South American Journal of Herpetology, 6(2), 2011, 119-126

POPULATION STRUCTURE AND REPRODUCTIVE PATTERN OF *PRISTIMANTIS* AFF. *FENESTRATUS* (ANURA: STRABOMANTIDAE) IN TWO NON-FLOODED FORESTS OF CENTRAL AMAZONIA, BRAZIL

Fabiano Waldez[1], Marcelo Menin[2,3], Diana Patricia Rojas-Ahumada[2], and Albertina P. Lima[1]

[1] *Coordenação de Pesquisas em Ecologia e Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia – INPA. Avenida André Araújo, 2.936, CEP 69011-970, Manaus, AM, Brazil.*
[2] *Departamento de Biologia e Programa de Pós-Graduação em Diversidade Biológica, Instituto de Ciências Biológicas, Universidade Federal do Amazonas – UFAM. Avenida General Rodrigo Otávio Jordão Ramos, 3.000, CEP 69077-000, Manaus, AM, Brazil.*
[3] *E-mail corresponding author: menin@ufam.edu.br*

Abstract. *Pristimantis* aff. *fenestratus* is a common species in non-flooded forests of central Amazonia, Brazil. Herein, we show the reproductive pattern and data on population structure of this species from two sites, using standardized sample methods (visual and auditory surveys), during three rainy seasons. The higher number of males in calling activity was detected in the beginning of the rainy season. However, sporadic male calls were also heard in the dry season. Females were significantly larger than males, and males captured at the end of the rainy season were larger than those captured in other periods. Females with eggs visible through the abdominal wall were found in all samplings at one site, but a larger number of juveniles were found at the end of the rainy season. The size of juveniles was variable and the smallest individuals were found at the end of the rainy season. According to nocturnal visual surveys males were significantly more abundant than females (1.9:1 adult sex ratio). According to data collected on gravid female occurrence, juvenile number variation, and presence of calling males, we suggest that *P.* aff. *fenestratus* reproduces during the rainy season showing marked seasonality.

Keywords. Abundance, gravid females, juveniles, size, temporal variation.

Introduction

Neotropical anurans exhibit different patterns of activity related to rainfall distribution throughout the year. In some areas with seasonal climate, calling males and gravid females are generally found throughout the rainy season (Aichinger, 1987), due to the presence of water bodies for reproduction. For species with terrestrial clutches and direct development, such as the genus *Eleutherodactylus* (see Hedges *et al.,* 2008 for new taxonomic arrangement), reproduction is expected to be continuous due to their independence from water bodies for reproduction. However, studies of species of *"Eleutherodactylus"* in the Neotropical region, indicate that population recruitment and the occurrence of juveniles is variable, occurring either during the rainy season (*e.g.,* Ovaska, 1991), the dry season (*e.g.,* Fogarty and Vilella, 2002; Watling and Donnelly, 2002) or throughout the whole year (*e.g.,* Crump, 1974; Towsend and Stuart, 1994; Bourne, 1997; Donnelly, 1999; Ortega *et al.,* 2005; Arroyo *et al.,* 2008; Fong *et al.,* 2010). Some species (*e.g., Craugastor bransfordii*) vary from seasonal to continuous reproduction (Crump, 1974). A juvenile biased population structure was reported for *C. bransfordii* in Costa Rica (Donnelly, 1999).

The genus *Pristimantis* (Strabomantidae, Strabomantinae) has about 439 named species, distributed mainly in Central and South America (Frost, 2011) but most of the species of the genus are only known taxonomically. Members of this genus and others from related families (see Hedges *et al.,* 2008) are terrestrial frogs with direct development (Lynch and Duellman, 1997) or viviparity (Wake, 1978). Although these species are common components of most Neotropical anuran communities (for example they account for 32% of the anuran fauna at La Selva Biological Station in Costa Rica) (Donnelly, 1999), aspects of distribution, population structure and reproduction are unknown for this high number of species.

Pristimantis aff. *fenestratus* (Steindachner, 1864) (= *Eleutherodactylus fenestratus* in Lima *et al.,* 2006) is a common species in central Amazonia, Brazil (Zimmerman and Rodrigues, 1990; Lima *et al.,* 2006; Menin *et al.,* 2007, 2008; Rojas-Ahumada and Menin, 2010), occurring in sympatry with *Pristimantis ockendeni* and *Pristimantis zimmermanae* (Lima *et al.,* 2006; Menin *et al.,* 2007, 2008). Based on nocturnal samples in the non-flooded forest of central Amazonia, the distribution of this species is related to topographic and edaphic factors (Menin *et al.,* 2007).

Males of this species call above the ground from the leaf litter, branches or shrubs at low height (Zimmerman and Rodrigues, 1990; Lima *et al.,* 2006). The calls can be heard at dusk and dawn throughout the forest and individuals call sporadically both during the day and at night (Zimmerman and Bogart, 1984). According to Lima *et al.* (2006) reproduction occurs

from November to May, a period when clutches are deposited in the soil under fallen leaves, suggesting that this species is a seasonal breeder in central Amazonia. However, data on population structure and reproductive pattern are not available for this species. Herein, we present data on abundance, calling activity, size of adults and juveniles, sex ration and presence of gravid females of *P.* aff. *fenestratus* in two areas of *terra firme* forest in central Amazonia, based on different rainy seasons using standardized sampling methods.

Material and Methods

Study area

Our study took place at Reserva Florestal Adolpho Ducke (RFAD: 02°55' and 03°01'S, 59°53' and 59°59'W), and Fazenda Experimental of the Universidade Federal do Amazonas (Fazenda UFAM: 02°37'17" and 02°39'41"S, 60°03'29" and 60°07'57"W), both near the city of Manaus, Amazonas state, Brazil. RFAD is site 1 of the Brazilian Long Term Ecological Research (PELD) program and the two areas are part of the Programa de Pesquisa em Biodiversidade (PPBio) of the Brazilian Ministry of Science and Technology (MCT) (http://ppbio.inpa.gov.br). RFAD covers 10,000 ha of *terra firme* (non-flooded) rainforest, a well-drained forest not subject to seasonal inundation. Fazenda UFAM has an area of 3,000 ha. A 30-37 m tall closed canopy characterizes the forest in both areas, with emergent trees growing to 40-45 m (Ribeiro *et al.,* 1999). The understory contains abundant sessile palms (*Astrocaryum* spp. and *Attalea* spp., Ribeiro *et al.,* 1999). The climate is characterized by a rainy season from November to May and a dry season during the rest of the year (Marques Filho *et al.,* 1981). Mean annual temperature is approximately 26°C (Marques Filho *et al.,* 1981) and mean annual rainfall was 2,489 mm between 1985 and 2004.

Data collection and analyses

We sampled adults and juveniles of *Pristimantis* aff. *fenestratus* during three diurnal surveys (November-December 2002, February-April 2003 and January-February 2004) and five nocturnal surveys (November-December 2002, March-May 2003, November-December 2003, February-March 2004 and April-May 2004) at RFAD and three nocturnal surveys at Fazenda UFAM (November-December 2008, January-February 2009 and April-May 2009). The sampling periods were determined according to the rainy season in central Amazonia: beginning (November-December), middle (January-March) and end of the rainy season (April-May). Sporadic observations were made throughout the dry season of the same years. Data were collected in 72 plots systematically distributed over a 64-km^2 grid formed by 8-km long trails at RFAD (Figure 1) and 41 plots distributed over a 24-km^2 grid formed by four 8-km long trails in the east-west direction and nine 3-km long trails in the north-south direction at Fazenda UFAM (Figure 1). At Fazenda UFAM each plot was at least 500 m distant from any other, but 31 plots were systematically distributed at every 1 km (Rojas-Ahumada and Menin, 2010). Plots were 250 m long and positioned to follow altitudinal contour lines, thus minimizing altitudinal and soil variation within each plot (Magnusson *et al.,* 2005). All plots were at least 1 km away from the edge of the study areas. Surveys occurred only during the rainy season (November to May). At RFAD diurnal surveys required a mean of 46 days to cover all 72 plots, and nocturnal surveys required a mean of 49 days to survey all 72 plots. Each sampling period lasted between 19 and 21 days at Fazenda UFAM.

The three diurnal surveys carried out at RFAD lasted about 2 hours per plot and were conducted between 08:00 and 16:00 h by two people walking along a 250 × 1 m (0.025 ha) plot (total sampled area was 1.8 ha/sampling period). Observers visually scanned and gently turned over the leaf-litter, detecting individuals by visual encounter. We conducted nocturnal surveys at the two areas by simultaneous visual encounter and auditory sampling (Crump and Scott, 1994; Zimmerman, 1994). These methods are complementary and adequate for surveying the distribution and abundance of anurans in long and short-term studies (Doan, 2003). Nocturnal sampling of each plot lasted about one hour between 18:30 and 22:00 h. At every 5 m, the two observers stopped and recorded the number of vocalizing individuals and searched the litter and vegetation for anurans. Only one observer recorded the number of calling males to avoid counting the same individual more than once during the survey. All individuals located within 20 m of the central line of the plot were recorded so that 1 ha was searched per plot (total sampled area was 72 ha by sampling period at RFAD and 41 ha by sampling period at Fazenda UFAM). We considered abundance in this study as the number of detections

of individuals using each sampling method in each period (diurnal and nocturnal samples).

Each time we captured a frog in the nocturnal visual survey we (1) recorded its snout-vent length (SVL) with a vernier calliper (0.05 mm), (2) classified it as adult or juvenile, and (3) recorded female reproductive condition (presence/absence of eggs visible through the abdominal wall). We considered juveniles individuals with SVL < 22.0 mm (the size of the smallest male found in calling activity). In diurnal samples, observers estimated the SVL and the sex of individuals was not determined.

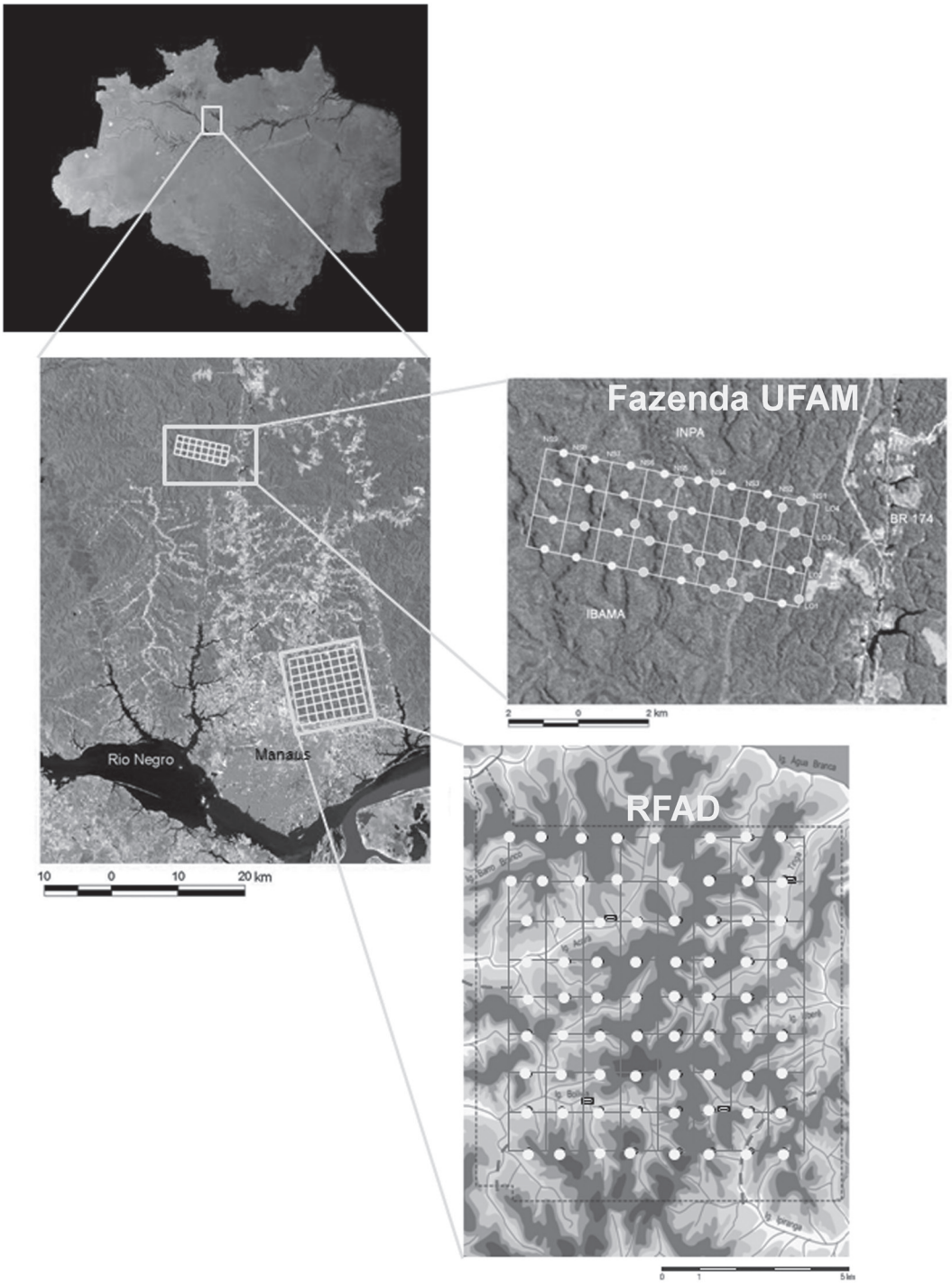

FIGURE 1. Geographical location of the study areas, Reserva Florestal Adolpho Ducke (RFAD) and Fazenda Experimental of the Universidade Federal do Amazonas (Fazenda UFAM), north of Manaus city, Amazonas State, Brazil, and the grid system inside the study areas. Circles indicate the plots.

We compared the sizes (snout-vent length, SVL) of both sexes by using the Mann-Whitney U-test (Zar, 1999). We checked the adult sex ratio by using the Chi-square test with Yates' Correction (Fowler *et al.,* 1998). The differences in size between males and females along sampling periods were tested by Kruskal-Wallis test (Zar, 1999). Voucher specimens were deposited in the Amphibians and Reptiles Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA-H 10872, 10879, 10882, 10885, 26016, 26022) in Manaus, Amazonas, Brazil.

Results

We detected 6,702 individuals of *Pristimantis* aff. *fenestratus* in nocturnal samplings at RFAD, both in visual and auditory surveys. Of these, 334 were found in visual surveys: 69 males, 35 females, and 162 juveniles (SVL < 22.0 mm). We could not determine the sex of 68 individuals (22.7 mm < SVL < 33.8 mm) due the absence of sexual dimorphism to distinguish between them (51 individuals were captured and released and 17 individuals escaped). Among individuals sampled, males were significantly more abundant than females (sex ratio 1.9:1; Chi-square = 10.47, df = 1, $p < 0.005$; Figure 2). Females with eggs visible through the abdominal wall were found in all sampling periods (Figure 2). The higher number of juveniles was found at the end of the second rainy season (Table 1 and Figure 2). Juveniles were found resting on leaves or small shrubs during the night. Based on audio surveys, the highest number of males in calling activity was detected at the beginning of the second rainy season (November-December 2003, auditory survey at Table 1) and the smallest number of males was found at the end of the two rainy seasons (second and fifth samplings, Table 1). Sporadic calls of males were heard in the dry season (June, July, September and October).

In diurnal samplings at RFAD, we detected 460 individuals (35 in November-December 2002; 127 in February-April 2003; 298 in January-February 2004), all on the ground in the leaf litter. The number of individuals increased from the first to the second sampling. Comparisons with data of the third sampling were ignored because the size of the frogs was not determined. The highest number of individuals was detected in the first size class (5 to15 mm), representing juveniles (Figure 3).

At Fazenda UFAM, we detected 667 individuals, 20 of which were found by visual surveys (7 males, 6 juveniles, 7 unidentified) (Table 1). The higher number of calling males was detected at the beginning of the rainy season and the smaller number was found at the end of the rainy season.

Based on nocturnal visual surveys (at RFAD and Fazenda UFAM), adult males averaged 29.77 mm SVL (SD = 3.10; range 22.0-36.2; N = 72); those captured at the end of the second rainy season were larger than those captured in other periods (Kruskal-Wallis = 10.459; df = 4; $p = 0.033$; Figure 4A). Calling males were found perched on tree trunks, on shrubs, or on fallen tree trunks. Adult females averaged 43.52 mm SVL (SD = 2.79; range 36.7-47.8; N = 35); those captured at the end of the second rainy season were smaller than those captured in other periods, but differences were not significant (Kruskal-Wallis = 4.193; df = 4; $p = 0.380$; Figure 4B). The minimum size of gravid females was 39.6 mm SVL. Females were found in the leaf-litter or on fallen tree

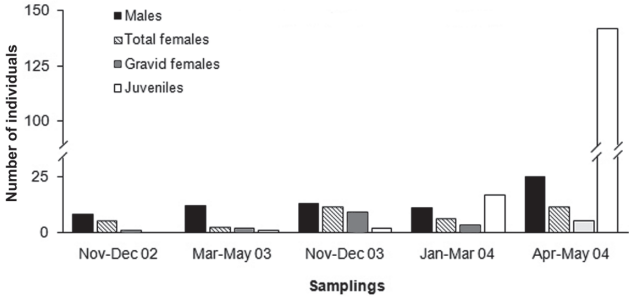

Figure 2. Number of males, females (total and only gravid), and juveniles of *Pristimantis* aff. *fenestratus* found in each nocturnal sampling by visual survey at Reserva Florestal Adolpho Ducke, Manaus, Brazil.

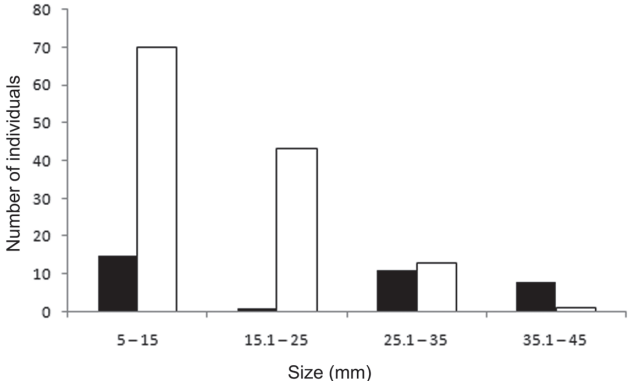

Figure 3. Number of individuals of *Pristimantis* aff. *fenestratus* recorded in diurnal samplings in different size categories of SVL (snout to vent length), Reserva Florestal Adolpho Ducke, Manaus, Brazil. Black bars: November-December 2002; white bars: February-April 2003.

Table 1. Number of individuals of *Pristimantis* aff. *fenestratus* recorded in nocturnal samplings based on two sample methods (visual and auditory surveys) conducted in 72 plots at Reserva Florestal Adolpho Ducke (RFAD) and 41 plots at Fazenda Experimental da Universidade Federal do Amazonas (Fazenda UFAM), Manaus, Brazil. Adults: snout-vent length (SVL) > 22.0 mm.

Sampling/Site	Nov-Dec/2002	Mar-May/2003	Nov-Dec/2003	Feb-Mar/2004	Apr-May/2004	Total
RFAD						
Visual survey						
Adults (males and females)	13	14	24	17	36	104
Juveniles	0	1	2	17	142	162
Undetermined	1	1	0	11	55	68
Auditory survey	1,005	604	2,406	1,416	937	6,368
Total	1,019	620	2,432	1,461	1,170	6,702
	Nov-Dec/2008	Jan-Feb/2009	Apr-May/2009			
Fazenda UFAM						
Visual survey						
Adults	2	3	2			7
Juveniles	2	3	1			6
Undetermined	2	2	3			7
Auditory survey	300	215	132			647
Total	306	223	138			667

trunks. Females were 47% larger than males in SVL (Mann-Whitney U = 2520.00; df = 1; $p < 0.001$). Juveniles were found in great number only in the middle and end of the second rainy season. Juvenile sizes varied and smaller individuals were found at the end of the two rainy seasons (Figure 4C). The smallest juvenile was 7.3 mm SVL.

Discussion

Adult males and females (gravid and non-gravid) of *Pristimantis* aff. *fenestratus* were captured in all samplings of the study period, which were conducted at different times during the rainy season. Juveniles were found mainly in the middle (February-March) and at the end (April-May) of the rainy season, and were more abundant than adults at the end of the rainy season. A similar pattern was also observed for *Craugastor bransfordii* (= *Eleutherodactylus bransfordii*) in Costa Rica (Donnelly, 1999) and other anuran species in central Amazonia (Menin *et al.,* 2008; Rojas-Ahumada and Menin, 2010).

Variation in the number of juveniles and body size of males observed in the present study suggests recruitment events. According to Donnelly (1999) the decrease in average body size suggests recruitment of juveniles into the adult class. On the other hand, data from Watling and Donnelly (2002) for populations of *Strabomantis biporcatus* (= *Eleutherodactylus biporcatus*), *Craugastor mimus* (= *Eleutherodactylus mimus*), and *Craugastor talamancae* (= *Eleutherodactylus talamancae*) from Costa Rica, indicated no significant differences in body size throughout the study period, but juvenile body size was low in the dry season and increased throughout the wet season. For populations that reproduce all year long, recruitment events are continuous (Bourne, 1997; Ortega *et al.,* 2005; Arroyo *et al.,* 2008; Fong *et al.,* 2010). In some studies the peak of reproductive activity and growth of juveniles occurs in the rainy season for species with terrestrial reproduction (Moreira and Lima, 1991; Ovaska, 1991).

Significant differences in sex ratios were probably the result of greater male conspicuousness throughout the study period, as observed by Ortega *et al.* (2005) for a population of *Eleutherodactylus johnstonei* from Colombia and *E. coqui* from Puerto Rico (Fogarty and Vilella, 2002). A male-biased sample was also observed in another anuran species and can be related to behavioral differences between sexes (Giaretta and Menin, 2004) or trapping/sampling methods (Fogarty and Vilella, 2002). Sexual size dimorphism was observed in 90% of anuran species and can be related to female fecundity (Shine, 1979), including *"Eleutherodactylus"* (Lynch and Duellman, 1997).

Gravid females were found throughout the rainy season, in contrast to that observed for *Haddadus binotatus* (= *Eleutherodactylus binotatus*) from the Atlantic Forest (Canedo and Rickli, 2006), in which the reproduction and call activity occur in the beginning of the rainy season. Seasonal reproduction was also observed in *Eleutherodactylus cooki* from Puerto Rico (Rogowitz *et al.,* 2001).

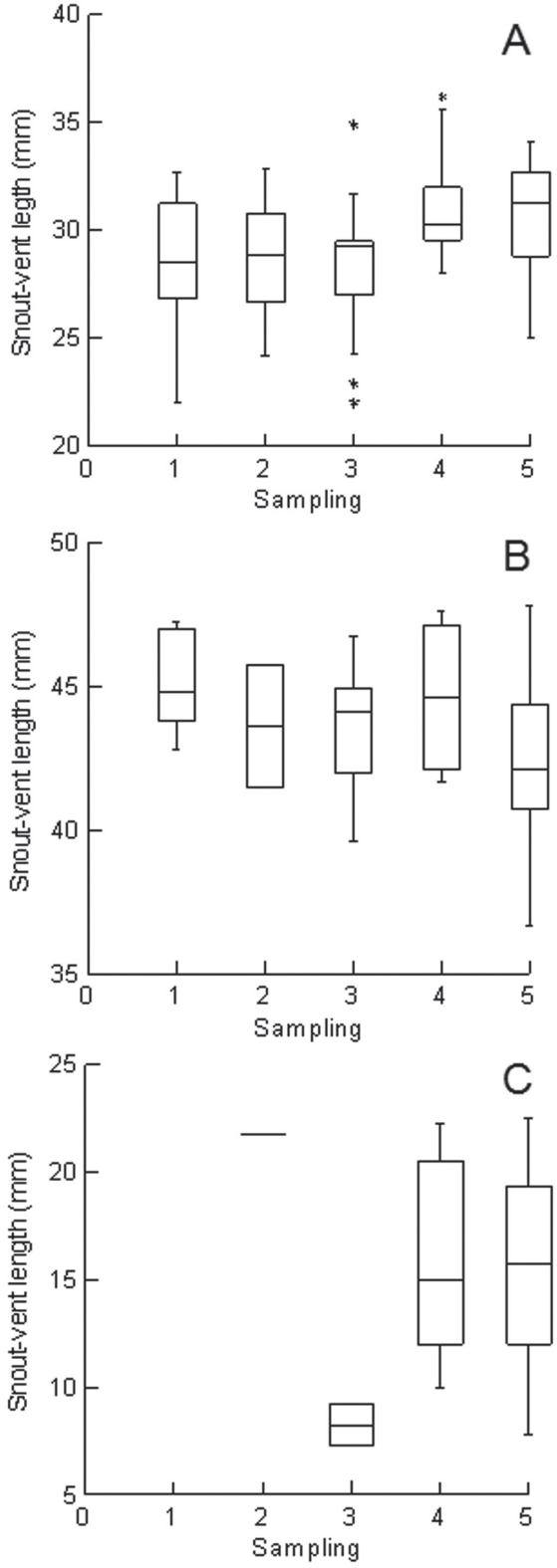

FIGURE 4. Variation in size of *Pristimantis* aff. *fenestratus* throughout the five nocturnal samplings (visual surveys) and among age classes, at Reserva Florestal Adolpho Ducke, Manaus, Brazil. (A) Males (N = 69 individuals); (B) females (N = 35 individuals); (C) juveniles (N = 162 individuals). Sampling periods: 1) November-December 2002, 2) March-May 2003, 3) November-December 2003, 4) February-March 2004, and 5) April-May 2004.

Our data show that *P.* aff. *fenestratus,* which is a terrestrial breeder, calls continuously, but shows a strong peak at the beginning of the rainy season. The data agrees partially with that from Gottsberger and Gruber (2004) for French Guiana on another species with direct development, where a slight peak in the calling activity was observed in the beginning of the rainy season, and from Menin *et al.* (2008) and Rojas-Ahumada and Menin (2010) for *Pristimantis zimmermanae* and *P. ockendeni* from central Amazonia. Other species in the Neotropical region have a continuous reproductive activity, showing seasonal variation only in the frequency of the reproductive activity (for example *C. bransfordii, E. cuneatus, E. johnstonei* and *E. coqui;* Bourne, 1997; Towsend and Stuart, 1994; Donnelly, 1999; Fong *et al.,* 2010). Continuous reproduction was also observed in *Pristimantis croceoinguinis* (= *Eleutherodactylus croceoinguinis*), *Pristimantis lanthanites* (= *Eleutherodactylus lanthanites*), *Pristimantis variabilis* (= *Eleutherodactylus variabilis*) and *E. coqui* (Crump, 1974; Towsend and Stuart, 1994). The pattern observed in central Amazonia could be related to differences in rainfall volume throughout the year, with months with lower rainfall than other tropical forest areas studied. Terrestrial eggs deposited by this species group are susceptible to dehydration, depending on substrate moisture available for embryo development (Duellman and Trueb, 1994). Areas with a low number of dry months favor the occurrence of continuous reproduction, mainly in Central America, in which the dry season is shorter and wetter than other areas of Amazonia (Watling and Donnelly, 2002).

Based on the occurrence and variation of gravid females, the presence of a higher number of juveniles at the end of the rainy season and the variation in the number of calling males, our data suggest that *P.* aff. *fenestratus* reproduces during the rainy season, showing marked seasonality.

RESUMO

Pristimantis aff. *fenestratus* é uma espécie comum e abundante em florestas de terra firme na Amazônia Central. Neste estudo, apresentamos dados de reprodução e estrutura populacional dessa espécie em duas áreas, durante três estações chuvosas, utilizando métodos de amostragem padronizados. Um maior número de machos em atividade de vocalização foi registrado no início das estações chuvosas. No entanto, cantos esporádicos de machos foram detectados na

estação seca. Machos capturados no final da estação chuvosa foram maiores que aqueles registrados em outros períodos. Fêmeas apresentaram óvulos visíveis através da parede do abdômen e foram detectadas em todas as amostragens de uma das áreas estudadas. Houve dimorfismo sexual no tamanho, sendo as fêmeas maiores que os machos. O maior número de jovens foi encontrado no final das estações chuvosas. O tamanho dos jovens foi variável e os menores indivíduos foram registrados no final das estações chuvosas. Com base nas amostragens noturnas, a razão sexual dos adultos foi 1,9:1 (machos:fêmeas). De acordo com a presença de fêmeas maduras, variação no número de jovens e variação na atividade de vocalização dos machos, acreditamos que essa espécie se reproduz durante a estação chuvosa e apresenta marcada sazonalidade.

Acknowledgements

We thank J. S. Lopes, M. M. Lima and E. V. Farias for field work assistance; Anne d'Heursel for reviewing the English; Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA) for collection permits (027/02, 036/03, 099/04, 095/05, and 11323-1), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (# 550651/01-2, 471453/03-0, 470375/2006-0, 555268/2006-3) for financial support. A Research Productivity Grant was provided to MM and APL by CNPq. Fellowships from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior to FW and DPRA.

Literature Cited

Aichinger, M. 1987. Annual activity patterns of anurans in a seasonal Neotropical environment. *Oecologia,* 71:583-592.

Arroyo, S. B., V. H. Serrano-Cardozo, and M. P. Ramírez-Pinilla. 2008. Diet, microhabitat and time of activity in a *Pristimantis* (Anura, Strabomantidae) assemblage. *Phyllomedusa,* 7(2):109-119.

Bourne, G. R. 1997. Reproductive behavior of terrestrial breeding frogs *Eleutherodactylus johnstonei* in Guyana. *Journal of Herpetology,* 31(2):221-229.

Canedo, C. and E. Rickli. 2006. Female reproductive aspects and seasonality in the reproduction of *Eleutherodactylus binotatus* (Spix, 1824) (Amphibia, Leptodactylidae) in an Atlantic rainforest fragment, Southeastern Brazil. *Herpetological Review,* 37(2):149-151.

Crump, M. L. 1974. Reproductive strategies in a tropical anuran community. *Miscellaneous Publications of the Museum of Natural History,* University of Kansas, 61:1-68.

Crump, M. L. and N. J. Scott Jr. 1994. Visual encounter surveys; pp. 84-92. In: W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek and M. S. Foster (Eds.), Measuring and Monitoring Biological Diversity: Standard methods for amphibians. Smithsonian Institution Press, Washington.

Doan, T. M. 2003. Which methods are most effective for surveying rain forest herpetofauna? *Journal of Herpetology,* 37(1):72-81.

Donnelly, M. A. 1999. Reproductive phenology of *Eleutherodactylus bransfordii* in Northeastern Costa Rica. *Journal of Herpetology,* 33(4):624-631.

Duellman, W. E. and L. Trueb. 1994. Biology of Amphibians. The Johns Hopkins University Press, Baltimore and London, 670 pp.

Fogarty, J. H. and F. J. Vilella. 2002. Population dynamics of *Eleutherodactylus coqui* in Cordillera forest reserves of Puerto Rico. *Journal of Herpetology,* 36(2):193-201.

Fong G., A. J.-M. Hero, R. Viña, and I. Bignotte-Giró. 2010. Population ecology of the riparian frog *Eleutherodactylus cuneatus* in Cuba. *Biotropica,* 42(3):348-354.

Fowler, J., L. Cohen, and P. Jarvis. 1998. Practical Statistics for Field Biology. John Wiley & Sons, Chichester, 259 pp.

Frost, D. R. 2011. Amphibian Species of the World: An online reference. Version 5.5, *American Museum of Natural History,* New York. Eletronic database accessible at http://research.amnh.org/vz/herpetology/amphibia (31 January 2011).

Giaretta, A. A. and M. Menin. 2004. Reproduction, phenology and mortality sources of a species of *Physalaemus* (Anura: Leptodactylidae). *Journal of Natural History,* 38:1711-1722.

Gottsberger, B. and E. Gruber. 2004. Temporal partitioning of reproductive activity in a Neotropical anuran community. *Journal of Tropical Ecology,* 20:271-280.

Hedges, S. B., W. E. Duellman, and M. P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa,* 1737:1-182.

Lima, A. P., W. E. Magnusson, M. Menin, L. K. Erdtmann, D. J. Rodrigues, C. Keller, and W. Hödl. 2006. Guia de sapos da Reserva Adolpho Ducke, Amazônia Central = Guide to the frogs to Reserva Adolpho Ducke, Central Amazonia. Atemma, Manaus, 168 pp.

Lynch, J. D. and W. E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in Western Ecuador: systematics, ecology, and biogeography. *The University of Kansas Natural History Museum,* Special Publication, 23:1-236.

Magnusson, W. E., A. P. Lima, R. C. Luizão, F. Luizão, F. R. C. Costa, C. V. Castilho, and V. F. Kinupp. 2005. RAPELD: uma modificação do método de Gentry para inventários de biodiversidade em sítios para pesquisa ecológica de longa duração. *Biota Neotropica,* 5(2). www.biotaneotropica.org.br/v5n2/pt/abstract?point-of-view+bn01005022005.

Marques Filho, A. O., M. N. G. Ribeiro, H. M. Santos, and J. M. Santos. 1981. Estudos climatológicos da Reserva Florestal Ducke – Manaus, AM. IV. Precipitação. *Acta Amazonica,* 11:759-768.

Menin, M., A. P. Lima, W. E. Magnusson, and F. Waldez. 2007. Topographic and edaphic effects on the distribution of terrestrially reproducing anurans in Central Amazonia: mesoscale spatial patterns. *Journal of Tropical Ecology,* 23:539-547.

Menin, M., F. Waldez, and A. P. Lima. 2008. Temporal variation in the abundance and number of species of frogs in 10,000 ha of a forest in Central Amazonia, Brazil. *South American Journal of Herpetology,* 3(1):68-81.

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(3):295-300.

Ortega, J. E., V. H. Serrano, and M. P. Ramírez-Pinilla. 2005. Reproduction of an introduced population of *Eleutherodactylus johnstonei* at Bucaramanga, Colombia. *Copeia,* 2005(3):642-648.

Ovaska, K. 1991. Reproductive phenology, population structure, and habitat use of the frog *Eleutherodactylus johnstonei* in Barbados, West Indies. *Journal of Herpetology,* 25(4):424-430.

Ribeiro, J. E. L. S., M. G. Hopkins, A. Vicentini, C. A. Sothers, M. A. S. Costa, J. M. Brito, M. A. D. Souza, L. H. P. Martins, L. G. Lohmann, P. A. C. L. Assunção, E. C. Pereira, C. F. Silva, M. R. Mesquita, and L. Procópio. 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra firme na Amazônia Central. Instituto Nacional de Pesquisas da Amazônia, Manaus, 800 pp.

Rogowitz, G. L., C. L. Candelaria, L. E. Denizard, and L. J. Meléndez. 2001. Seasonal reproduction of a Neotropical frog, the cave coquí (*Eleutherodactylus cooki*). *Copeia,* 2001(2):542-547.

Rojas-Ahumada, D. P. and M. Menin. 2010. Composition and abundance of anurans in riparian and non-riparian areas in a forest in Central Amazonia, Brazil. *South American Journal of Herpetology,* 5(2):157-167.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. *Copeia,* 1979(2):297-306.

Towsend, D. S. and M. M. Stewart. 1994. Reproductive ecology of the Puerto Rican frog *Eleutherodactylus coqui*. *Journal of Herpetology,* 28(1):34-40.

Wake, M. H. 1978. The reproductive biology of *Eleutherodactylus jasperi* (Amphibia, Anura, Leptodactylidae), with comments on the evolution of live-bearing systems. *Journal of Herpetology,* 12(2):121-133.

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.

Zar, J. H. 1999. Biostatistical Analysis, 4th ed. Englewood Cliffs, Prentice Hall, 718 pp.

Zimmerman, B. L. 1994. Audio Strip Transects; pp. 92-97. In: W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L.-A. C. Hayek, M. S. Foster (Eds.), Measuring and Monitoring Biological Diversity. Standard methods for amphibians. Smithsonian Institution Press, Washington.

Zimmerman, B. L. and J. P. Bogart. 1984. Vocalizations of primary forest frog species in the Central Amazon. *Acta Amazonica,* 14:473-519.

Zimmerman, B. L. and M. T. Rodrigues. 1990. Frogs, snakes, and lizards or the INPA-WWF reserves near Manaus, Brazil; pp. 426-454. In: A. H. Gentry (Ed.), Four Neotropical Rainforest. Yale University Press, New Haven.

Submitted 14 February 2011
Accepted 08 June 2011