaves in Ceará state, northeastern Brazil. White, black, and gray columns represent the mountains of Meruoca, Baturité, and Maranguape, respectively.

not find sufficient evidence to state that the usage of these microhabitats varied significantly among the three mountains (H = 3.6137, P = 0.1642). Despite this result, the individuals collected on Mt. Maranguape were associated more frequently with herbaceous vegetation and on the ground, whereas those collected on Mt. Baturité were more frequently associated with shrubs, and those from Mt. Meruoca were more frequently associated with trees (Figure 3).

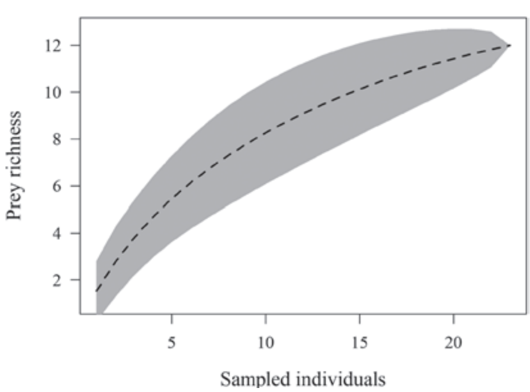

Figure 4. Accumulation curve of the prey items consumed by *Pristimantis relictus* in the studied mountains.

Of the 89 observed individuals, we collected 48 (20 males and 28 females), of which 31 (10 males and 21 females) had full stomachs (65%). Prey diversity was high (12 prey categories), with beetles (IRI = 26.2) and larvae (IRI = 22.3) the most consumed prey items (Table 1). Pieces of plants were found in the stomachs of seven individuals. Our accumulation curve did not reach the asymptote (Figure 4), in which the estimators Jackknife 1 and Chao 1 indicated around four (15.8 ± 1.91) and two (13.9 ± 2.54) more prey categories, respectively, in the diet composition of *P. relictus* at the sampled sites.

We recorded only five prey types in males (Acaridae, Formicidae, Gastropoda, larvae, and plant pieces), whereas 11 prey items were found in female stomachs (Acaridae, Aranae, Blattaria, Coleoptera, Dermaptera, Diptera, Formicidae, Hemiptera, Orthoptera, larvae, and plant pieces). Discrepancies between males and females sampled prohibited intersexual statistical analyses. Neither anuran SVL (R = 0.171, $p > 0.05$) or mouth width (R = 0.307, $p > 0.05$) influenced the choice of prey volume.

Our literature search revealed a generalist pattern of diet composition for the genus *Pristimantis* with 25 prey categories recorded for 29 species distributed in five countries from the Americas. The most frequently consumed items were Coleoptera, Araneae, Diptera, Formicidae, Blattaria, and Orthoptera. Overall, the prey number found in each species ranged from one to 16 (Figure 5, Appendix I).

Discussion

Pristimantis relictus occurs only in the "Brejos de Altitude" of Ceará state in northeastern Brazil. It usually lives in dry and wet forests (Roberto *et al.* 2022).

Some individuals were found near disturbed sites; for example, at Mt. Meruoca, most

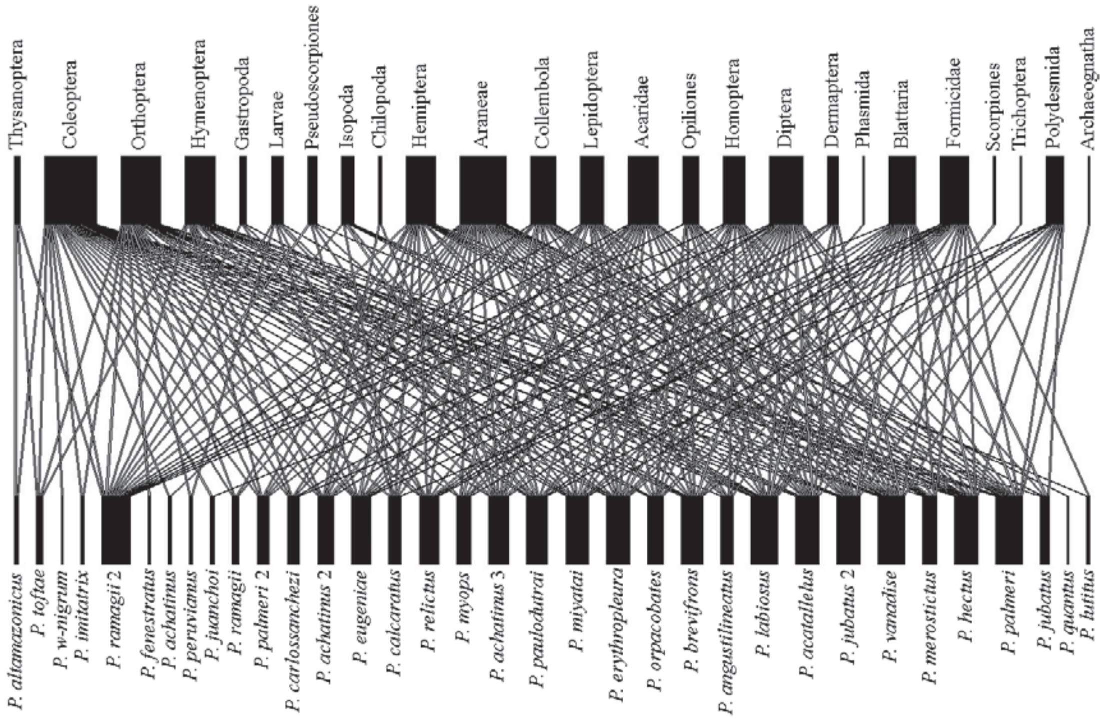

Figure 5. Bipartite network diagram representing predator-prey interactions among different species of the genus *Pristimantis.* The bar width of the predators (left side column, with *Pristimantis* species names) represents niche breadth, and the bar width of the prey (right side column, with arthropod order names) is the level of importance for the diet of the species of *Pristimantis.*

individuals were primarily found in bamboo trees. Although the microhabitat used by *P. relictus* did not vary significantly among the mountains, most individuals at Mt. Baturité were located on the ground. In contrast, at Mt. Maranguape, individuals were predominantly found in herbaceous plants (Figure 2). This plasticity of microhabitat use was observed in other *Pristimantis* species (e.g., Arroyo *et al.* 2008). Direct-developing frogs do not need lentic ponds to reproduce because they have terrestrial eggs and lack a free-living larval stage (Wells 2007, Padial *et al.* 2014), which makes them habitat generalists.

Pristimantis relictus consumed high prey diversity, indicating that it is a generalist predator as observed in most congenerics (e.g., Arroyo *et al.* 2008, García-R *et al.* 2015, Gutiérrez-Cárdenas *et al.* 2016, Alves-dos-Santos *et al.* 2021). Coleopterans and larvae were the most common prey, as observed in other congenerics such as *P. altamazonicus* (Barbour and Dunn, 1921), *P. imitatrix* (Duellman, 1978), *P. toftae* (Duellman, 1978) (e.g., Parmelee 1999), *P. eugeniae* (Lynch and Duellman, 1997) (e.g., Guayasamin *et al.* 2004), and *P. labiosus* (Lynch, Ruiz-Carranza, and Ardila-Robayo, 1994) (e.g., Gutiérrez-Cárdenas *et al.* 2016). Beetles are usually abundant and diverse in the environment, in addition to being difficult to digest. Insect larvae are abundant during the rainy season (Leite-Filho *et al.* 2015),

Table 1. Diet composition of *Pristimantis relictus* from rainforest enclaves in Ceará state, northeastern Brazil. The absolute values and proportion (%) number (*N*), frequency of occurrence (*F*), volume (V) and index of relative importance (IRI) are given. *Prey items consumed exclusively by males, ** prey items consumed exclusively by females.

Prey category	*N*	*N*%	V	V%	*F*	*F*%	IRI
Arachnida							
Acaridae	8	22.2	3.21	0.15	4	14.2	12.2
Aranae**	1	2.78	8.38	0.38	1	3.57	2.24
Insecta							
Blattaria**	2	5.56	47.5	2.18	2	7.14	4.96
Coleoptera**	10	27.7	407.5	18.6	9	32.1	26.2
Dermaptera**	1	2.78	5.75	0.26	1	3.57	2.20
Diptera**	1	2.78	68.4	3.14	1	3.57	3.16
Formicidae	5	13.8	84.8	3.89	2	7.14	8.31
Gastropoda*	1	2.78	31.6	1.45	1	3.57	2.60
Hemiptera**	2	5.56	217.0	9.95	2	7.14	7.55
Orthoptera**	2	5.56	258.3	11.8	2	7.14	8.18
Other Items							
Larvae	3	8.33	1049.8	48.1	3	10.7	22.3

coinciding with the anuran reproductive period. Larvae are a great energy source because of their nutritional content (Marconi *et al.* 2002). Of the 31 individuals, seven had plant pieces in their stomachs, which may be consumed unintentionally during arthropod predation (Hirai and Matsui 1999, Brito *et al.* 2012). The hypothesis of accidental consumption is supported by our findings because plant material was consistently associated with the consumption of other food items and was recorded in a smaller number of individuals. However, consumption of plant material may be beneficial for anurans because it can aid digestion or provide a supplementary source of nutrients and water (Anderson *et al.* 1999). The role of plant material in the diet of *P. relictus* requires further investigation.

We found no relationship between prey volume and SVL or mouth width, as reported for other anurans (e.g., Lima *et al.* 2010, Sabagh *et al.* 2012, Solé *et al.* 2009, 2019), including *P. labiosus* (Gutiérrez-Cárdenas *et al.* 2016). This relationship is typically more apparent when comparing adults and juveniles (Solé and Rödder 2010). The absence of a relationship between anuran size and prey volume may occur when only adult individuals are sampled (Sugai *et al.* 2012), as in the present study. In addition to this discussion, foraging strategy might be the most important driver of prey selection by anurans (Blanco-Torres *et al.* 2020). Our findings suggest that *P. relictus* eats whatever is available in the environment with no prey selectivity; consequently, SVL and mouth width do not appear to be key factors for prey selection.

Although discrepancies between sampled males and females inhibited intersexual analyses, we observed that females consumed a higher prey diversity (10 prey types) compared with males that consumed just five prey types, of which Gastropoda was found only in males. Differences in selectivity of some prey items between males and females may be the result of chance (Sugai *et al.* 2012) given the generalist diet pattern observed. Similarity in other prey items may reflect prey availability in the environment (Sant'Anna *et al.* 2022). Further studies with larger sample sizes are needed to understand intersexual variation in this species.

We observed that species of *Pristimantis* have a generalist diet and consume a high diversity of prey, which is probably a phylogenetically conserved trait (Alves-dos-Santos *et al.* 2021). The various studies were carried out in different locations and periods, which might have contributed to high prey diversity. Among them, *P. ramagii* consumed the highest prey diversity (Leite-Filho *et al.* 2017), whereas *P. quantus* (Lynch, 1998) and *P. w-nigrum* (Boettger, 1892) consumed the lowest, likely because just one individual of each species was examined (García-R *et al.* 2015). In general, the most commonly consumed prey items were Coleoptera, Araneae, Diptera, Formicidae, Blattaria, and Orthoptera, which are frequently found in diets of anurans. This study supports a generalist diet in species of *Pristimantis.*

Pristimantis relictus is a generalist species regarding microhabitat use and feeding habits, which can be linked. As individuals explore different microhabitats, they encounter different prey categories. This plasticity in diet and microhabitat use may be crucial for their persistence and geographic distribution, including their response to environmental changes. In addition, the large variety of prey categories observed in species of *Pristimantis* may suggest a generalist diet, with individuals consuming a high prey diversity wherever they forage. Our study contributes to the understanding of the natural history of the recently described and endemic mountain frog *P. relictus.*

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Appendix I. *The most common prey items in the diet of species of* Pristimantis *in the Americas.*

Species	First Prey	Second Prey	Third Prey	Country	References
P. acatallelus	Diptera	Collembola	Araneae	Colombia	García-R *et al.* 2015
P. achatinus	Araneae	Coleoptera	-	Colombia	García-R *et al.* 2015
P. achatinus 2	Coleoptera	Hymenoptera	Hemiptera	Colombia	Hoyos-Hoyos *et al.* 2012
P. achatinus 3	Coleoptera	Hymenoptera	Araneae	Colombia	Moreno-Barbosa and Hoyos-Hoyos 2014
P. altamazonicus	Thysanoptera	Coleoptera	-	Peru	Parmelee 1999
P. angustilineatus	Diptera	Araneae	Homoptera	Colombia	García-R *et al.* 2015
P. brevifrons	Diptera	Coleoptera	Araneae	Colombia	García-R *et al.* 2015
P. calcaratus	-	-	-	Colombia	García-R *et al.* 2015
P. carlossanchezi	Coleoptera	Araneae	-	Colombia	Arroyo *et al.* 2008
P. erythropleura	Araneae	Formicidae	Diptera	Colombia	García-R *et al.* 2015
P. eugeniae	Coleoptera	Araneae	Hemiptera	Ecuador	Guayasamin *et al.* 2004
P. fenestratus	Orthoptera	-	-	Peru	Parmelee 1999
P. hectus	Diptera	Coleoptera	Araneae	Colombia	García-R *et al.* 2015
P. imitatrix	Coleoptera	Orthoptera	-	Peru	Parmelee 1999
P. juanchoi	Coleoptera	Blattaria	-	Colombia	García-R *et al.* 2015
P. jubatus	Araneae	Hymenoptera	Acari	Colombia	García-R *et al.* 2015
P. jubatus 2	Diptera	Hymenoptera	Araneae	Colombia	García-R *et al.* 2012
P. labiosus	Hymenoptera	Hemiptera	Orthoptera	Colombia	Gutiérrez-Cárdenas *et al.* 2016
P. lutitus	Formicidae	Hemiptera	-	Colombia	Arroyo *et al.* 2008
P. merostictus	Coleoptera	Araneae	Formicidae	Colombia	Arroyo *et al.* 2008
P. miyatai	Collembola	Coleoptera	Formicidae	Colombia	Arroyo *et al.* 2008
P. myops	Diptera	Formicidae	Hymenoptera	Colombia	García-R *et al.* 2015
P. orpacobates	Coleoptera	Araneae	Formicidae	Colombia	García-R *et al.* 2015
P. palmeri	Coleoptera	Diptera	Blattaria	Colombia	García-R *et al.* 2015
P. palmeri 2	Hymenoptera	Hemiptera	Araneae	Colombia	Hoyos-Hoyos *et al.* 2012
P. paulodutrai	Araneae	Isopoda	Formicidae	Brazil	Alves-dos-Santos *et al.* 2021
P. peruvianus	Orthoptera	Larvae	-	Peru	Parmelee 1999
P. quantus	Araneae	-	-	Colombia	García-R *et al.* 2015
P. ramagii	Coleoptera	Hemiptera	Araneae	Brazil	Caldas *et al.* 2019
P. ramagii 2	Hemiptera	Formicidae	Orthoptera	Brazil	Leite-Filho *et al.* 2017
P. relictus	Coleoptera	Larvae	Acaridae	Brazil	**Present study**
P. toftae	Orthoptera	Coleoptera	-	Peru	Parmelee 1999
P. vanadise	Coleoptera	Diptera	Acari	Venezuela	Piñero and Durant 1993
P. w-nigrum	Coleoptera	-	-	Colombia	García-R *et al.* 2015