

Patterns of Community Structure and Microhabitat Usage in Peruvian *Pristimantis* (Anura: Strabomantidae)

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We examined patterns of community structure and microhabitat requirements of *Pristimantis* frogs at sites of high geographic proximity in the Tambopata region of southeastern Peru. Herpetofaunal surveys were conducted at five sites encompassing approximately 131 square km of Tambopata Province, including EcoAmazonía (EA), Reserva Amazónica (RA), Explorer's Inn (EI), Sachavacayoc Centre (SC), and Tambopata Research Center (TRC). In addition to sampling and identifying all species of *Pristimantis* captured, environmental variables, including substrate, perch height, leaf litter depth, tree cover, and time of day, were collected and analyzed. Total frog encounters, species richness, diversity, and community similarity differed significantly among sites. Generally, similarity, richness, and diversity were not closely related to geographic proximity, but total abundance was. More individuals were captured at SC and TRC, whereas more total species were captured at TRC and EI. Diversity was the highest at TRC, followed by RA, EI, EA, and SC. Encounters of *P. toftae* and *P. peruvianus* also differed significantly among sites, with one species rarely encountered where the other was prevalent. Generally, more individuals of *Pristimantis* were captured during the wet season at all five sites. Significantly more individuals were captured during the night than the day. Significantly more individuals as well as species were captured on leaves and the ground versus all other substrate types, with more on leaves at night and on the ground during the day. Significantly more adults were captured higher off the ground than juveniles, with males found higher than females. There was no significant relationship between frog encounters and leaf litter or tree cover. *Pristimantis peruvianus* was shown to exhibit differences in microhabitat usage from *P. toftae*. We conclude that many factors contribute to the observed differences in diversity among the sites, requiring future studies that will also examine other environmental variables such as forest type, soil characteristics, and prey availability.

Investigamos la estructura de comunidad y los requisitos de microhábitat de ranas *Pristimantis* en localidades de proximidad alta en la región de Tambopata del sudeste del Perú. Para lograr los objetivos, realizamos censos de herpetofauna en cinco lugares cubriendo aproximadamente 131 km cuadrados de la Provincia Tambopata, incluyendo EcoAmazonía (EA), Reserva Amazónica (RA), Explorer's Inn (EI), Sachavacayoc Centre (SC) y Tambopata Research Center (TRC). Además de capturar y identificar todas las especies de *Pristimantis*, colectamos y analizamos datos ambientales, incluyendo substrato, altura de percha, profundidad de hoja rasca, cobertura de árboles y hora. Los encuentros de ranas, riqueza de especies, diversidad y semejanza de comunidad fueron diferentes entre localidades. Generalmente, semejanza, riqueza y diversidad no fueron relacionadas a proximidad geográfica pero abundancia sí fue relacionada. Más individuos fueron capturados en SC y TRC, pero más especies fueron capturadas en TRC y EI. Diversidad fue más alta en TRC, con RA, EI, EA y SC siguientes. También, encuentros de *P. toftae* y *P. peruvianus* fueron diferentes entre lugares, con una especie encontrada raramente donde la otra fue abundante. Generalmente, más individuos de *Pristimantis* fueron capturados durante la época lluviosa en todas las localidades. Más individuos fueron capturados durante la noche que el día. Más individuos y especies fueron capturados en hojas y el suelo versus todos los otros tipos de substrato, con más en hojas por noche y en el suelo por día. Más adultos que juveniles fueron capturados en alturas más altas, con machos encontrados más altos que las hembras. No había una relación significativa entre profundidad de hoja rasca o cobertura de árboles y los encuentros de ranas. *Pristimantis peruvianus* mostró diferencias de *P. toftae* en uso de microhábitat. Concluimos que muchos factores contribuyen a las diferencias observadas de diversidad entre lugares requiriendo estudios futuros que examinan otros variables ambientales, como tipo de bosque, características del suelo y la disponibilidad de presas.

INVESTIGATING and quantifying species diversity and community structure has been a long-term goal of both community ecologists and evolutionary biologists, especially in tropical regions, which tend to have high species diversity (Duellman, 2005). Generally, when investigating community structure over large geographic areas it is often imperative to examine historical influences as well as current environmental variables (Tuomisto and Ruokolainen, 1997). However, when studying community structure over a much smaller area, history becomes less significant and thus, the local environment becomes the main driving force shaping these communities (Tuomisto and Ruokolainen, 1997). Strabomantid frogs have undergone large adaptive radiations throughout the Neotropics,

colonizing a multitude of macro- as well as microhabitat types (Duellman, 2005; Heinicke et al., 2007). Strabomantid frogs serve as ideal organisms for studying aspects of community ecology and diversity due to their sheer abundance and species richness resulting from the successful colonization of a multitude of habitat types throughout the Neotropics (Duellman, 2005).

The recently defined strabomantid genus *Pristimantis* encompasses almost 400 species; nearly 50 of those species occur in the Amazon Basin (Duellman, 2005; Heinicke et al., 2007). Although the diversity of *Pristimantis* is high, few studies have been conducted investigating environmental variables that influence these populations and assemblages, particularly among sites of high geographic proximity.

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The Tambopata region of Peru, located at the southwestern edge of the Amazon Basin, is a biodiversity hotspot, with the highest recorded herpetofaunal diversity in the world (Doan and Arizábal, 2002). The fauna and flora of multiple localities within the Tambopata Province have been studied, and the herpetofaunal assemblages at each have been investigated in detail, with 15 species of *Pristimantis* recorded (Doan and Arizábal, 2002). The region presents an ideal area to address the following questions about common frogs such as *Pristimantis*: to what extent do assemblages of *Pristimantis* vary on a microgeographic scale among sites and what are the microhabitat factors that are important in determining assemblages of *Pristimantis*?

Many species of *Pristimantis* undergo diel variations in choice of substrate. For example, most species are primarily terrestrial and inhabit the leaf litter during the day, whereas during the night they are found perched on leaves above the ground (Miyamoto, 1982). However, a small number of species remain in the litter at night, possibly to feed (Miyamoto, 1982; Duellman, 2005). Miyamoto (1982) hypothesized that moisture requirements restrict *Pristimantis* to the leaf litter during the day, whereas at night abiotic conditions are more favorable to allow frogs to ascend the vegetation to call for mates. Therefore, we predicted that more *Pristimantis* would be encountered closer to the ground during the day, whereas at night they would be found perched on vegetation, with adult males encountered on higher perches than females to adequately call for receptive mates. Several authors have also stated that species of *Pristimantis* partition vertical microhabitats, thus utilizing slightly different resources (Heatwole, 1963; Miyamoto, 1982; Toft, 1985; Parmelee, 1999), so we predicted that there would be species-specific variation in capture height characteristics. We also predicted a direct relationship of the abundance of *Pristimantis* versus leaf litter depth (Lieberman, 1986; Fauth et al., 1989; Whitfield and Pierce, 2005) and tree cover (Voris, 1977; Whitfield and Pierce, 2005).

Whether certain species of *Pristimantis* are encountered more commonly during the wet or dry season depends on many factors such as sampling methodologies, location, climatic conditions, and several other ecological factors including reproduction and prey availability (Toft, 1980a; Allmon, 1991; Watling and Donnelly, 2002). Toft and Duellman (1979) found that both *P. toftae* and *P. peruvianus* breed primarily during the dry season in Amazonian Peru, when they were also more abundant. However, we hypothesized that more frogs would be captured during the wet season than the dry season, due to the increased prey abundance, moisture, and litter depth associated with the wet seasons in Neotropical forests of South America (Watling and Donnelly, 2002). Few studies have examined diel activity, microhabitat preferences, and physiological tolerances of these species in the Neotropics, and thus the results of this study will contribute knowledge regarding the ecology of Amazonian strabomantine frogs.

MATERIALS AND METHODS

Sites sampled.—Site descriptions and sampling methodology follow Doan and Arizábal (2002) and Doan (2003). The five sites sampled included EcoAmazonía (EA), Reserva Amazónica (RA), Explorer's Inn (EI), Sachavacayoc Centre (SC), and Tambopata Research Center (TRC), all of which are located in the Tambopata Province of the Madre de Dios Department,

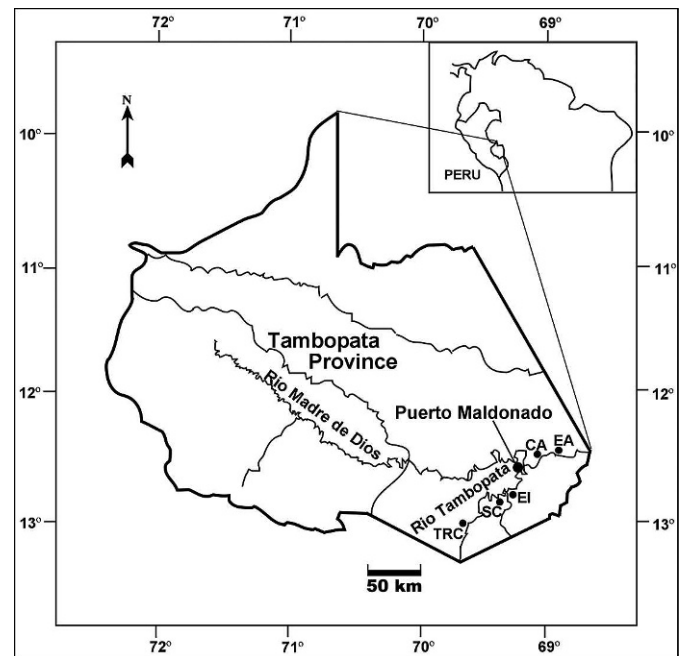


Fig. 1. Map of Tambopata province of the Madre de Dios Department, Peru showing the geographic locations of the five sites examined in this study. EA = EcoAmazonía, RA = Reserva Amazónica, EI = Explorer's Inn, SC = Sachavacayoc Centre, TRC = Tambopata Research Center.

ment, Peru and are separated from each other by approximately 7–131 km (Fig. 1). Two main rivers flow through this region: Río Madre de Dios and Río Tambopata. The five lowland sites sampled averaged 212 m above sea level. The degree of human perturbation at each of the sites is minimal due to the difficulty of access (only by boat); therefore, most of the region consists of primary forest at the western edge of the Amazon basin (Duellman and Koechlin, 1991; pers. obs.).

Sampling methodology.—The surveys for this study were conducted over a two-year span from January 1997 to November 1998 with sites visited on a rotating schedule (Doan and Arizábal, 2002). Both quadrat and visual encounter survey (VES) methodologies were used (Doan and Arizábal, 2000, 2002; Doan, 2003). At each site, four quadrat parcels and two VES parcels were installed. Each quadrat parcel measured 80 × 70 m and contained 56–8 × 8 m quadrats, whereas each VES parcel was 1 ha and held 24 transects 4 m apart, each 100 m in length. Each site was visited five times over the two-year period with 18 days spent per site visit (Doan and Arizábal, 2002). Quadrats were intensively searched by four individuals lifting cover objects and sifting through leaf litter until the entire area was searched (Doan, 2003). During each site visit, half of the 224 quadrats were sampled randomly with more quadrats sampled at night because the capture rate was much higher. Because of the disruptive sampling scheme, each quadrat was sampled only once per site visit. Also, during each site visit, each of the 48 transects were sampled both at night and during the day. All sampling was conducted from the ground up to 2 m in height (Doan, 2003). Identical sampling of parcels occurred at each site. Along with identifying the species of *Pristimantis* captured, snout-vent length (SVL), mass, sex, capture height, substrate type, leaf litter depth, tree cover, air temperature, date, and time of day were also recorded. All captured anurans were released

at the point of capture. Voucher specimens of each species were taken at each site outside of the sampling parcels and deposited at the Museo de Historia Natural of the Universidad Nacional de San Antonio Abad de Cusco (MHNC WAA119, WAA137, WAA141, WAA156, WAA189, WAA202, WAA203, WAA245, WAA247, WAA260, WAA272).

In each quadrat sampled in the study, 16 measurements of leaf litter depth were taken, four on each side. Litter depth was estimated by counting the number of leaves (or leaf fragments) from the surface to the soil along a wire placed through the leaves. Although this is not an actual depth measurement, number of leaves was used as a proxy for depth. Thickness of leaves varies to some extent but not substantially enough that the approximation is invalid (Torti et al., 2001). The four values per side were summed to obtain a single value per side. These four sums were then averaged together to obtain the mean leaf litter depth per quadrat. After a single value was obtained for all quadrats within a particular sampling interval/parcel, those values were then summed to obtain a single leaf litter depth value for the entire parcel during a particular sampling period.

Within each quadrat sampled at the five sites, all tree diameters at breast height (dbh) greater than 10 cm were measured. These values were summed to obtain a single value for tree diameter within a specific quadrat/date. Next, all the tree sums within a specific parcel were averaged to obtain a single tree diameter value for a particular date/parcel. Finally, all the tree diameters for each parcel/date were summed to obtain a single value for the entire parcel/sampling interval. Tree diameter was used as an estimate of tree cover as wider trees produce wider canopies (Gill et al., 2000; Archibald and Bond, 2003).

To obtain perch height statistics that were used in these analyses, all capture height data for quadrats and transects were averaged for a particular day within a sampling period, and summed to obtain a single height value for a particular parcel during a particular sampling interval. Substrate types used by *Pristimantis* during this study included leaf, ground, trunk, root, branch, vine, log, and bamboo. During each individual encounter, the substrate on which the frog was first seen was recorded. Individual parcels were analyzed as the sampling unit for each site; thus, individual quadrats and transects were pooled for each parcel. All quadrat and transect data were averaged and summed across sampling interval and parcel for each site as described above. All statistical tests were performed using SYSTAT V. 7.0 (SYSTAT Inc., Chicago, IL), JMP-IN V. 4.0 (SAS Institute, Cary, NC), or SAS (SAS Institute, Cary, NC).

Community data analysis.—Species diversity at each site was estimated using the Shannon-Weiner diversity index calculated with BIO-DAP (Thomas, 2000). Similarity between sites was calculated using the Bray-Curtis index of similarity. Subsequently, non-metric multidimensional scaling (nMDS) was used to interpret differences in similarity between sites. In addition, cluster diagrams were constructed over the nMDS plot in order to show how the sites grouped with each other. Similarity and nMDS analyses were performed using PRIMER (Clark and Warwick, 2001).

Analysis of variance (ANOVA) was used to determine if total frog, species, and sex class (male, female, juvenile) encounters differed significantly among the five sites. Tukey *post-hoc* tests were then performed to determine which sites were statistically similar to each other. Kruskal-

Wallis tests were used to determine if the encounters of *P. peruvianus* and *P. toftae* differed significantly among sites, because they were the two most frequently encountered species.

Microhabitat data analysis.—For examination of microhabitat, data from all sites were combined. First, data of all individuals and species of *Pristimantis* were pooled to examine general patterns. Subsequent analyses were then performed on the most common species for a more comprehensive examination of the microhabitat requirements of western Amazonian *Pristimantis*.

T-tests and ANOVAs determined if more individuals, species, and sex classes were captured during the day or night. Because more quadrats were sampled during the night than during the day (Doan, 2003), all diurnal data were multiplied by a calculated factor of 2.04 to account for the diel difference in sampling effort for each test that examined differences in diel activity. Because multiple t-tests were performed, a Bonferroni adjustment was used to correct *P*-values. To determine if more individuals and species were more commonly found on certain substrate types at certain times of the day, Friedman two-factor ANOVAs were used. T-tests then were used to quantify if more individuals were captured on leaves or the ground, whereas a Wilcoxon Signed-Rank test was used to quantify if more total species were captured on leaves or the ground.

The values for perch height, leaf litter depth, and tree cover per quadrat sampling date/parcel were compared to the total number of individuals and species at the corresponding parcel/sampling date using multiple regression analyses. We detected no significant correlation between tree cover and litter depth, so each variable was treated independently in subsequent analyses. Because leaf litter and tree cover data were not measured in transects, subsequent simple linear regressions were performed examining the relationship between perch height and abundance (using all quadrat and VES data). Wilcoxon Signed Rank tests were used to determine if adults versus juveniles and males versus females were found higher off the ground, and a Kruskal-Wallis test determined if there was a difference in leaf litter depth for sampling date. Leaf litter data were also analyzed using regression analysis to determine if more individuals or sex classes were captured in deeper leaf litter.

Data for *Pristimantis toftae* and *P. peruvianus* were analyzed in more detail in this study because they were found in high numbers at more than two sites. For *P. toftae*, EA and EI were not included due to small sample sizes or absence from the site. For *P. peruvianus*, SC was not included in these analyses because only 12 individuals of this species were captured at that site (Table 1). Multiple regression analyses were conducted to determine if leaf litter depth, tree cover, and perch height contributed to the encounters of both species. As with the overall data of *Pristimantis* above, subsequent simple linear regressions were performed to determine if height alone had an effect on the encounters of both species. A Mann-Whitney U test was used to determine if one species was found at higher perches than the other, and a t-test was used to examine any difference in overall body size (SVL) between the two species. Finally, seasonal encounters of both species were examined graphically to determine if one or both species were more common during certain times of the year.

Table 1. *Pristimantis* Species Richness, Shannon-Weiner Diversity, Species Encounters, and Total Encounters for Five Sites. EA = EcoAmazonía, RA = Reserva Amazónica, EI = Explorer's Inn, SC = Sachavacayoc Centre, TRC = Tambopata Research Center.

| | Sites | | | | |
|----------------------------|------------|------------|------------|------------|-------------|
| | EA | RA | EI | SC | TRC |
| Richness | 6 | 7 | 4 | 5 | 8 |
| Diversity | 0.5 | 1 | 0.53 | 0.27 | 1.22 |
| Species | Encounters | | | | |
| <i>P. altamazonicus</i> | 28 | 20 | 12 | 27 | 43 |
| <i>P. carvalhoi</i> | 0 | 1 | 0 | 3 | 0 |
| <i>P. cruralis</i> | 1 | 8 | 50 | 11 | 92 |
| <i>P. diadematus</i> | 1 | 0 | 0 | 0 | 0 |
| <i>P. lacrimosus</i> | 0 | 0 | 0 | 0 | 5 |
| <i>P. martiae</i> | 2 | 0 | 0 | 0 | 0 |
| <i>P. ockendeni</i> | 0 | 1 | 0 | 0 | 21 |
| <i>P. peruvianus</i> | 197 | 32 | 381 | 12 | 106 |
| <i>P. skydmainos</i> | 1 | 1 | 0 | 0 | 133 |
| <i>P. toftae</i> | 0 | 135 | 5 | 936 | 751 |
| <i>P. ventrimarmoratus</i> | 0 | 0 | 0 | 0 | 14 |
| Totals | 230 | 198 | 448 | 989 | 1165 |

RESULTS

Community statistics.—A total of 3033 individuals of 11 species of *Pristimantis* were captured during the entire study, 728 of which were *P. peruvianus* and 1827 of which were *P. toftae*. Table 1 shows total encounters, individual species encounters, species richness, and species diversities calculated with the Shannon-Weiner diversity index. The site with the highest species richness, diversity, and highest number of *Pristimantis* captures was TRC. The next most diverse site was RA followed by EI, EA, and SC. Following TRC, species richness was highest at RA, EA, SC, and EI, and total frog abundance was greatest at SC, EI, EA, and RA. By examining the nMDS plot (Fig. 2), it can be seen that SC and TRC were most similar to one another (60%) and EA and EI were most similar to each other (60%). Although SC and TRC were shown to be quite similar, diversity at SC was much lower due to the extremely high abundance of *P. toftae* (Table 1). Reserva Amazónica was more different from all the sites, but more similar to both SC and TRC than to EA and EI.

Statistically significant differences were found in the average number of individuals captured by sampling date and parcel with TRC and SC having the highest catch averages ($F_{4,147} = 19.549$; $P < 0.001$). A Tukey *post-hoc* test showed EA, RA, and EI to be statistically similar, whereas SC and TRC were similar to one another. A statistically significant difference was found in the average number of species captured by sampling date/parcel among sites ($F_{4,147} = 44.432$; $P < 0.001$). The sites EA, RA, EI, and SC were statistically similar to one another, but different from TRC.

There were significant differences in the number of juveniles, males, and females captured at each site and for all sites combined ($F = 4.629$ – 18.630 ; $P = 0.001$ – 0.011). Significantly more juveniles were captured at RA, SC, and TRC and for all sites combined, whereas more adult males were captured at EA and EI. Figure 3 shows the fluctuations

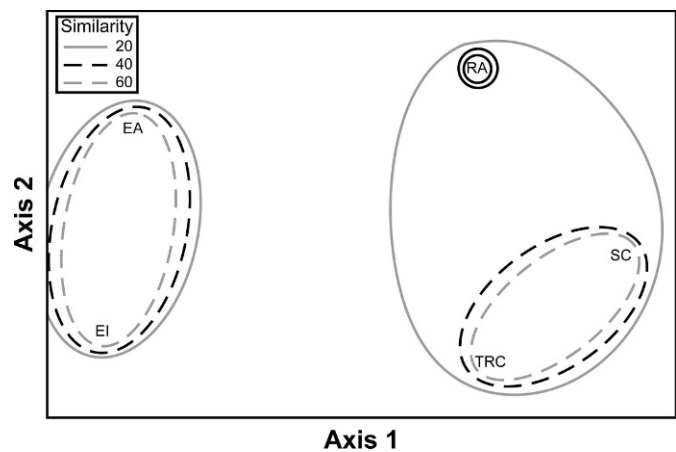


Fig. 2. Results of the nMDS showing similarity between the five sites constructed using the Bray-Curtis Index of Similarity with a stress level of 0. Values in the similarity legend illustrate the percent similarity between sites. For example, SC and TRC are 60% similar, as indicated by the line pattern closely encompassing these two locations. SC and TRC together are 20% similar to RA, and EA and EI are 60% similar to one another.

in juvenile and adult encounters throughout the two years sampled at each site. The wet season in Amazonian Peru commences in October and lasts until approximately April (Duellman, 2005; pers. obs.). Patterns were similar at most sites with more total frogs captured during the wet season versus the dry, although results from SC deviated slightly. Adult encounters peaked slightly after juvenile encounters at EI (Fig. 3C) and TRC (Fig. 3E), whereas at EA (Fig. 3A) and RA (Fig. 3B) juvenile and adult encounters were similar and at SC (Fig. 3D) they were almost completely opposite.

Pristimantis toftae was the most abundant species encountered throughout the entire study (Table 1). However, there was a significant difference in the average number of *P. toftae* captured among sites ($H_4 = 129.779$; $P < 0.001$; Fig. 4). No individuals of this species were captured at EA. Both TRC and SC had significantly more individuals of this species than all other sites. *Pristimantis peruvianus* was the second most common species captured in this study (Table 1). Unlike *P. toftae*, it was captured at all five sites, although there was a significant difference in the average number captured among sites ($H_4 = 85.961$; $P < 0.001$; Fig. 4). Most individuals of this species were captured at EA, EI, and TRC. These results are strikingly different from those of *P. toftae*, where very few individuals were captured at EI and none were present at EA. Thus, assemblages of *Pristimantis* at each site tend to be dominated by a single species.

Pristimantis peruvianus was more abundant during the wet season, but *P. toftae* showed high encounters during both seasons (Fig. 5). At RA for example, more *P. toftae* were captured in the dry season, whereas *P. peruvianus* was more common during the wet season. *Pristimantis toftae* was more common during the dry season at SC, whereas it was more common during the wet season at TRC. *Pristimantis peruvianus*, on the other hand, was more common during the wet season at EA, RA, and TRC, whereas it was nearly equally as common during both seasons at EI.

Diel and substrate influences.—There were significant diel differences in total individuals captured with more frogs

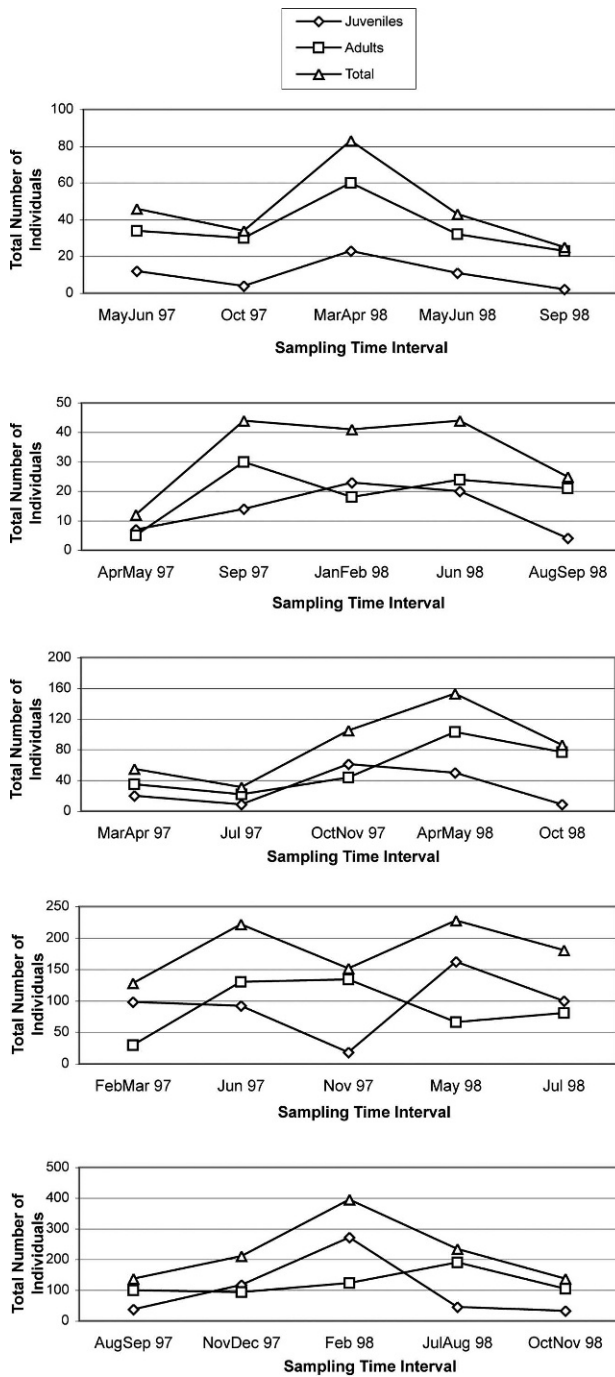


Fig. 3. Sampling time interval versus juvenile, adult, and total encounters. (A) EcoAmazonía, (B) Reserva Amazónica, (C) Explorer's Inn, (D) Sachavacayoc Centre, and (E) Tambopata Research Center.

captured during the night than during the day ($t_{151} = -6.615$; $P < 0.001$). However, there was no diel difference in the number of species captured ($F_{1,338} = 0.013$; $P = 0.911$). More males, females, and juveniles were captured during the night versus the day (Fig. 6), but there was no significant sex \times time of day interaction on abundances ($F_{2,1062} = 3.693$; $P = 0.068$).

Frogs were captured on a variety of substrate types throughout the course of this study (Fig. 7). However, ground and leaves were the most common substrates by far. More individuals of *Pristimantis* (Fig. 7A; χ^2_r day = 150.144; $P < 0.001$; χ^2_r night = 478.809; $P < 0.001$) and more species (Fig. 7B; χ^2_r day = 134.132; $P < 0.001$; χ^2_r night

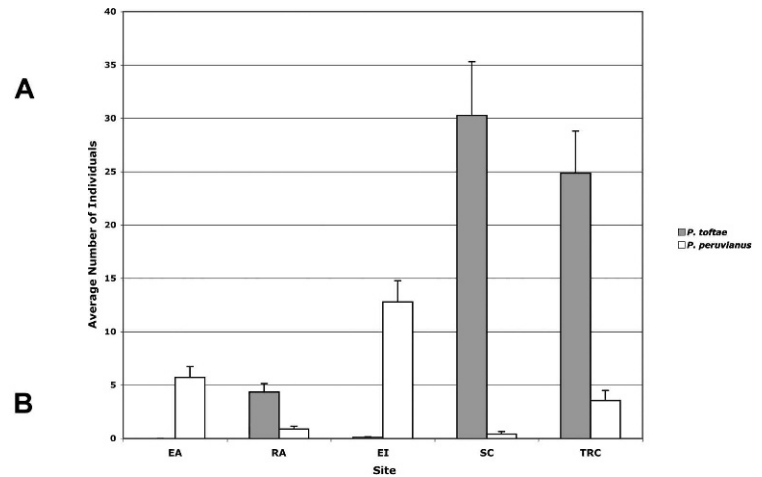


Fig. 4. Average (+SE) number *Pristimantis toftae* and *P. peruvianus* captured at each site per sampling date and parcel.

= 448.328; $P < 0.001$) were captured on the ground during the day and on leaves at night. Significant differences between leaf and ground encounters without taking time of day into account were also found, with more captured on leaves versus the ground ($t_{151} = 5.106$; $P < 0.001$), but there was no difference in species richness between leaves and ground ($Z = 0.760$; $P = 0.447$).

Capture height, leaf litter depth, and tree cover influences.—No significant relationship was found between perch height, leaf litter depth, and tree cover versus either total *Pristimantis* abundance ($F_{3,94} = 0.52$; $R^2 = 0.0162$; $P = 0.6724$) or species richness ($F_{3,94} = 0.50$; $R^2 = 0.0156$; $P = 0.6859$). However, simple linear regression showed significantly more individuals ($F_{1,150} = 12.845$; $R^2 = 0.079$; $P < 0.001$) and more species ($F_{1,150} = 12.810$; $R^2 = 0.079$; $P < 0.001$) were found higher off the ground (up to the 2 m sampling limit) versus closer to the surface.

Adults were captured significantly higher off the ground than juveniles ($\chi^2_1 = 64.057$; $P < 0.001$). The mean height of adults was 26.5 cm, whereas the mean height of juveniles was 17.2 cm. Males were captured significantly higher off the ground than females ($\chi^2_1 = 8.140$; $P < 0.001$). The mean height of males was 28.9 cm, whereas the mean height of females was 25.5 cm.

There was a significant difference among sampling dates with respect to leaf litter depth, with deeper litter during the onset of the wet season ($H_{25} = 90.559$; $P < 0.001$; Fig. 8). However, no significant relationship was found between litter depth and total number of individuals ($R^2 = 0.006$; $F_{1,96} = 0.597$; $P = 0.442$), adults ($R^2 = 0.01$; $F_{1,96} = 0.932$; $P = 0.337$), juveniles ($R^2 = 0.002$; $F_{1,96} = 0.206$; $P = 0.651$), males ($R^2 = 0.008$; $F_{1,96} = 0.760$; $P = 0.385$), or females ($R^2 = 0.005$; $F_{1,96} = 0.495$; $P = 0.483$).

Ecological factors influencing *Pristimantis toftae* and *P. peruvianus*.—No significant relationship was found between leaf litter depth, tree cover, or perch height on the abundance of *P. toftae* ($F_{3,94} = 0.13$; $R^2 = 0.0041$; $P = 0.9426$). However, with capture height data from transects included (simple regression), there was a significant relationship between perch height and *P. toftae* encounters ($R^2 = 0.120$; $F_{1,87} = 11.917$; $P = 0.001$), with more individuals captured higher off the ground versus closer to the surface.

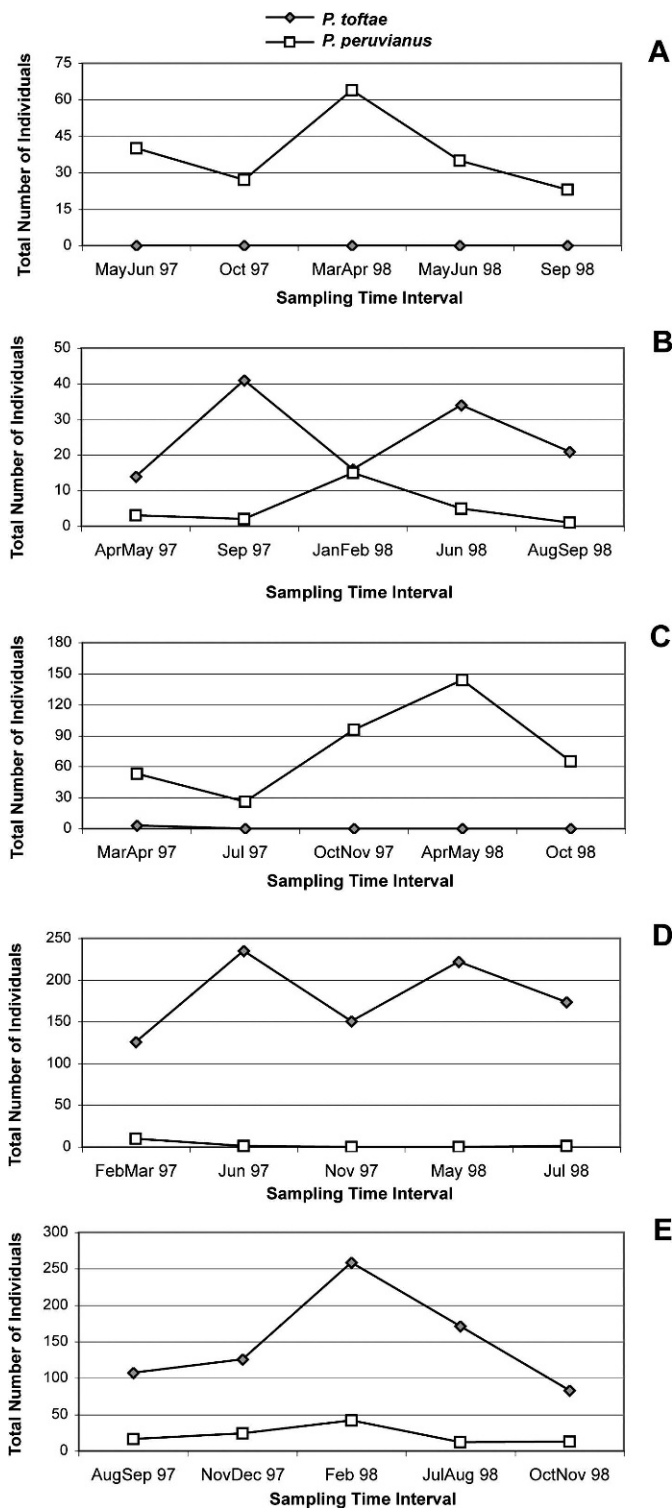


Fig. 5. Sampling interval versus total *Pristimantis toftae* and *P. peruvianus* encounters. (A) EcoAmazonía, (B) Reserva Amazónica, (C) Explorer's Inn, (D) Sachavacayoc Centre, and (E) Tambopata Research Center.

Unlike the results for *P. toftae*, there were significant relationships between perch height, leaf litter depth, and tree cover versus *P. peruvianus* encounters ($F_{3,94} = 3.54$; $R^2 = 0.1016$; $P = 0.0175$), with litter depth having the greatest influence ($P = 0.0137$). When all transect data were included, significant relationships between perch height and *P. peruvianus* encounters were found ($R^2 = 0.126$; $F_{1,120} = 17.355$; $P < 0.001$).

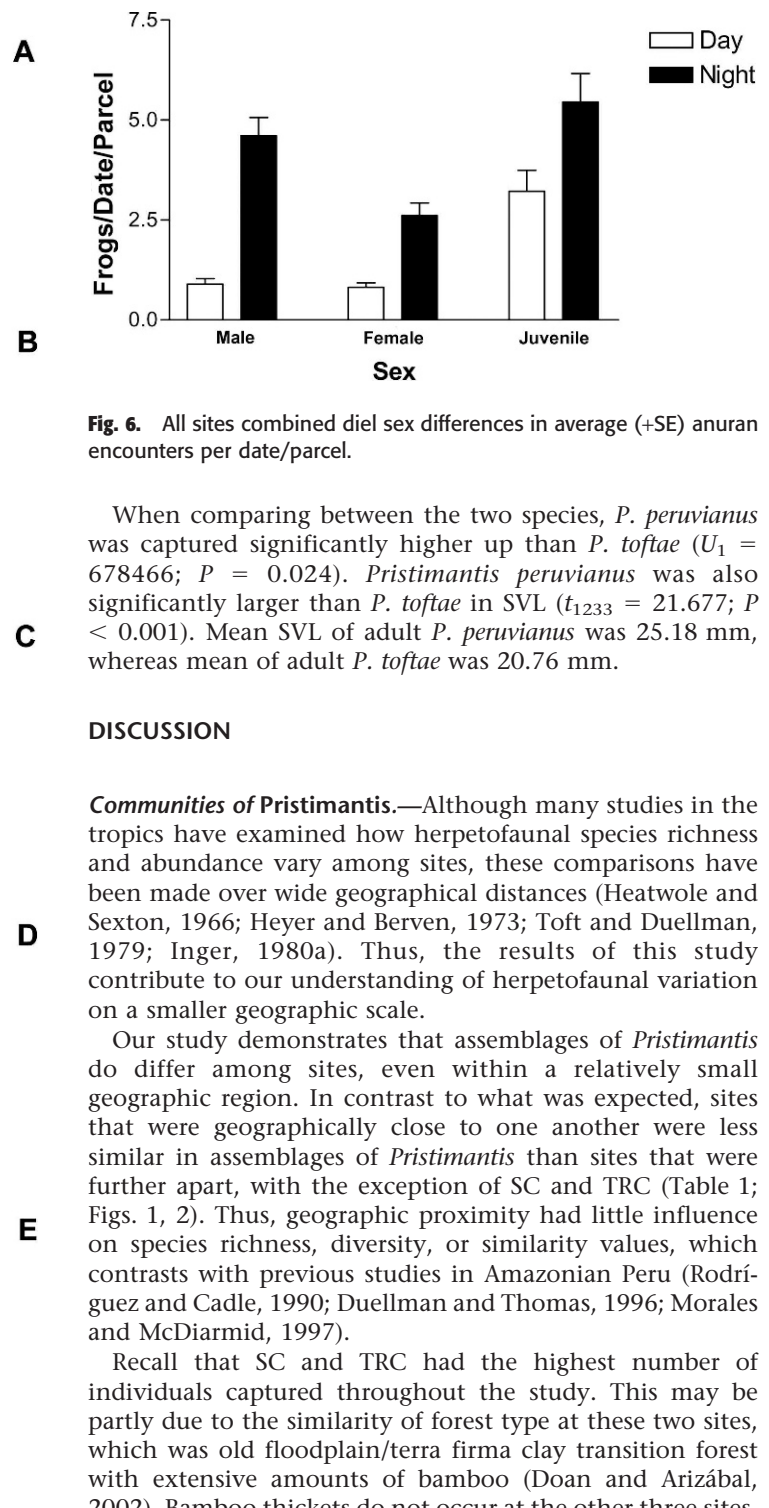


Fig. 6. All sites combined diel sex differences in average (+SE) anuran encounters per date/parcel.

When comparing between the two species, *P. peruvianus* was captured significantly higher up than *P. toftae* ($U_1 = 678466$; $P = 0.024$). *Pristimantis peruvianus* was also significantly larger than *P. toftae* in SVL ($t_{1233} = 21.677$; $P < 0.001$). Mean SVL of adult *P. peruvianus* was 25.18 mm, whereas mean of adult *P. toftae* was 20.76 mm.

DISCUSSION

Communities of *Pristimantis*.—Although many studies in the tropics have examined how herpetofaunal species richness and abundance vary among sites, these comparisons have been made over wide geographical distances (Heatwole and Sexton, 1966; Heyer and Berven, 1973; Toft and Duellman, 1979; Inger, 1980a). Thus, the results of this study contribute to our understanding of herpetofaunal variation on a smaller geographic scale.

Our study demonstrates that assemblages of *Pristimantis* do differ among sites, even within a relatively small geographic region. In contrast to what was expected, sites that were geographically close to one another were less similar in assemblages of *Pristimantis* than sites that were further apart, with the exception of SC and TRC (Table 1; Figs. 1, 2). Thus, geographic proximity had little influence on species richness, diversity, or similarity values, which contrasts with previous studies in Amazonian Peru (Rodríguez and Cadle, 1990; Duellman and Thomas, 1996; Morales and McDiarmid, 1997).

Recall that SC and TRC had the highest number of individuals captured throughout the study. This may be partly due to the similarity of forest type at these two sites, which was old floodplain/terra firma clay transition forest with extensive amounts of bamboo (Doan and Arizabal, 2002). Bamboo thickets do not occur at the other three sites. It is possible that forest type is contributing, at least partially, to the observed differences in species diversity among these sites (Watling, 2005). To our knowledge there have been no studies comparing encounters and diversity of *Pristimantis* to the amount of bamboo present, although other studies have shown a positive relationship between bamboo density and bird diversity in Tambopata (Kratter, 1997). It is possible that bamboo may provide an additional microhabitat that frogs are able to exploit.

Toft and Duellman (1979) found similar anuran assemblages in comparable habitats in Ecuador and Peru, mostly due to microhabitat and reproductive similarities. All *Pristimantis* inhabiting our five sites have similar microhab-

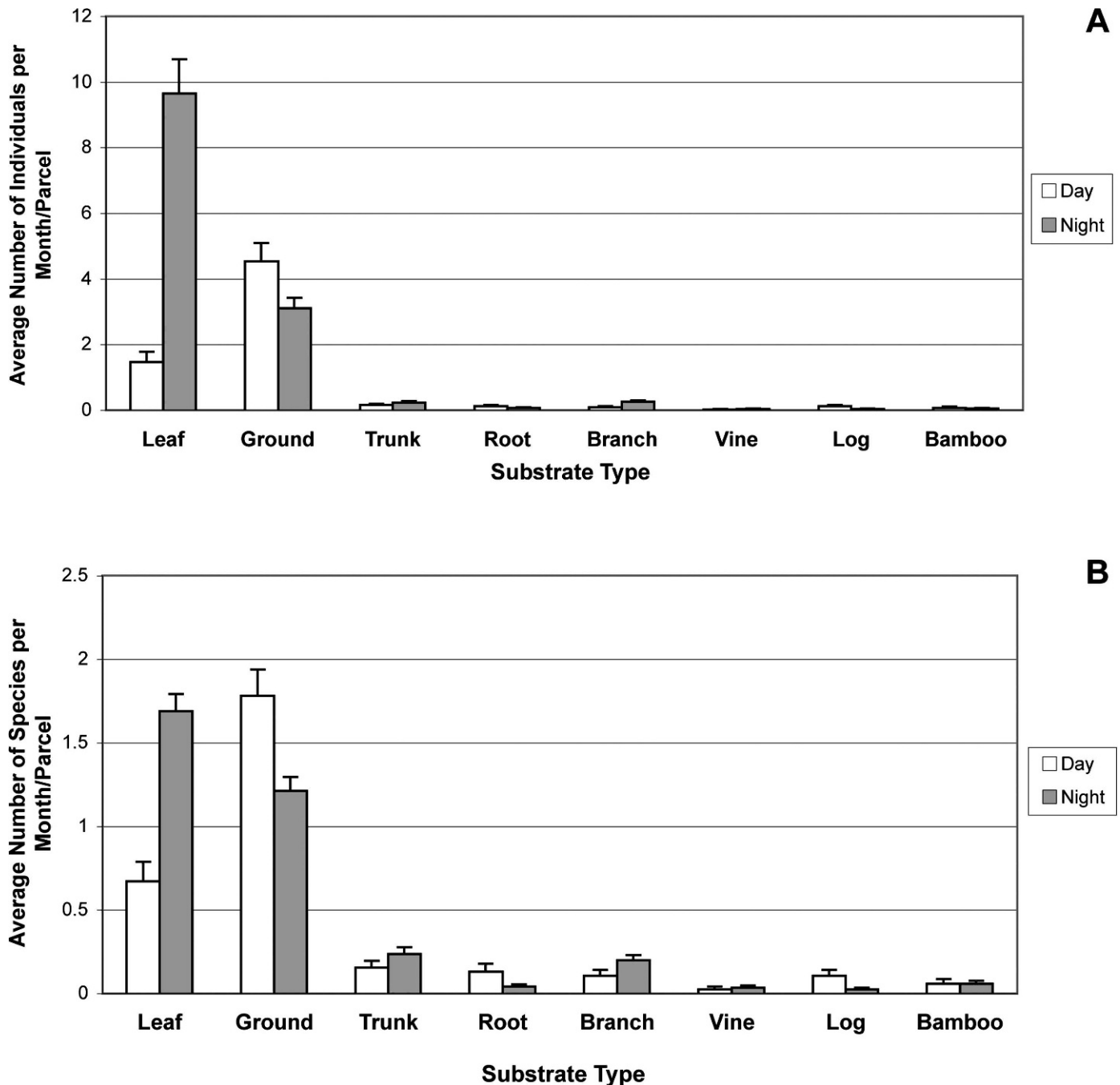


Fig. 7. All sites combined mean (\pm SE) diel differences per substrate type in (A) frog encounters and (B) total species richness.

itats as well as reproductive type, yet species compositions were drastically different. However, there did seem to be a geographic component to total frog abundance, with capture numbers increasing westward towards the Andes. Rodríguez (1994) concluded that species richness of *Pristimantis* was lower at EI than TRC due to the proximity of TRC to the Andean foothills, and Duellman (1979, 1999, 2005) stated that *Pristimantis* has been found to have high diversity at middle elevations. Our study extends those findings to include both higher species richness and higher encounters of *Pristimantis* at TRC, the site with moderately higher elevation nearest the Andean foothills.

In most cases ecology and evolution both play a vital role in shaping Neotropical communities. Generally, resource use in herpetofauna is tightly linked to the phylogenetic

history of the taxa in question and not ecological interactions (Vitt and Pianka, 2005). However, when looking at species variation over a smaller geographic area, ecology tends to be a more important factor (Tuomisto and Ruokolainen, 1997). A species may have evolved to fit a particular niche at a given time (history), but modern environmental processes and variables (ecology) are what maintain these species in these specific habitats. Moreover, as the species in question are so similar genetically and morphologically, ecological interactions may play a more vital role in determining resource use in these assemblages. We suggest that history enabled strabomantine frogs to evolve to fit their niches that they currently inhabit in this region, but that modern ecological processes are influencing distributions on a daily, monthly, seasonal, and yearly basis.

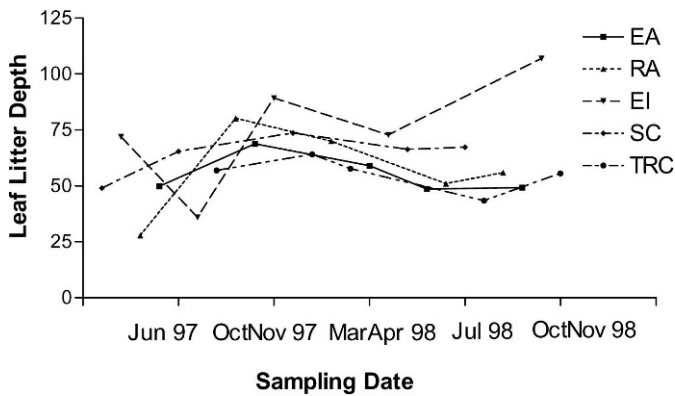


Fig. 8. Sampling date versus total leaf litter depth for the five sites sampled in Tambopata. Leaf litter values were obtained by summing litter depth at all parcels within a sampling date/site.

Many frogs within the genus have the same ecological requirements (food, habitat/microhabitat, climate, etc.); thus, in order for populations to coexist in the same location, some form of niche partitioning must take place. As more than one species was captured at all sites, it is presumed that some degree of niche partitioning is occurring, but not to the extent of permitting large populations of many species to occur sympatrically. What is interesting is that *P. toftae* was abundant at SC and TRC, which are adjacent sites, and also at RA, which is further away (Table 1; Figs. 1, 4). Similar results were found for *P. peruvianus*, with encounters greater at EA, EI, and TRC, none of which are adjacent to one another.

Considerably more juveniles, adults, and total individuals were captured during the wet season at all sites (Fig. 3). These results agree with several other studies that concluded that anuran encounters and diversity are greater during the wet season in South America (Toft, 1980a; Aichinger, 1987; Moreira and Lima, 1991; Duellman, 1995). We also found distinct seasonal patterns of leaf litter depth (Fig. 8). At each site, litter depth was greater during the wet season, particularly during the onset of the wet season around October/November. However, recall that we found no significant relationships between litter depth and abundance of *Pristimantis*, even though both litter depth and total abundance were greater during the wet season. It is probable that there are a multitude of factors causing seasonal differences in frog abundances, with leaf litter characteristics being just one. For example, the increase in litter depth during the wet season may provide more refuge space/microhabitats for these frogs, in turn increasing abundance and diversity. Alternatively, increases in invertebrate assemblages associated with the wet season may contribute to higher anuran abundances (Toft, 1980a; Lieberman, 1986; Watling and Donnelly, 2002).

There were also seasonal differences in the encounters of *P. toftae* and *P. peruvianus* (Fig. 5). *Pristimantis peruvianus* was more common during the wet season at all sites, although the exact month of peak encounters differed slightly between sites. *Pristimantis toftae*, however, was more abundant during the dry season at RA and SC, whereas at TRC encounters were greater during the wet season (Fig. 5). This contrasts with the study of Toft and Duellman (1979), which concluded that both *P. toftae* and *P. peruvianus* breed primarily and are more abundant in the dry season in Amazonian Peru.

Diel and substrate influences.—Throughout the tropics, most frog species tend to be encountered more frequently during the night than during the day (Toft and Duellman, 1979; Inger, 1980b; Miyamoto, 1982; Slowinski et al., 1987) and this was evident in our study. The fact that no relationship was found between time of day and total number of species may reflect that only 11 species were examined in this study with only one or two species dominant at a site.

Our results also showed that significantly more individuals and species were captured on leaves and ground versus all other substrate types analyzed (Fig. 7), with more frogs on the ground during the day and on leaves at night, in concordance with the results of Toft and Duellman (1979). *Pristimantis* calls from leaves at night, so perhaps males climb at night to call to females. Other possible explanations are moisture or other physiological constraints (Miyamoto, 1982). These frogs may be restricted to leaf litter retreats during the day to prevent desiccation, whereas during the night they are able to expose their bodies fully without having to consider that selective pressure.

Capture height.—More individuals were captured at higher versus lower perch heights when including data from all encounters. We hypothesize that the juvenile/adult differences in capture height were detected due to adults ascending to higher vegetation at night for feeding and mating encounters, whereas juveniles might prefer to remain hidden in the leaf litter to conceal themselves from potential predators. In addition, more males were captured higher off the ground than females, presumably to be able to better call for mates. Significantly more *P. peruvianus* were captured higher off the ground than *P. toftae*, suggesting evidence of niche partitioning. Miyamoto (1982), Parmelee (1999), and Toft (1985) demonstrated that frog species can partition their vertical microhabitats. Heatwole (1963) also concluded that *P. terraebolvaris* and *Strabomantis cornutus* were able to coexist without one out-competing the other by occupying different vegetation heights during the night, thus utilizing different available resources. Perhaps the size differences found between *P. toftae* and *P. peruvianus* enable them to partition their vertical microhabitat in order to reduce competitive pressures. However, the exact effectiveness of this microhabitat partitioning would have to be questioned as we found that sites that were extremely abundant in one species were generally lacking in the other. Although Miyamoto (1982) found that larger/heavier species within the genus ascended to significantly lower perches versus lighter species, the larger *P. peruvianus* was found higher up than *P. toftae* in our populations.

Influences of leaf litter depth.—Slowinski et al. (1987) stated that tropical leaf litter provides herpetofauna with shelter, food, breeding, and oviposition sites. Scott (1976), Fauth et al. (1989), and Allmon (1991) found positive relationships between litter depth or volume and total abundance and diversity. However, Allmon (1991) also suggested that differences in litterfall among sites are not adequate explanations for the differences in diversity that are observed in many tropical herpetofaunal comparisons. Our results are consistent with this suggestion, because of the lack of relationships between litter depth and abundance of *Pristimantis*. Although leaf litter characteristics no doubt have the ability to influence herpetofaunal species richness and abundance (Scott, 1976; Lieberman, 1986; Fauth et al.,

1989; Vonesh, 2001), there must be other ecological/environmental variables playing an important role in shaping these assemblages. Of the variables measured, *P. peruvianus* encounters were influenced most strongly by leaf litter depth. Leaf litter is one variable that contributes to habitat heterogeneity, and this heterogeneity may be one of the main driving forces shaping these frog communities (Scott, 1976; Fauth et al., 1989).

Influence of tree cover.—There was no significant relationship between tree diameter and total frog encounters. Allmon (1991) and Watling (2005) also analyzed tree cover data and found no relationship between these variables and frog abundance or diversity. It appears that other microhabitat variables are more important in determining encounters of *Pristimantis* than tree cover.

Conclusions.—The results of our study showed significant differences in *Pristimantis* among sites. However, these differences could not be attributed to leaf litter depth and tree cover, although there was a relationship between perch height and abundance of *Pristimantis*. In addition, *P. peruvianus* and *P. toftae* were shown to exhibit differences in microhabitat. Clearly, there are other potentially significant environmental variables that may help explain the observed differences in abundance and diversity of *Pristimantis* in Amazonian Peru (Blair, 2006), including forest type (Watling, 2005), soil moisture and chemistry (Watling, 2005), prey availability (Toft, 1980b; Lieberman, 1986; Parmelee, 1999), bamboo density (Kratler, 1997), vegetation characteristics, and proximity to the Andes (Rodríguez, 1994). Although only one genus was examined in this study, similar comparisons should be conducted utilizing a diverse array of taxa. This will allow for more novel conclusions to be drawn regarding relationships between ecological heterogeneity and patterns of community structure in Neotropical organisms.

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LITERATURE CITED

- Aichinger, M. 1987. Annual activity patterns of anurans in a seasonal neotropical environment. *Oecologia* 71:583–592.
- Allmon, W. D. 1991. A plot study of forest floor litter frogs, Central Amazon, Brazil. *Journal of Tropical Ecology* 7:503–522.
- Archibald, S., and W. J. Bond. 2003. Growing tall vs. growing wide: tree architecture and allometry of *Acacia karoo* in forest, savanna, and arid environments. *Oikos* 102:3–14.
- Blair, C. 2006. Ecological factors influencing *Eleutherodactylus* (Anura: Leptodactylidae) abundance and distribution at five sites in southeastern Peru. Unpubl. Masters thesis, Central Connecticut State University, New Britain, Connecticut.
- Clark, K. R., and R. M. Warwick. 2001. Changes in marine communities: an approach to statistical analysis and interpretation. Second edition. PRIMER-E, Plymouth, U.K.
- Doan, T. M. 2003. Which methods are most effective for surveying rain forest herpetofauna? *Journal of Herpetology* 37:72–81.
- Doan, T. M., and W. Arizábal. 2000. The impact of tourism on the herpetofauna of Tambopata, south-eastern Peru, p. 63–76. *In: Tourism Development and the Status of Neotropical Lowland Wildlife in Tambopata, South-eastern Peru: Recommendations for Tourism and Conservation/El Desarrollo Turístico, su Impacto sobre la Fauna Neotropical de Tambopata, Sureste del Perú: Recomendaciones para el Turismo y la Conservación.* C. A. Kirkby, T. M. Doan, H. Lloyd, A. Cornejo F., W. Arizábal A., and A. Palomino M. (eds.). Tambopata Reserve Society, London.
- Doan, T. M., and W. Arizábal. 2002. Microgeographic variation in species composition of the herpetofaunal communities of Tambopata Region, Peru. *Biotropica* 34:101–117.
- Duellman, W. E. 1979. The South American herpetofauna: a panoramic view, p. 1–28. *In: The South American Herpetofauna: Its Origin, Evolution and Dispersal.* W. E. Duellman (ed.). Museum of Natural History, University of Kansas, Lawrence, Kansas.
- Duellman, W. E. 1995. Temporal fluctuations in abundances of anuran amphibians in a seasonal Amazonian rainforest. *Journal of Herpetology* 29:13–21.
- Duellman, W. E. 1999. Distribution patterns of amphibians in South America, p. 255–328. *In: Patterns of Distribution of Amphibians.* W. E. Duellman (ed.). Johns Hopkins University Press, Baltimore, Maryland.
- Duellman, W. E. 2005. Cusco Amazónico. The Lives of Amphibians and Reptiles in an Amazonian Rainforest. Comstock Publishing Associates, Ithaca, New York.
- Duellman, W. E., and J. E. Koechlin. 1991. The reserva Cuzco Amazonico, Peru: biological investigations, conservation, and ecotourism. *Occasional Papers of the Museum of Natural History, The University of Kansas* 142:1–38.
- Duellman, W. E., and R. Thomas. 1996. Anuran amphibians from a seasonally dry forest in southeastern Peru and comparisons of the anurans among sites in the upper Amazon Basin. *Occasional Papers of the Natural History Museum, the University of Kansas* 180:1–34.
- Fauth, J. E., B. I. Crother, and J. B. Slowinski. 1989. Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica* 21:178–185.
- Gill, S. J., G. S. Biging, and E. C. Murphy. 2000. Modeling conifer tree crown radius and estimating canopy cover. *Forest Ecology and Management* 126:405–416.
- Heatwole, H. 1963. Ecologic segregation of two species of tropical frogs in the genus *Eleutherodactylus*. *Caribbean Journal of Science* 3:17–23.
- Heatwole, H., and O. J. Sexton. 1966. Herpetofaunal comparisons between two climatic zones in Panama. *American Midland Naturalist* 75:45–60.
- Heinicke, M. P., W. E. Duellman, and S. B. Hedges. 2007. Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences of the United States of America* 104:10092–10097.
- Heyer, W. R., and K. A. Berven. 1973. Species diversities of herpetofaunal samples from similar microhabitats at two tropical sites. *Ecology* 54:642–645.
- Inger, R. F. 1980a. Densities of floor-dwelling frogs and lizards in lowland forests of southeast Asia and Central America. *American Naturalist* 115:761–770.
- Inger, R. F. 1980b. Relative abundances of frogs and lizards in forests of Southeast Asia. *Biotropica* 12:14–22.

- Kratter, A. W.** 1997. Bamboo specialization by Amazonian birds. *Biotropica* 29:100–110.
- Lieberman, S. S.** 1986. Ecology of the leaf litter herpetofauna of a Neotropical rain forest: La Selva, Costa Rica. *Acta Zoologica Mexicana* 15:1–66.
- Miyamoto, M. M.** 1982. Vertical habitat use by *Eleutherodactylus* frogs (Leptodactylidae) at two Costa Rican localities. *Biotropica* 14:141–144.
- Morales, V. R., and R. W. McDiarmid.** 1997. Annotated checklist of the amphibians and reptiles of Pakitza, Manu National Park Reserve Zone, with comments on the herpetofauna of Madre de Dios, Peru, p. 503–522. *In: Manu: The Biodiversity of Southeastern Peru*. D. E. Wilson and A. Sandoval (eds.). Smithsonian Institution Press, Washington, D.C.
- Moreira, G., and A. P. Lima.** 1991. Seasonal patterns of juvenile recruitment and reproduction in four species of leaf litter frogs in Central Amazonia. *Herpetologica* 47:295–300.
- Parmelee, J. R.** 1999. Trophic ecology of a tropical anuran assemblage. *Scientific Papers, Natural History Museum, The University of Kansas* 11:1–59.
- Rodríguez, L.** 1994. Herpetofauna of the Ccolpa de Guacamayos, p. 50–51. *In: The Tambopata-Candamo Reserved Zone of Southeastern Peru: A Biological Assessment*. R. B. Foster, T. A. Parker, III, A. H. Gentry, L. H. Emmons, A. Chicchón, T. Schulenberg, L. Rodríguez, G. Lamas, H. Ortega, J. Icochea, W. Wust, M. Romo, J. A. Castillo, O. Phillips, C. Reynel, A. Kratter, P. K. Donahue, and L. J. Barkley (eds.). Conservation International, Washington, D.C.
- Rodríguez, L. B., and J. E. Cadle.** 1990. A preliminary overview of the herpetofauna of Cocha Cashu, Manu National Park, Peru, p. 410–425. *In: Four Neotropical Rainforests*. A. H. Gentry (ed.). Yale University Press, New Haven, Connecticut.
- Scott, N. J., Jr.** 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* 8:41–58.
- Slowinski, J. B., B. I. Crother, and J. E. Fauth.** 1987. Diel differences in leaf-litter abundances of several species of reptiles and amphibians in an abandoned cacao grove in Costa Rica. *Revista de Biología Tropical* 35:349–350.
- Thomas, G.** 2000. BIO-DAP Software. Princeton University Press, Princeton, New Jersey.
- Toft, C. A.** 1980a. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia* 47:34–38.
- Toft, C. A.** 1980b. Feeding ecology of thirteen synoptic species of anurans in a seasonal tropical environment. *Oecologia* 45:131–141.
- Toft, C. A.** 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- Toft, C. A., and W. E. Duellman.** 1979. Anurans of the lower Rio Llullapichis, Amazonian Peru: a preliminary analysis of community structure. *Herpetologica* 35:71–77.
- Torti, S. D., P. D. Coley, and T. A. Kursar.** 2001. Causes and consequences of monodominance in tropical lowland forests. *The American Naturalist* 157:141–153.
- Tuomisto, H., and K. Ruokolainen.** 1997. The role of ecological knowledge in explaining biogeography and biodiversity in Amazonia. *Biodiversity and Conservation* 6:347–357.
- Vitt, L. J., and E. R. Pianka.** 2005. Deep history impacts present-day ecology and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* 102:7877–7881.
- Vonesh, J. R.** 2001. Patterns of richness and abundance in a tropical African leaf-litter herpetofauna. *Biotropica* 33:502–510.
- Voris, H. K.** 1977. Comparison of herpetofaunal diversity in tree buttresses of evergreen tropical forests. *Herpetologica* 33:375–380.
- Watling, J. I.** 2005. Edaphically-biased distributions of amphibians and reptiles in a lowland tropical rainforest. *Studies on Neotropical Fauna and Environment* 40:15–21.
- Watling, J. I., and M. A. Donnelly.** 2002. Seasonal patterns of reproduction and abundance of leaf litter frogs in a Central American rainforest. *Journal of Zoology* 258:269–276.
- Whitfield, S. M., and M. S. F. Pierce.** 2005. Tree buttress microhabitat use by a Neotropical leaf-litter herpetofauna. *Journal of Herpetology* 39:192–198.