

Diet, microhabitat and time of activity in a *Pristimantis* (Anura, Strabomantidae) assemblage

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Abstract

Diet, microhabitat and time of activity in a *Pristimantis* (Anura, Strabomantidae) assemblage. We tested if the richness and abundance of six closely related species of *Pristimantis* significantly varied among three transects located at different distances from a creek in an Andean cloud forest. We found that richness and abundance of frogs varied significantly among transects, being the transect located at the forest interior the richest in frog species and number of individuals. We chose these more crowded sites to evaluate resource use differences among the species. We evaluated ecological variables such as microhabitat, diet, and time of activity in these species that are similar in morphology and body size, to determine whether they have differences in the use of these resources. Most specimens perch on leaves at heights within 1.5 and 2.0 m of the ground and are nocturnal; only *P. douglasi* was found with diurnal and nocturnal activity. The species had similar diets, they ingested a wide spectrum of prey sizes that are similar among species, months, and between transects. Almost all collected frogs were juveniles and were found during every single month of sampling suggesting continuous reproduction; however, adults and juveniles of *P. douglasi* were absent during some of the drier months, indicating seasonality. Thus, we found that most of these *Pristimantis* species occupy the forest interior and that there is no a strong segregation in the use of the evaluated resources, only one species had a slight difference in activity and reproductive time.

Keywords: Anura, Strabomantidae, Andean anurans, cloud forest, resource segregation.

Introduction

Within an ecological community or local assemblage, sympatric species should differ substantially in body size or in other aspects of

morphology (Hutchinson 1959, Grant 1972). Morphological similarity among coexisting animal species sets the stage for potential interactions that may lead to competition and niche segregation (Huey and Pianka 1977). Morphologically similar species are more likely to interact than dissimilar species simply because a major portion of the behavioral and ecological activities of animals are linked with morphology (Ricklefs *et al.* 1981, Losos 1990).

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In an Andean cloud forest of the Cordillera Oriental of Colombia, we found an assemblage of ten species of *Pristimantis* (*P. anolirex*, *P. bicolor*, *P. carlossanchezi*, *P. douglasi*, *P. jorgevelosai*, *P. lutitus*, *P. merostictus*, *P. miyatai*, and one undescribed species, *Pristimantis* sp. 1) (Arroyo *et al.* 2003). Six of these species are easily found (*P. carlossanchezi*, *P. douglasi*, *P. lutitus*, *P. merostictus*, *P. miyatai*, and *Pristimantis* sp. 1), whereas the other four species are rare in this locality. Four of these species belong to the *P. unistrigatus* group (Lynch 1984), whereas *P. carlossanchezi* belongs to the taxonomic *P. conspicillatus* group (Arroyo 2007) and *P. douglasi* belongs to the *P. galdi* phylogenetic group (Lynch 1996). The adult individuals of these six species are similar in body size and in morphology; in fact we need to do a morphometric analysis to differentiate taxonomically these species (Arroyo *et al.* 2005).

We evaluated the diet, microhabitat, and time of activity of these six *Pristimantis* species in order to determine whether these species differ in the use of these resources. Furthermore, we evaluated these resources across the sampling months to determine seasonal variation. Because nothing is known about natural history and differences in trophic and other niches in sympatric assemblages of *Pristimantis*, we presented these fundamental data herein.

Materials and Methods

Study area

The study was conducted at the Estación Experimental y Demostrativa El Rasgón, in the Municipality of Piedecuesta, Departamento de Santander, Colombia (07°03' N, 72°57' W, 2400 m elevation). The area is a cloud forest reserve, located on the western flank of the northern Cordillera Oriental. Mean annual rainfall is 1645 mm and the mean temperature is 15.02°C. The rainfall regime is bimodal, with one peak in

April–May and a second peak in October. November to March and July to August are the months with the lowest rainfall.

Frog sampling and ecological data collection

Frogs were surveyed by transects (Heyer *et al.* 1994). The use of transects is related to topography; the area has marked slopes that facilitates the use of transects preferably to quadrats. Transects can provide data of species presence/absence, richness, relative abundance, and density (number of individuals/area surveyed). We established three different transects of 100 x 2 m. One transect was located in the forest interior (200 m from the next creek and forest edge, Interior Forest Transect); the second was located in a creek (Creek Transect), and the third transect was parallel to it, 20 m above the creek (Parallel Creek Transect). These three sites have differences in the vegetation and were surveyed and samples were collected no more than once per day to avoid excessive disturbance. We collected in 7 mo (from March 1999 to March 2000; see months in Figure 1B). We visited the locality for one week each one of the sampled months. During this week, all the three transects were sampled. The specimens were collected by hand and kept in individually labelled bags. Because, frogs are capable of digesting their prey rapidly (Vitt and Caldwell 1994), the frogs were killed within 3 h of the capture. Individuals were fixed in 10% formalin, preserved in 70% ethanol and are housed in the herpetological collection of the Museo de Historia Natural, Escuela de Biología, Universidad Industrial de Santander, Colombia (UIS–A). This scientific herpetological collection is registered by the Ministerio del Ambiente of the Colombian government.

We employed a G–test to assess whether species richness of *Pristimantis* varied among transects using the data of all sampling months together. For the most abundant species we put together the abundance data of the transects to

detect a significant variation among the months of sampling using a Serial run test. We also checked whether the abundance of the most abundant species significantly changed between seasons (rainy and drier months) using a G-test.

Microhabitat use and time of activity

Habitat use data such as perch height (measured with a metric tape) and substrate type (leaf litter, branch, leaf, stone, and trunks) were recorded for each sampled frog. We performed a Kruskal–Wallis nonparametric test in order to detect perch height preferences among *Pristimantis* species in each sampled transect. For the most abundant species we put together the perch height data of the two transects to test whether perch height varied for each species among sampling months. Also, for the common species we used Spearman correlation to test the effect of body size on perch height.

Activity time was measured sampling each transect in the morning (from 9:00 h to 11:00 h), in the afternoon (from 15:00 h to 17:00 h) and in the night (from 18:00 h to 22:00 h) during different days to avoid continuous disturbance.

Diet

Dietary studies have demonstrated that post-metamorphic frogs change both prey type and prey size as they grow (Donnelly 1991, Lima and Magnusson 1998). Because juvenile and adult *Pristimantis* occur in the same microhabitats and forage at the same place (leaf litter and on the bushes [J. D. Lynch, pers. comm. and pers. obs.]), we analyzed the diet for both juveniles and adults combined. Stomachs of frogs were removed and dissected, and prey items were sorted in a Petri dish. Prey items were counted and their lengths measured to an accuracy of 0.02 mm with either dial calipers or micrometer on a microscope, depending on prey size. Prey items were classified and identified to order taxonomic level. We did not use

individual volumes because some prey were disarticulated or were so small that we could not measure them accurately.

Kruskal–Wallis nonparametric test was used to compare sizes of prey ingested among *Pristimantis* species. Species of the two transects together with at least five items in their stomachs were included in the analysis of prey size. We tested whether the lengths of the most frequently consumed items by species were similar among species by means of a Kruskal–Wallis nonparametric test. To test for the effect of body size on prey size, we used Spearman correlation for the most common species.

Other ecological data

For each specimen, we measured snout–vent length (SVL) and mouth width with Vernier callipers (± 0.02 mm). We used a Kruskal–Wallis nonparametric test to determine whether members of the *Pristimantis* assemblage are similar in body size. We dissected and preserved the reproductive and digestive tracts. The condition of the oviduct and ovary was recorded as oviduct width (at midlength, measured with an ocular micrometer) and the number of large–yolked follicles in the ovaries. For males, left testis length was measured with an ocular micrometer and the convolution of the deferent ducts was observed. Based on the anterior data of the macroscopic observation of the gonads and ducts we determined age structure and reproductive condition. Individuals were assigned to one of three age–sex groups (adult female, adult male, and juveniles). Adult females were considered those females with yolked follicles and females with non yolked follicles but with distended oviducts, and adult males those individuals with large testes and convoluted deferent ducts. We classified the adult females as previtellogenic (ovaries without yolked follicles) and vitellogenic (ovaries containing vitellogenic follicles and convoluted oviducts). The reproductive stage determined for each specimen allowed us

to establish the reproductive activity for males and females in each month and during the whole sampling time, as well as the minimum size of sexual maturity for females of each population. The minimum size at sexual maturity was determined by the body size (SVL) of the smallest female with yolked follicles.

Results

Pristimantis assemblage and species abundance

Of the three transects, The Forest Interior Transect had the most species and individuals (Figure 1A). All six species of *Pristimantis* studied were found in this transect. The Creek Parallel Transect had fewer species and individuals, and the transect on the creek had the lowest number of species and individuals; during the year of sampling only one *P. carlossanchezi* was collected on this transect (Figure 1A). For this reason, we did not consider this transect in the ecological analyses. Then, the species richness of *Pristimantis* varied significantly among transects ($G_{0.05, 2} = 6.26$, $P < 0.05$).

On the Interior Forest Transect, *P. miyatai* was the most abundant species; this species represented 42.8 % of the total abundance and therefore is the most common species in this study, followed by *P. douglasi* with 16.3% of the total abundance.

On the Parallel Creek Transect, *P. merostictus* was the most abundant species and was the third most abundant in this study with 12.8 % of the total abundance. *P. lutitus*, *Pristimantis* sp. 1 and *P. carlossanchezi* were the rarest, with a percent abundance lower than 5.0%.

We included only the three most abundant species (*P. miyatai*, *P. douglasi* and *P. merostictus*) in the analysis of seasonal variation. For these three species, we put together the abundance data for the two transects (Interior Forest Transect and Parallel Creek Transect). The relative abundance of these three most common species was not different between dry

and rainy seasons ($G_{0.05, 1, 2} = 12.1$, $P > 0.25$). The resulting seasonal comparison demonstrates that *Pristimantis miyatai* and *P. merostictus* did not vary significantly in abundance during the year ($C_{0.05, 2, 2} = 3.4$, $P = 0.8$ and $C_{0.05, 2, 2} = 3.4$, $P = 0.2$), whereas *P. douglasi* showed significant differences in the number of individuals among the months of sampling (serial run test— $C_{0.05, 1, 1} = 5$, $P = 0.02$) (Figure 1B).

Microhabitat and time of activity

Frogs of all observed species of *Pristimantis* were found on vegetation within 0–2.0 m of the ground. Heights between 1.5 and 2.0 m were most frequently observed (74.6%, Figure 2A). Leaves were the preferred (88.6%) perch site among the frogs.

Kruskal–Wallis test results showed that there was no significant difference in the use of perch height among species on The Interior Forest Transect and on Parallel Creek Transect respectively ($H_{5, 97} = 7.49$, $P = 0.1864$; $H_{2, 26} = 1.22$, $P = 0.543$). For *P. miyatai*, *P. douglasi* and *P. merostictus*, no monthly variation was observed in the use of this spatial resource ($H_{1, 20} = 0.91$, $P = 0.33$) and none of these three most common species showed correlation between body size and vertical position (*P. miyatai*, $R = 0.024$, $P < 0.85$, $n = 60$; *P. douglasi*, $R = 0.031$, $P < 0.88$, $n = 24$; *P. merostictus*, $R = 0.485$, $P < 0.09$, $n = 16$).

Most individuals were active beginning at about 18:30 h. A few individuals were collected during the day (6.5%, Figure 2B); these were juvenile *P. miyatai* moving around in leaf litter, and few calling males *P. douglasi* perched on vegetation.

Diet

Diet data for this study are based on 123 stomachs from the six studied species of *Pristimantis*. One hundred and fifty prey items belonging to 17 prey categories were identified to the level of order in insects and to higher

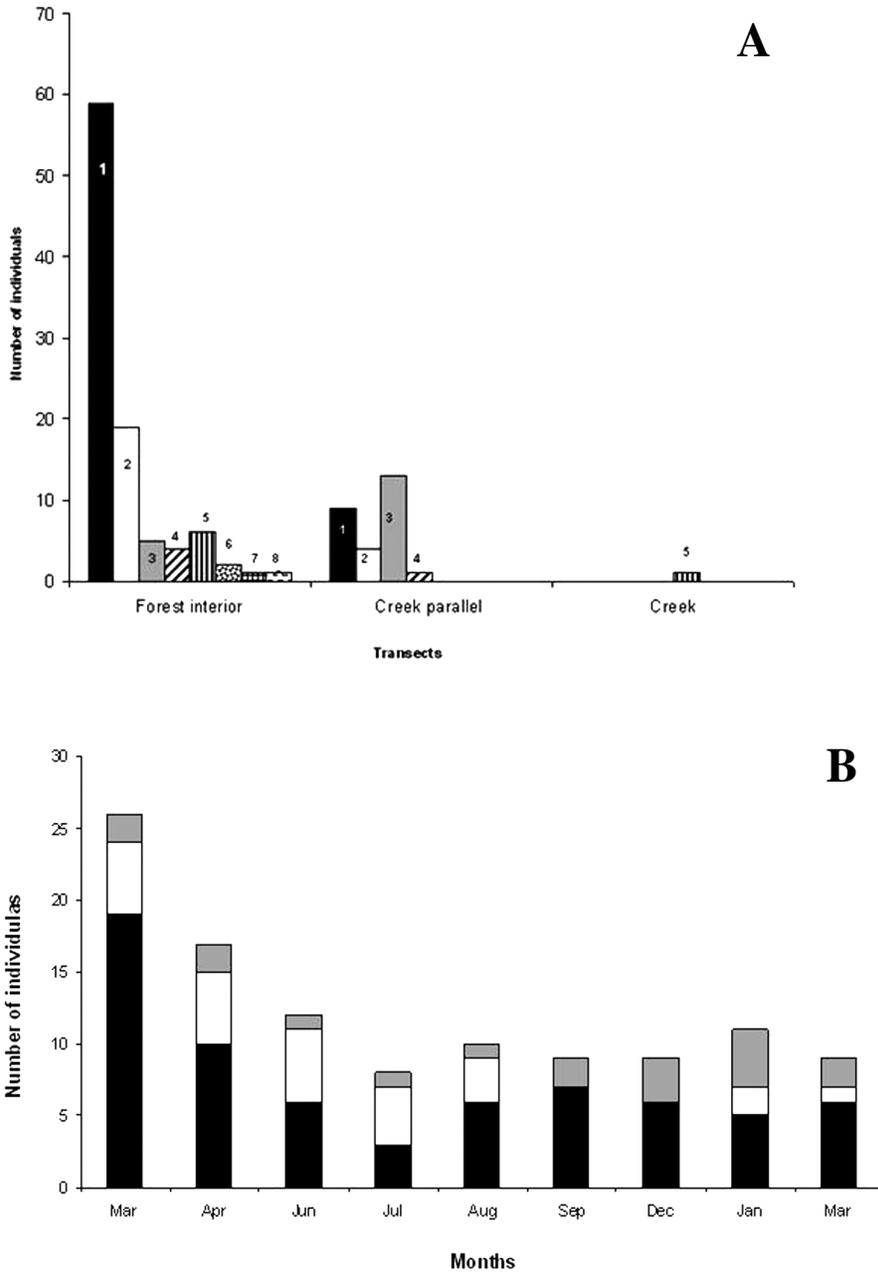


Figure 1 - (A) Distribution of *Pristimantis* species at El Rasgón in the three transects sampled. The number of species drops with transition from forest interior to aquatic habitat. (B) *Pristimantis douglasi* (in white) showed significant differences in the relative abundance of individuals collected during the months of sampling, individuals were not observed from September to December whereas *P. miyatai* (in black) and *P. merostictus* (in gray) were observed during the year of sampling from March 1999 to March 2000. (1) *Pristimantis miyatai*, (2) *P. douglasi*, (3) *P. merostictus*, (4) *P. lutitus*, (5) *P. carlossanchezi*, (6) *Pristimantis* sp. 1, (7) *P. anolirex*, (8) *P. prolixodiscus*.

taxonomic levels in other arthropod prey item groups (Table 1). The taxonomic orders with the highest frequency of occurrence (percentage of stomachs containing each prey type) were Collembola, Coleoptera, Isopoda, and Araneae, and these preys items were found in the stomachs of the three most common species. Spiders and coleopterans were the most abundant prey items consumed by individuals of *P. miyatai*. Also, collembolans are an important item in *P. miyatai*, whereas isopods seem to be commonly consumed by both *P. miyatai* and *P. douglasi* (Table 1).

Coleopterans were observed in stomach contents of all species, except for *P. lutitus*. However, the sample of stomach contents for this species was small. Individuals of *Pristimantis* sp. 1 also contained few prey items in their stomachs. Hence, we did not consider the diet of *P. lutitus* or *Pristimantis* sp. 1 in the prey size analysis. Then, species included in the analysis of prey size were *P. miyatai*, *P. douglasi*, *P. merostictus* and *P. carlossanchezi*.

The comparison of prey size among species of *Pristimantis* reveals that frogs collected along the Forest Interior Transect differ significantly in the size of the prey that they eat ($H_{3,116} = 18.3$, $P = 0.0162$) (Figure 3A). In contrast, no significant differences were observed in prey size consumed by species observed on the Creek Parallel Transect (*P. douglasi*, *P. miyatai* and *P. merostictus*) ($H_{2,37} = 0.52$, $P = 0.5869$). We tested whether the lengths of the two most frequently consumed items (Coleoptera and Araneae) by species collected at the Forest Interior Transect were similar among species. *Pristimantis douglasi* and *P. carlossanchezi* eat significantly differently sized Araneae (Figure 3B), whereas the Coleoptera consumed by *P. miyatai*, *P. douglasi* and *P. merostictus* are not significantly different in length ($H_{2,23} = 4.72$, $P = 0.0941$). Only *P. miyatai* shows a significant correlation between prey size and jaw width ($R = 0.1071$, $P < 0.002$). In *Pristimantis douglasi* and *P.*

merostictus, mouth size and prey length are uncorrelated ($R = 0.0005$, $P < 0.889$, $R = 0.0687$, $P < 0.264$, respectively).

Other ecological data

Almost all captured individuals of *P. miyatai*, *P. merostictus*, *P. lutitus*, and *Pristimantis* sp 1 and *P. carlossanchezi* were juveniles (less than 17 mm; Lynch, 1984) and were observed every sampling month. Adult individuals of the six species have similar body sizes ($H_{4,66} = 9.38$, $P = 0.052$).

Pristimantis douglasi was not found or heard at the beginning of the dry season. Reproductive activity in *P. douglasi* was evident from the male calling activity and from the observation of vitellogenic follicles in females. Some yolked follicles were also observed in females of *P. miyatai*, but calling activity was never heard in *P. miyatai*, *P. lutitus*, *P. merostictus*, *P. carlossanchezi* and *Pristimantis* sp. 1 males. Sexually mature females had enlarged and convoluted oviducts or large yellow–orange ovarian follicles. The minimum size at sexual maturity is 24.72 mm SVL for *P. miyatai* females (adult females range from 24.72–27.19 mm SVL), and 23.03 for *P. douglasi* females (range 23.02–26.08 mm). Reproductive females of *P. miyatai* were observed during the months of March, July, August, and October; whereas reproductive females of *P. douglasi* were found only during the first months of the year.

Discussion

Species richness and abundance vary significantly among the three transects. The abundance of species among transects seems to depend on the distance to the nearest body of water; the number of species in vegetation over the aquatic habitats is lower than in the forest interior. The *Pristimantis* assemblage at El Rasgón is not tied to aquatic environments. This result is in accordance with the reproductive

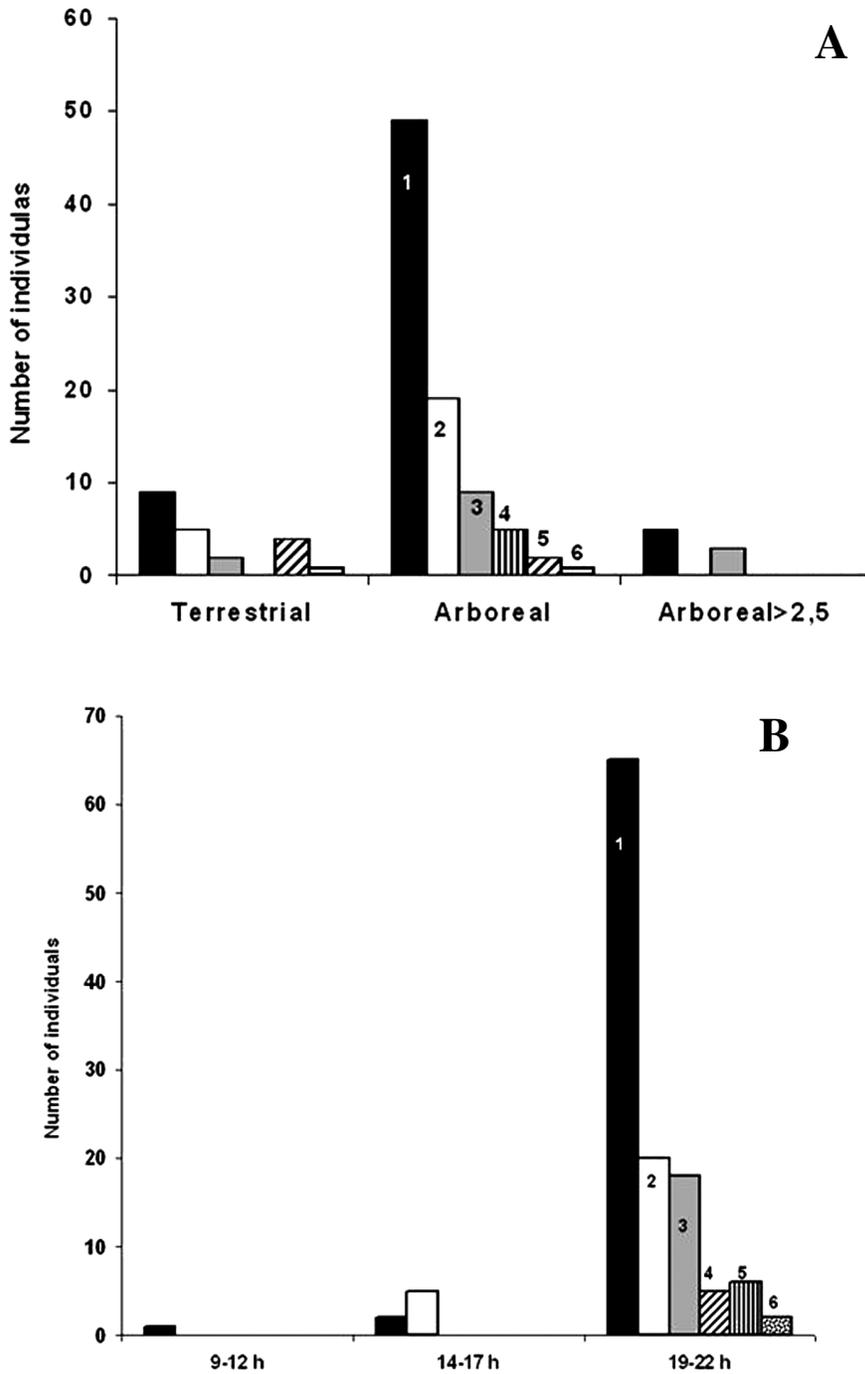


Figure 2 - (A) Microhabitat use in *Pristimantis* assemblage. (B) Time of activity. The majority of individuals were observed at heights within 1.5 m of the ground and showed nocturnal activity. (1) *Pristimantis miyatai*, (2) *P. douglasi*, (3) *P. merostictus*, (4) *P. luitus*, (5) *P. carlossanchezi*, (6) *Pristimantis* sp. 1.

Table 1 - Prey taxa found in six species of *Pristimantis* at El Rasgón, Santander, Colombia. Numbers of individuals per prey taxon (N) and percent of the total number of prey accounted by the particular prey type (%).

	<i>P. miyatatai</i>		<i>P. douglasi</i>		<i>P. merostictus</i>		<i>P. luttitus</i>		<i>P. carlossanchezi</i>		<i>Pristimantis</i> sp. 1	
	N	%	N	%	N	%	N	%	N	%	N	%
Insecta												
Colembolla	28	36.36	2	5.41	1	5.26	0	0	1	8.33	0	0
Homoptera	1	1.3	1	1.3	1	5.26	0	0	0	0	0	0
Dermoptera	0	0	1	1.3	0	0	0	0	0	0	0	0
Diptera	1	1.3	1	1.3	0	0	0	0	1	8.33	0	0
Lepidoptera (larvae)	1	1.3	0	0	0	0	0	0	0	0	0	0
Coleoptera	12	15.58	6	7.79	6	31.52	0	0	1	8.33	1	50
Hymenoptera	4	5.19	1	1.3	1	5.26	0	0	1	8.33	1	50
Formicidae	6	7.79	2	5.41	2	10.53	1	50	1	8.33	0	0
Blattidae	2	2.6	6	7.8	1	5.26	0	0	0	0	0	0
Hemiptera	0	0	0	0	0	0	1	50	0	0	0	0
Orthoptera	4	5.2	1	1.3	0	0	0	0	3	25	0	0
Diplopoda	5	6.49	1	1.3	0	0	0	0	0	0	0	0
Neuroptera (larvae)	0	0	1	1.3	0	0	0	0	0	0	0	0
Aracnida												
Araneae	1	1.3	4	10.81	6	31.52	0	0	3	25	0	0
Acarinae	1	1.3	1	1.3	0	0	0	0	0	0	0	0
Crustacea												
Isopoda	9	11.68	9	24.32	2	10.53	0	0	0	0	0	0

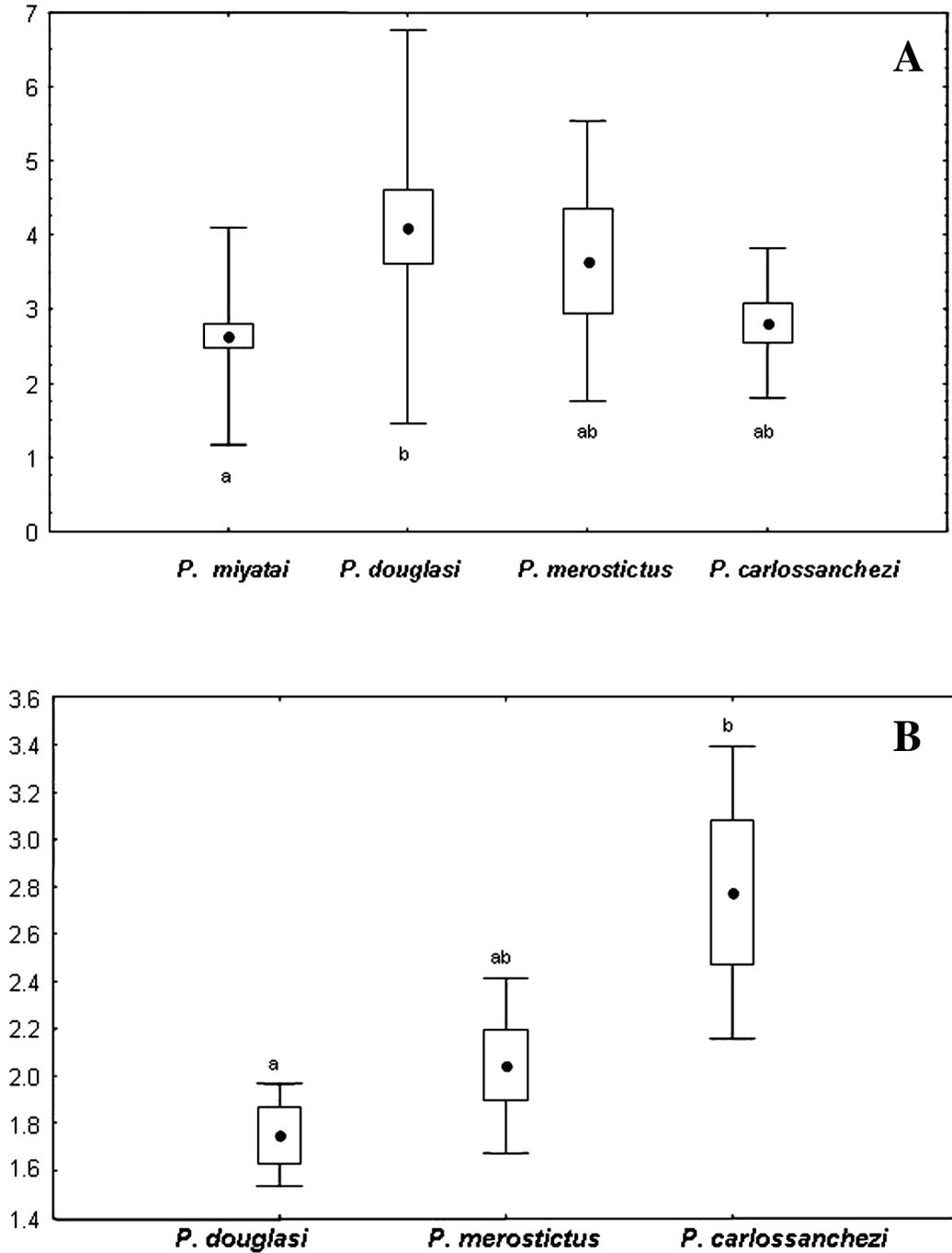


Figure 3 - Length of ingested prey (mm) by *Pristimantis* species. (A) Species of Forest Interior Transect showed significant differences in prey size. (B) There were significant differences in the prey size of Araneae. Different superscripts indicate significant differences. point = Mean box = Standard Error whiskers= Standard Deviation.

mode of *Pristimantis*, direct development, in which females deposit terrestrial eggs that hatch directly into miniature adults (Townsend and Stewart 1985, Woolbright 1985).

The species of *Pristimantis* studied does not differ in the space they occupy. Most species of *Pristimantis* were observed perched on leaves at heights below 210 cm. Our results about microhabitat use are consistent with other *Pristimantis* assemblage studies that show use of vertical position at heights within 150 cm of the ground (Miyamoto 1982, Lynch and Duellman 1997, Höbel 1999). Furthermore, we found that perch site use is not influenced by seasonal changes. Because most individuals are active beginning at about 18:30 h, we think that the *Pristimantis* assemblage at El Rasgón is arboreal/nocturnal in the use of microhabitat and time of activity, although one species, *P. douglasi* is characterized as arboreal with diurnal and nocturnal activity. We think that the number of *P. douglasi* males collected could be more, we heard a lot of *P. douglasi* calling males but they were hard to collect because calling sites were often too difficult to access.

In *Pristimantis miyatai*, there is a significant correlation between prey size and mouth size, suggesting that size of consumer determines prey size; however, this species did not show significant differences in prey size. Generally in anurans, there is a positive correlation between body size and prey size (Toft 1980, 1981, 1985, Lima 1998, Parmalee 1999), but this generalization has limited application to frogs that are dietary generalists (Lynch and Duellman 1997). The generalization about body size and prey size applies to maximum-size prey that can be captured and ingested, but generalist frogs do not forage only at maximum prey size (Lynch and Duellman 1997). Our results in *P. miyatai* are consistent with the argument of Lynch and Duellman (1997). Moreover, we conclude that species of *Pristimantis* at El Rasgón select their prey according to their abundance because we did not observe differences in prey ingested within species between transects. This result is

not unexpected because most species of *Pristimantis* are characterized as dietary generalists. Members of *Pristimantis* and *Eleutherodactylus* have been characterized as insectivorous generalists that choose prey depending on food availability (Ovaska 1991, Lynch and Duellman 1997, Woolbright and Stewart 1997). Species of *Pristimantis* in this study ingested a wide spectrum of prey sizes and types.

We also observed a slight segregation by individuals of *P. douglasi* during the mating season. *P. douglasi* seems to show more seasonality in its reproduction than the other species of *Pristimantis* studied. We did not find or hear individuals of *P. douglasi* at the beginning of the dry season, and most of the adult males were heard and observed in the rainy season. In contrast, the populations of *P. miyatai*, *P. merostictus*, *P. lutitus*, *Pristimantis* sp. 1 and *P. carlossanchezi* consisted of individuals of small body size during all months of sampling.

In summary, we did not find strong differences in the use of the diet, microhabitat and time of activity among the six species of *Pristimantis* at El Rasgón, just a slight segregation was observed by *P. douglasi* individuals in activity time and reproductive time.

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