

## Diversity and Abundance of Litter Frogs in a Montane Forest of Southeastern Brazil: Seasonal and Altitudinal Changes<sup>1</sup>

A. A. Giaretta<sup>2</sup>, K. G. Facure, R. J. Sawaya, J. H. De M. Meyer, and N. Chemin

Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C.P. 6109, 13083-970, Campinas, SP, Brasil.

### ABSTRACT

We sampled litter frogs in an 1800-ha mid-elevation seasonal forest in southeastern Brazil. One hundred 8 × 8-m plots were sampled during the dry/cold season and wet/warm season (unburned areas); we also examined the effects of fire in recently burned areas. A total of 267 frogs (305 g), belonging to 16 species (4 families) were caught. A single species comprised 78.5 percent of the individuals in the dry/cold season and 54.3 percent in the wet/warm season. The density of individuals did not change significantly with season, biomass did. Density and biomass of frogs were positively correlated with altitude. A Mantel test indicated that biological data (species and their abundance) were significantly associated with environmental parameters. The burned areas showed low values in richness, density and biomass of frogs. Harsh seasonal climate and a history of human disturbance may produce the low observed diversity values. The greater densities of frogs in sites of higher elevation may primarily result from mist-generated humidity, which diminishes the harshness of the dry/cold season in relation to lower sites.

### RESUMO

Amostramos a anurofauna de serapilheira de um fragmento de floresta sazonal de altitude (1800 ha) no Sudeste do Brasil. Cem parcelas de 8 × 8-m foram amostradas na estação fria e seca, em áreas não queimadas na estação quente e úmida e em áreas de queimada recente. No total 267 sapos foram coletados (305 g), pertencendo a 16 espécies (4 famílias). Uma única espécie representou 78,5 por cento dos indivíduos na estação fria e seca e 54,3 percent na quente e úmida. A densidade de indivíduos não variou sazonalmente, a biomassa sim. A densidade e a biomassa de sapos se correlacionaram positivamente com a altitude. Um teste de Mantel indicou que os dados biológicos (espécies e suas abundâncias) se correlacionaram significativamente com as variáveis ambientais. As áreas queimadas apresentaram baixos valores de riqueza, densidade e biomassa de sapos. O clima sazonalmente estressante e a história de perturbação humana no local devem estar agindo em conjunto para produzir os baixos valores de diversidade observados. A maior densidade de sapos em locais mais altos deve ser resultado principalmente da umidade gerada pela neblina, a qual diminui o rigor da estação fria e seca em relação a locais mais baixos.

*Key words:* abundance; altitudinal changes; biomass; *Brachycephalus ephippium*; *Bufo*; cloud forest; conservation; dominance; *Elcutherodactylus* spp.; fire effects; human disturbance; *Hyla*; litter frog assemblage; *Physalaemus*; *Proceratophrys*; seasonal changes; seasonal forest; southeastern Brazil; species diversity.

SPECIES COMPOSITION AND ABUNDANCE OF LITTER FROGS are influenced by local environmental conditions, such as altitude and climate (Scott 1976, Toft 1980b), in addition to historical factors, such as human disturbance (Lieberman 1986, Heinen 1992). In seasonal environments, a long dry season may adversely affect the litter herpetofauna directly by restricting the availability of moist microhabitats and indirectly by lowering primary production and slowing decomposition (Scott 1976). In South America, samples of litter frogs are restricted to

Amazon forest (Allmon 1991), and possible regional patterns cannot be evaluated because studies related to the Atlantic forest domains (sensu Ab'Saber 1977) are scarce (Giaretta et al. 1997). We present and discuss data on diversity and abundance of litter frogs in a seasonally dry altitudinal forest in the Mantiqueira range, Atlantic forest in southeastern Brazil. We also looked for seasonal and altitudinal changes and fire effects on litter frogs, and investigated the influence of environmental variables on the diversity and abundance of these animals.

### STUDY AREA

This study was carried out in a mid-elevation seasonal forest at the Parque Florestal do Itapetinga

<sup>1</sup> Received 15 September 1996; revision accepted 25 April 1998.

<sup>2</sup> Current address: Departamento de Biosciências, Universidade Federal de Uberlândia, CP 593, CEP 38400-902, Uberlândia, MG, Brazil.

(PFI) and adjacent areas (*ca* 23°15'S, 46°45'W; 900–1250 m elev.; 1400–1700 mm rainfall/yr; *ca* 1800 ha). This site is in the municipality of Atibaia, Mantiqueira range of the state of São Paulo, southeastern Brazil. The regional climate is seasonal, with a dry/cold season (DC) from April to September (with occasional frosts in June and July) and a wet/warm season (WW) from October to March (maximum 38°C). In some months of the DC, the precipitation can be zero. The vegetational type is "altitudinal semi-deciduous forest" (Meira-Neto et al. 1989, Grombone et al. 1990); at *ca* 1200 m elevation, a montane cloud forest (*sensu* Bruijnzeel & Proctor 1995) occurs. The terrain is sloping; buttressed trees and tank bromeliads are rare. At the periphery of the forest, there are orchards, pastures, and agricultural fields. Natural bodies of water include forest rivulets and oxbow ponds; there are two small artificial lakes in the area. In the past, trees in some areas of the park were cut and burned for charcoal, as indicated by old roads and charcoal pits. Occasional human-generated forest fires occur, mainly during the DC. Public visitation to the park is minimal.

## MATERIALS AND METHODS

The sample units used in this project were 8 × 8-m plots, sampled as in Jaeger and Inger (1994). The plots were distributed along trails and streams, mainly on the west face of the hill, as defined by a sequence of three randomizing steps—the first roughly determined a numbered point on the map, the second indicated the side of the trail or stream, and the third, the number of paces (1–500) perpendicular to the trail or stream to the sample point; minor adjustments were occasionally made to maintain uniform declivity. The 50 DC plots were sampled from late May to mid August 1994 and the 50 WW plots from January to early February 1995. Eleven of the WW plots were in burned areas (BA) caused by fires four months prior to sampling. These fires affected portions of both cloud and lower forests. Hereafter, WW will refer only to 39 plots in unburned areas. Each plot perimeter was delimited by ropes and strips of bare ground. The plots were examined once during the daytime by four or five of us. We turned over the litter with garden forks, superficially examined holes in the ground with flashlights, and rolled logs looking for frogs. All frogs were weighed to the nearest 0.01 g. A few small frogs that were lost before identification were used only for calculations of density and biomass (estimates according to

size). We used a topographic relief map and an altimeter (WW plots) to determine altitudes. To examine effects of altitude in the DC, we grouped plots *a posteriori* as belonging to three altitudinal belts: low (900–1050 m), mid-elevation (*ca* 1100 m), and cloud forest (1200–1250 m).

We searched for associations between environmental variables and biological data (species and their abundance) in WW plots containing at least one frog. We calculated a correlation coefficient between distance matrices (species and environmental) using the Mantel test (Luo & Fox 1996). Environmental data used in multivariate analyses and evaluation of some seasonal changes were: number of large- (diameter >110 cm), medium- (71–109 cm) and small-sized (20–70 cm) trees; soil cover depth (litter + root mat); estimated percentage of canopy, understory and herb cover; maximum tree height above a plot; slope; density of litter insects; dried litter mass; area inside the plot occupied by fallen trunks (diameter above 10 cm); and litter moisture. Soil cover depth was measured in each corner and at the center of each plot. We used a 30-cm diameter ring to delimit the areas for litter samples, inside of which we counted insects (two samples) and measured litter mass and moisture (three samples). Insects were extracted from the litter in Berlese funnels (Borror & DeLong 1988). Litter moisture, expressed as percentage of weight, was determined by drying the sample at 90°C for 24 h. We used insect density as an indicator of potential prey abundance. The significance of the correlation in the Mantel test was evaluated by 9999 random permutations made in the NT-SYS package (Rohlf 1988). For environmental data, we used Euclidian distance over the standardized matrix (Digby & Kempton 1987) and for biological data, the Bray-Curtis measure. Correlations and local and seasonal variation in biological and environmental parameters were tested with nonparametric methods (Zar 1974). The Shannon-Wiener diversity index, using the natural logarithms of the proportions, was calculated and statistical differences between seasons were tested as in Magurran (1988). We refer to dominance as the relative abundance of the most common species. The index of dispersion (variance–mean ratio) was calculated for each season as an indicator of spatial distribution of frogs; the pattern of spatial distribution was investigated and the goodness of fit to theoretical statistical distributions was tested as in Krebs (1989). The expected richness of each sample was estimated by a jackknife method (Krebs 1989). The three most abundant species in this study were

TABLE 1. Species and its proportional contribution (%) to the litter sample at Parque Florestal do Itapetinga (Atibaia, SP, Brazil) by season.

Family Species	Season	
	Dry/cold	Wet/ warm
Brachycephalidae		
<i>Brachycephalus ephippium</i>	78.6	54.4
Bufo		
<i>Bufo crucifer</i>	0	3.1
<i>B. ictericus</i>	0	0.8
Hylidae		
<i>Hyla faber</i> <sup>a</sup>	0.7	0.8
<i>H. leucopygia</i> <sup>a</sup>	1.5	0
<i>H. luctuosa</i>	1.5	7.9
<i>H. prasina</i> <sup>a</sup>	0.7	0
<i>Scinax biemalis</i>	0	1.6
Leptodactylidae		
<i>Crossodactylus</i> sp. n.	0.7	0.8
<i>Eleutherodactylus guentheri</i>	1.5	8.6
<i>E. juipoca</i>	0.7	0
<i>E. parvus</i>	12.7	11.8
<i>E. spanios</i>	0.7	4.7
<i>Hylodes</i> sp. (gr. <i>lateristrigatus</i> )	0	0.8
<i>Physalaemus</i> sp. (cf. <i>olferstii</i> )	0.7	3.1
<i>Proceratophrys boiei</i>	0	1.6
Total number of plots and frogs	50/135	39/127

<sup>a</sup> Casual species in the litter.

direct developing; basic biological data for most of the frog species reported here can be found in Haddad and Sazima (1992), Heyer et al. (1990), and Pombal et al. (1994). Voucher frog specimens were deposited in the Museu de História Natural da Universidade Estadual de Campinas (ZUEC).

## RESULTS

In our leaf litter samples at PFI, we caught a total of 267 frogs belonging to 16 species and four families, with a total biomass of 305 g. The propor-

tional contributions (in no. of individuals) of each species and for each season are given in Table 1. The absolute values of richness, number of individuals, and biomass (by samples) were: DC = 11, 135, 103 g; WW = 13, 127, 195 g; BA = 4, 5, 7 g (50, 39, and 11 plots, respectively). The overall density for the area was, when adjusted to 100 m<sup>2</sup>, was 4.6 frogs (DC + WW). A single snake (*Bothrops jararaca*) and one lizard (*Enyalius perditus*) were caught.

*Brachycephalus ephippium* had the greatest number of individuals in both seasons, followed by *Eleutherodactylus parvus* (Table 1). In the DC, *B. ephippium* also dominated in biomass, but in the WW, some less abundant but larger species (e.g., *Proceratophrys boiei* and *Hyla luctuosa*) had greater biomass values. The jackknife estimate of richness did not differ between seasons, each season averaging 17 species; BA had a lower value (6 spp.). The Shannon-Wiener diversity index for DC ( $H' = 0.856$ ) was lower than for WW ( $H' = 1.641$ ;  $t = 4.99$ ;  $P < 0.001$ ;  $df = 262$ ). No new species were added to the sample after 80 plots.

In the WW the biomass of frogs (Table 2) was greater than for the DC. The density of individuals did not show a significant seasonal difference (Table 2).

The Mantel test of WW data indicated that biological dissimilarity (species and their abundance) among the plots was significantly associated with the environmental dissimilarity among them ( $r = 0.211$ ,  $t = 2.60$ ;  $P = 0.006$ ,  $N = 31$  plots). In the WW, the abundance of frogs was significantly correlated with: soil cover depth ( $r_s = 0.38$ ,  $P < 0.05$ ,  $N = 31$ ); altitude ( $r_s = 0.59$ ,  $P < 0.01$ ,  $N = 31$ ); dried litter mass ( $r_s = -0.44$ ,  $P < 0.02$ ,  $N = 31$ ); and fallen trunk area ( $r_s = 0.47$ ,  $P < 0.01$ ,  $N = 31$ ). The biomass of frogs ( $r_s = 0.506$ ;  $P < 0.001$ ,  $N = 39$ ) and the density of insects ( $r_s = 0.447$ ,  $P = 0.01$ ,  $N = 38$ ) were positively correlated with elevation. We also detected an increase

TABLE 2. Seasonal variation in environmental and biological parameters for the litter frogs of Parque Florestal do Itapetinga (Atibaia, SP, Brazil).

	Dry/cold season			Wet/warm season			U	P
	Median	(Range)	N	Median	(Range)	N		
Litter moisture (%)	34	(11-75)	45	70	(44-81)	39	112	<0.001
Temperature (°C)	17	(2-23)	44	23	(20-27)	33	57	<0.001
Litter mass (g/0.21 m <sup>2</sup> )	137	(65-242)	45	104	(34-181)	39	427	<0.001
Insects (ind./0.14 m <sup>2</sup> )	17	(1-171)	41	31	(1-179)	38	498	0.006
Frogs/plot	1	(0-16)	50	1	(0-23)	39	859	0.325
Biomass (g/plot)	0.4	(0-41)	50	1.4	(0-52)	39	740	0.049

TABLE 3. A comparison of density ( $DI = \text{individuals/plot}$ ) and biomass ( $B = \text{g/plot}$ ) for litter frog assemblages at Parque Florestal do Itapetinga, Atibaia, SP, Brazil. Categories of altitude are Low (900–1050 m), Medium (ca 1100 m), and Cloud Forest (1200–1250 m). Within a season, different superscripts indicate differences ( $P \leq 0.05$ ).

Season		Altitude			Kruskal-Wallis $H$
		Low DI/B	Medium DI/B	Cloud Forest DI/B	
Dry/cold	Median	0 <sup>a</sup> /0.0 <sup>a</sup>	1/0.6	2 <sup>b</sup> /1.2 <sup>b</sup>	7.90/6.19
	Maximum	3/2.6	8/8.0	16/41.0	
	$N$ (plots)	15	16	19	
Wet/warm	Median	1 <sup>a</sup> /0.9 <sup>a</sup>	1 <sup>a</sup> /0.8 <sup>a</sup>	4 <sup>b</sup> /8.3 <sup>b</sup>	12.29/8.43
	Maximum	6/9.8	6/22.5	23/51.8	
	$N$ (plots)	16	12	11	

in density and biomass of frogs when plots were grouped into altitudinal belts, including DC data (Table 3). In the WW, soil cover depth also correlated with elevation ( $r_s = 0.376$ ,  $P < 0.05$ ,  $N = 39$ ). In the DC, litter moisture in cloud forest was marginally greater than the lower adjacent areas (Mann-Whitney  $U$ -test:  $U = 162.0$ ,  $0.05 < P < 0.10$ ). The cloud forest also had the greatest seasonal variation in biological parameters (Tables 3 and 4), and the density of litter frogs (5.6/plot) was about four times greater than the lower areas (DC + WW). *Brachycephalus ephippium* was the dominant species in the three altitudinal belts and in both seasons (Table 4). Despite the altitudinal differences in frog density and dominance, no species was restricted to a given altitudinal belt (Giaretta, pers. obs.).

Litter frogs of PFI were aggregated during both seasons, and the negative binomial adequately described the frequencies distribution (WW:  $\chi^2 = 11.79$ ; DC:  $\chi^2 = 4.08$ ; both with  $df = 6$  and  $P > 0.05$ ); the degree of aggregation was greater in the DC (lower  $k$ , negative binomial exponent). In the DC, plots having at least one frog had moister litter than empty ones ( $U = 162$ ,  $P = 0.05$ ). The proportion of juveniles in the samples of WW (22%) was not significantly greater than for the DC (14%;  $\chi^2 = 2.34$ ,  $df = 1$ ,  $P = 0.13$ ).

TABLE 4. Percent contribution (dominance) of *Brachycephalus ephippium* to the litter frogs at Parque florestal do Itapetinga, Atibaia, SP, Brazil, in each altitude and season.

Altitude	Season	
	Dry/cold	Wet/warm
Low (900–1050 m)	36.4	37.5
Medium (ca 1100 m)	66.7	41.2
Cloud Forest (1200–1250 m)	87.9	61.6

The burned areas had drier litter ( $U = 60.5$ ,  $P = 0.001$ ), lower soil cover depth ( $U = 132.5$ ,  $P = 0.05$ ), lower density of individuals (0.45 frogs/plot;  $U = 80.5$ ,  $P = 0.001$ ) and lower biomass (0.64 g/plot;  $U = 79.0$ ,  $P = 0.001$ ) than the unburned WW plots.

## DISCUSSION

We have conducted herpetological studies at the PFI since 1992, and all frog species known to occur in the leaf litter were collected within the study plots. High values of dominance, such as those found for *B. ephippium* at PFI, are typical of seasonally stressed or early successional environments (for herpetological examples, see Lieberman 1986, Heinen 1992). At Serra do Japi, another site in the Mantiqueira range, Giaretta et al. (1997) also found high values of dominance for litter frogs, due to two *Eleutherodactylus* species. At PFI and Japi, long dry periods (4–6 months), winter frosts, sporadic occurrence of fires, and a history of human disturbance may be responsible for the high dominance values. Differences in the dominant species between PFI and Japi can be attributed in part to differences in the considered altitudinal ranges and sampling design.

The inland montane forests of southeastern Brazil are seasonal in litter production, flowering, and fruiting; litter peaks in the late dry season (Morellato 1992). We found that the density of potential arthropod prey was lower in the DC and that the litter frog assemblage had a lower diversity and biomass in the harsher period. Scott (1976) found a negative correlation between the number of dry months at a locality and the richness of litter frogs. The richness we observed at PFI (13 regular spp.; Table 1) agrees with his model. The greater diversity of litter frogs in the wetter season was expected, based on other studies (Scott 1976, Toft 1980b,

Rodriguez 1992). The greater seasonal variation in the diversity observed in the cloud forest was due mainly to a reduction in the dominance of *B. ephippium*.

In general, litter frog assemblages increase in density with altitudes (until 1800 m) and display reduced evenness and richness with increasing elevation (Scott 1976). The observed pattern at PFI, even over this small altitudinal range, agrees with the first two (density and evenness) generalizations. The greater density of frogs in the cloud forest may be related to the greater soil cover depth, but mainly to the mist-generated humidity, which diminishes harshness during the DC. In the Serra do Japi, the density of litter frogs is also greatest at higher sites (Giaretta et al. 1997).

The frogs at PFI concentrate their reproduction in the wet/warm months (Giaretta, pers. obs.) and we expected juveniles to contribute to the greater density of litter frogs in the WW. The lack of statistically significant seasonal differences in the density of litter frogs is possibly due to recruitment occurring later in March; the finding of two *Eleutherodactylus* egg clutches during summer sampling corroborates this idea. The density of litter frogs is variable among South American sites, with a range of 2 to 12 frogs/100 m<sup>2</sup> (Toft 1980a, Allmon 1991, Rodriguez 1992, Gascon 1996, Giaretta et al. 1997, this study), but consistently lower than in Central America (review in Allmon 1991).

Several studies have shown a seasonal dispersal of the litter frogs in the rainy season (Toft 1980b, Rodriguez 1992, this study). The spatial aggregation of litter frogs at PFI may be mediated by hu-

midity, as indicated by a tendency of frogs to be absent from drier places. The harshness of the DC may select against dispersal behavior because of the risk of entering seasonally dry sites. In Japi, the litter frog fauna is aggregated along stream margins in the DC (Giaretta et al. 1997).

At PFI, fire has deleterious effects on the litter frogs, decreasing richness and abundance. Although the soil becomes covered with some leaves soon after burns, there is little leaf compaction so that the litter cannot retain humidity. This most likely prevents immediate recolonization by frogs. Prior to human occupation, fires may have been rare in seasonal forest of southeastern Brazil and may not represent an evolutionary force in this ecosystem. Management plans for these forests need to include fire avoidance programs.

Long (1995) and Leo (1995) commented on the importance of conserving the tropical montane cloud forest for threatened vertebrate species. Most cloud forests in southern and southeastern Brazil occur as small isolates (Falkenberg & Voltolini 1995), and the example of PFI may stimulate the preservation of these areas as important reservoirs of the many specialized litter frogs in the region.

## ACKNOWLEDGMENTS

We thank to the Prefeitura Municipal de Atibaia for permission to work in the Parque Florestal do Itaperinga. Drs. K. S. Brown Jr., W. R. Heyer, C. Gascon, and W. W. Benson made helpful suggestions on the draft. H. F. de Medeiros and R. Bredariol helped in the fieldwork. The Fundação Boticário de Proteção à Natureza gave financial support. Grants were awarded by CNPq (AAG) and CAPES (KGF).

## LITERATURE CITED

- AB'SABER, A. N. 1977. Os domínios morfoclimáticos na América do Sul. *Geomorfologia* 52: 1-23.
- ALLMON, W. D. 1991. A plot study of forest floor litter frogs, central Amazon, Brazil. *J. Trop. Ecol.* 7: 503-522.
- BORROR, J. D., AND D. M. DELONG. 1988. Introdução ao Estudo dos Insetos. Edgard Blucher Ltda, São Paulo, Brasil.
- BRIJNZEEL, L. A., AND J. PROCTOR. 1995. Hydrology and biogeochemistry of tropical montane cloud forest: what do we really know? In J. Hamilton, J. O. Juvik, and E. N. Scatena (Eds.). *Tropical montane cloud forest*, pp. 38-78. Springer-Verlag, New York, New York.
- DICBY, P. G. N., AND R. A. KEMPTON. 1987. *Multivariate analysis of ecological communities*. Chapman & Hall, New York, New York. 206 pp.
- FALKENBERG, D. DE B., AND J. C. VOLTOLINI. 1995. The montane cloud forest in southern Brazil. In L. S. Hamilton, J. O. Juvik, and E. N. Scatena (Eds.). *Tropical montane cloud forests*, pp. 138-149. Springer-Verlag, New York, New York.
- GASCON, C. 1996. Amphibian litter fauna and river barriers in flooded and non-flooded Amazonian rain forest. *Biotropica* 28: 136-140.
- GIARETTA, A. A., R. J. SAWAYA, G. MACHADO, M. S. ARAÚJO, K. G. FACURE, H. F. DE MEDEIROS, AND R. NUNES. 1997. Diversity and abundance of litter frogs at altitudinal sites at Serra do Japi, southeastern Brazil. *Rev. bras. Zool.* 14(2): 341-346.
- GROMBONE, M. T., L. C. BERNACCI, J. A. A. MEIRA-NETO, J. Y. TAMASHIRO, AND H. F. LEITÃO-FILHO. 1990. Estrutura fitossociológica da floresta semidecídua de altitude do Parque Municipal da Grota Funda (Atibaia-Estado de São Paulo). *Acta Bot. Bras.* 4(2): 47-64.

- HADDAD, C. F. B., AND I. SAZIMA. 1992. Anfíbios anuros da Serra do Japí. In L. P. C. Morellato (Org.), História natural da Serra do Japí: ecologia e preservação de uma área florestal no sudeste do Brasil, pp. 188–210. Editora da Unicamp/FAPESP, Campinas, SP, Brasil.
- HEINEN, J. T. 1992. Comparisons of the leaf-litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. *Biotropica* 24: 431–439.
- HEYER, W. R., A. S. RAND, C. A. G. DA CRUZ, O. L. PEIXOTO, AND C. E. NELSON. 1990. Frogs of Boracéia. *Arq. Zool.* 31: 231–410.
- JAEGER, R. G., AND R. F. INGER. 1994. Standard techniques for inventory and monitoring: quadrat sampling. In W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (Eds.), *Measuring and monitoring biological diversity. Standard methods for amphibians*, pp. 97–98. Smithsonian Institution Press, Washington, DC.
- KREBS, C. J. 1989. *Ecological methodology*. Harper & Row Publishers, New York, New York.
- LEO, M. 1995. The importance of tropical montane cloud forest for preserving vertebrate endemism in Peru: the Río Abiseo National Park as a case study. In L. S. Hamilton, J. O. Juvik, and E. N. Scatena (Eds.), *Tropical montane cloud forests*, pp. 198–211. Springer-Verlag, New York, New York.
- LIEBERMAN, S. S. 1986. Ecology of the leaf litter herpetofauna of a Neotropical rain forest: La Selva, Costa Rica. *Acta Zool. Mex. (NS)* 15: 1–71.
- LONG, A. J. 1995. The importance of tropical montane cloud forest for endemic and threatened birds. In L. S. Hamilton, J. O. Juvik, and E. N. Scatena (Eds.), *Tropical montane cloud forests*, pp. 79–106. Springer-Verlag, New York, New York.
- LUO, J., AND B. J. FOX. 1996. A review of the Mantel test in dietary studies: effect of sample size and inequality of sample size. *Wildl. Res.* 23: 267–288.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Croom Helm, London, England.
- MEIRA-NETO, J. A. A., L. C. BERNACCI, M. T. GROMBONE, J. Y. TAMASHIRO, AND H. F. LEITÃO-FILHO. 1989. Composição florística da floresta semidecídua de altitude do Parque Municipal da Gruta Funda (Atibaia, Estado de São Paulo). *Acta Bot. Bras.* 3: 51–74.
- MORELLATO, L. P. C. 1992. Nutrient cycling in two south-east Brazilian forests. I. Litterfall and litter standing crop. *J. Trop. Ecol.* 8: 205–215.
- POMBAL, J. P. JR., I. SAZIMA, AND C. F. B. HADDAD. 1994. Breeding behavior of the pumpkin toadlet, *Brachycephalus ephippium* (Brachycephalidae). *J. Herpetol.* 28: 516–519.
- RODRIGUEZ, L. O. 1992. Structure et organization du peuplement d'anoures de Cocha Cashu, Parc National Manu, Amazonie Péruvienne. *Rev. Ecol. (Terre Vie)* 47: 151–197.
- ROHLF, F. J. 1988. NT-SYS-pc. Numerical taxonomy and multivariate analysis system, version 1.50. Exeter Publ., Ltd., New York, New York.
- SCOTT, N. J. 1976. The abundance and diversity of herpetofaunas of tropical forest litter. *Biotropica* 8: 41–58.
- TOFT, C. A. 1980a. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical rain forest. *Oecologia (Berl.)* 45: 131–141.
- . 1980b. Seasonal variation in populations of Panamanian litter frogs and their prey: a comparison of wetter and drier sites. *Oecologia (Berl.)* 47: 34–38.
- ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, New Jersey. 718 pp.