Seasonal patterns of reproduction and abundance of leaf litter frogs in a Central American rainforest

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Abstract
Patterns of reproductive phenology and temporal variation in species composition and age structure were investigated for a sample of terrestrial leaf litter frogs from a lowland tropical rainforest in north-eastern Costa Rica. Recruitment of most species showed a seasonal pattern in which the growth of juveniles occurred during the dry season. The phenology of the assemblage was also seasonal, with a peak in abundance during the dry season. Variation in abundance was driven by seasonal patterns of juvenile recruitment in one species, Eleutherodactylus brandsfordii. We suggest that the timing of reproduction and patterns of frog phenology may be tied to the availability of arthropod prey items. A comparison of our data with data collected at other rainforest sites in Central America and the Amazon basin of South America indicates that patterns of recruitment and abundance, while correlated with arthropod abundance on both continents, show divergent seasonal patterns. This and other studies indicate that peaks in abundance and recruitment of juvenile frogs are concentrated in the dry season in Central America, whereas in South American rainforests, the wet season is the period of highest abundance and juvenile recruitment. We suggest that the length and severity of dry periods in the Amazon basin limits the ability of terrestrial frogs to reproduce successfully, while in Central America a more benign dry season, while strong enough to create distinct seasonal trends in the phenology of rainforest animals, is not strong enough to prohibit frogs from recruiting juveniles during the dry season.

Key words: age structure, amphibians, Costa Rica, reproductive phenology, species composition, temporal variation

INTRODUCTION
Field researchers have described seasonal reproductive patterns among terrestrial vertebrates at several tropical locations (Fogden, 1972; Leigh, Rand & Windsor, 1982 and references therein; van Schaik, Terborgh & Wright, 1993; Sinclair, Mduma & Arcese, 2000; Wikelski, Hau & Wingfield, 2000). Data indicate that many tropical species time their reproduction to coincide with peaks in food resources, which generally occur during the rainy season (Russell, 1982; Goldizen et al., 1988; Poulin, Lefebvre & McNeil, 1992). Some species will reproduce during the dry season, however, if preferred food items are available at this time (Sinclair et al., 2000). Although there are several studies describing seasonal patterns of reproduction among individual species of tropical vertebrates, there are relatively few data quantifying seasonal variation in the composition and dynamics of multi-species tropical assemblages (but see Stiles, 1980; Gascon, 1991a). If species composition and age structure differ throughout the year, interactions among species (e.g. predator–prey dynamics) may also be expected to vary seasonally. Therefore, our understanding of how communities are structured, as well as the interactions among organisms at a site, hinges in part on understanding how individuals and species are distributed in time.

Crump (1974) quantified reproductive patterns among 74 sympatric species of frogs at a site in Amazonian Ecuador, making her study the most thorough description of anuran reproductive ecology in the Neotropics. Among 22 species of leaf litter frogs in her sample, 11 (50%) were continuous breeders, two (9%) were sporadic breeders (one of which bred sporadically during the wet season, while the other one was a sporadic dry season breeder), and nine (41%) were unknown with respect to the timing of reproduction. In the central Amazon, Moreira & Lima (1991) described seasonal patterns of reproduction in four species of leaf
litter frogs. They found that two species bred primarily in the wet season, whereas the other two species were dry-season breeders. These studies show that Amazonian leaf litter frogs exhibit some variability in the timing of reproduction, though the most complete data set available indicates that most terrestrial species breed continuously or during the wet season. However, these two studies do not necessarily represent broad patterns of anuran reproductive phenology from throughout the Neotropics. We are interested in determining whether seasonal patterns of reproduction are characteristic of anurans at one site in Central America and to what extent there is variation in the composition of the anuran community throughout the year. Therefore, our goals in this study are: (1) to quantify the phenology of reproduction of several abundant frog species from a rainforest in northeastern Costa Rica and compare our findings to what is known from South America; (2) to describe temporal patterns of species composition and age structure based on the abundance of frogs in monthly quadrat samples.

**MATERIALS AND METHODS**

A sample of anurans collected over 14 months from November 1973 to December 1974 at the La Selva Biological Station, Heredia Province, Costa Rica was examined. Most of the 1536 ha of the La Selva reserve is in primary forest, with the rest occurring in secondary forest, pasture and abandoned plantations (McDade & Hartshorn, 1994). Rainfall at La Selva averages 3962 mm, with a short dry season from February to April (Sanford et al., 1994).

Frogs were obtained in three ways. Most frogs (n =1690) were collected in 1-ga pitfall traps containing picric acid. Traps were placed 10 m apart along a 100 m transect and emptied every 4–6 h during the 4 days per month that traps were opened. Some frogs (n = 1326) were collected from 8 × 8 m litter plots, which were sampled monthly by 2–4 observers. Six different focal litter plots were sampled each month during the study period, with the exception that the first 6 quadrats were sampled in late November and early December 1973. November and December 1973 samples were combined into 1 period, so samples used to describe patterns of community phenology reflect 13 sample periods across 14 months. The litter plots and pitfall-trap transects were located in primary forest and in an adjacent fallow cacao grove. Finally, 508 individuals were collected opportunistically in the laboratory clearing and along trails in both habitat types. All captured frogs were placed in plastic bags and transported to the laboratory where they were killed by submersion in a chlorobutanol solution, then preserved in 10% formalin and stored in 70% ethanol.

The snout–vent length (SVL) of each frog was measured to the nearest 0.5 mm with a plastic ruler. The presence of secondary sexual characteristics, including nuptial pads and vocal slits, was recorded. Frogs were dissected and gonad size and condition were recorded. For females of the genera Eleutherodactylus and Gastrophryne, the number of mature ova contained in the ovaries was counted. An ocular micrometer was used to measure the width of left and right oviducts at mid-length and their condition described as straight, semi-convoluted, or convoluted. Convoluted oviducts may indicate sexual maturity (Donnelly, 1999). For sub-adult females the presence of immature (unpigmented) follicles was noted and the width and condition of left and right oviducts were recorded. For males, the length and width of left and right testes were recorded. Total volume of the testes was calculated using the equation for the volume of a prolate spheroid (Johnson, 1999):

\[
\text{testis volume} = \frac{4}{3}\pi(1/2 \text{ testis length})(1/2 \text{ testis width})^2.
\]

The volume of each testis was calculated separately and then the 2 values combined to estimate total testis volume.

Frogs were placed into 1 of 3 age-sex categories (juvenile, adult male, or adult female) based on body size, gonad condition, and the presence of secondary sexual characteristics. Individuals were classified as adult females if SVL was at least the minimum size at which mature ovarian eggs were recorded for each species. For males of all species except E. biporcatus, the minimum SVL at which vocal slits were noted was the size at which individuals were considered adults. Since E. biporcatus lacks vocal slits and nuptial pads, we were not able to assign individuals to sex classes using secondary sexual characteristics. Because E. biporcatus is comparable in size to E. rugulosus, we chose 25 mm (approximately the size of the smallest adult male in E. rugulosus) as the minimum SVL of adult males in E. biporcatus.

**Reproductive phenology of individual species**

The reproductive phenology for 6 species of frogs (Bufo haematiticus, E. biporcatus, E. fitzingeri, E. minus, E. talamancae, and G. pictiventris) was quantified based on monthly variation in mean body size and mean testis volume. Variation in the size of the ovarian complement during the study period was not analysed because of the small sample sizes for adult females. To maximize the sample size available for analyses of body size and testis size variation, data were included from individuals collected using all 3 sampling methods.

Variation in body size across the 14 months of the study was analysed because months with relatively low SVLs may indicate periods of recruitment to the adult age classes (Donnelly, 1989, 1999). Because our data did not meet the assumption of equal variance across all months of the study, a Kruskall–Wallis nonparametric test was used to determine how mean body size varied among months for males, females, and juveniles of each species.

Mean testis volume of all individuals for each month
was used as an indirect measure of the reproductive activity of males. Seasonal variation in testis size has been documented in other tropical vertebrate taxa (Kanamadi & Jirankali, 1992; Kappeler, 1997; Wikelski et al., 2000). Here it is assumed that significant changes in mean testis volume per month reflect differential allotment of energy to reproductive activity (Kanamadi & Jirankali, 1992). Because testis volume was linearly related to male SVL, a 1-way analysis of covariance (ANCOVA), using (ln) SVL as a covariate to determine if total testis volume varied significantly by month once the influence of body size on testis volume was removed. Months which did not have a minimum of 3 data points were excluded from this analysis.

Species composition and age structure

Data from quadrat sampling were used to describe patterns of abundance across the study period for the most common leaf litter species at La Selva. Quadrats are an effective method for sampling leaf litter amphibians (Jaeger & Inger, 1994). Only the quadrat data were used because more species were sampled using this method than using pitfall traps, and the data are easily standardized in terms of number of individuals/plot. The analyses described below include 5 species represented by > 20 individuals from quadrat sampling, including D. pumilio and E. brandsfordii, for whom individual patterns of reproductive phenology have been described previously (Donnelly, 1989, 1999).

First, a 2-way analysis of variance (ANOVA) using months and species as factors and quadrat counts as the dependent variable was used to test hypotheses about the distribution of species throughout the study period. This analysis was run twice, once including all 5 species in the model, and a second time excluding E. brandsfordii (the most abundant frog at La Selva) to determine if monthly variation in abundance was attributable to E. brandsfordii alone. Post-hoc tests used Dunnett’s C to determine which months and species differed significantly from one another in quadrat counts. Another 2-way ANOVA with months and age-sex classes as factors and quadrat counts as the dependent variable was used to investigate the temporal distribution of age-sex classes. As before, post-hoc tests were conducted using Dunnett’s C to determine which months and age-sex classes differed significantly from one another.

χ² statistics were calculated to determine if the appearance of individuals in a species or age-sex class was evenly distributed throughout the year. First, we tested the hypothesis that the distribution of each species among months did not differ from an even distribution throughout the study period, calculating a χ² value for each species separately. Then 3 separate χ² tables were used to test the hypotheses that the total number of individuals in each age class (male, female, or juvenile) was evenly distributed among months throughout the study period. All other statistical methods were conducted using SPSS 8.0 (SPSS, 1997).

RESULTS

Reproductive phenology

Adults of all six species showed no significant differences in body size across the 14 month study period. Juveniles of four species, however, showed significant monthly variation in body size (for G. pictiventris, \(H = 30.19, P = 0.001\); for E. biporcatus, \(H = 35.86, P = 0.001\); for E. mimus, \(H = 23.41, P = 0.003\); for E. talamancae, \(H = 16.03, P = 0.042\), Fig. 1). In three species, juvenile body size was low at some point in the dry season (January–April) and increased monthly throughout the wet season August–September 1974, when the signal dampened. In E. talamancae, SVL was low during the dry season and increased every month from March to September 1974 with the exception of June, when SVL was lower than April and May.

Males of most species did not show variation in gonadal condition during the 14-month study. Only G. pictiventris showed significant variation in testis volume among months once the effect of body size on testis volume was removed (\(F = 3.312, P = 0.001\); for E. fitzingeri, \(F = 1.275, P = 0.297\); for E. biporcatus, \(F = 2.065, P = 0.112\); for B. haematiticus, \(F = 0.981\), \(P = 0.344\), Fig. 2).
In *G. pictiventris*, testis volume was lowest from January–April 1974. 

**Abundance**

A total of 1205 individuals of five species was represented by >20 individuals in quadrat surveys. The five species represented three families: Dendrobatid (*Dendrobates pumilio*), Leptodactylidae (*E. biporcatus, E. brandsfordii, and E. talamancae*), and Microhylidae (*G. pictiventris*). *Eleutherodactylus brandsfordii* and *D. pumilio* were the most abundant species in the sample, accounting for 86% of quadrat observations (Fig. 2). All five species were caught in 9 of the 13 months of quadrat sampling. The 4 months in which fewer than five species were recorded were August 1974 (four species), September 1974 (four species), October 1974 (three species), and November 1974 (four species).

There were significant differences in the abundance of species across all months, and monthly abundance across all species (Table 1a, Fig. 2). All five species were caught in 9 of the 13 months of quadrat sampling. The 4 months in which fewer than five species were recorded were August 1974 (four species), September 1974 (four species), October 1974 (three species), and November 1974 (four species).

There were significant differences in the abundance of species across all months, and monthly abundance across all species (Table 1a, Fig. 2). The interaction between the main effects was not significant, which indicates that there were no differences in the relative importance of each taxon in the community throughout the year. Post-hoc tests using Dunnett’s C indicated that the abundance of *E. biporcatus* was not different from the abundance of *E. talamancae* or *G. pictiventris* across months. All other combinations of species were significantly different from one another. Post-hoc tests did not indicate the months for which quadrat counts differed significantly from one another, but the frequency histogram of the abundance of all species across months indicates that frogs were more abundant from February–July and December 1974 than the other 5 months of the study period (Fig. 2). When *E. brandsfordii* was excluded from the analysis, abundance varied significantly among species, but differences in quadrat counts among months were no longer significant (Table 1b). The interaction between months and species was not significant. There were significant monthly differences in the quad rates of the three age–sex classes during the 14-month study (Table 1c, Fig. 4). Individuals (especially juveniles) were more abundant from February to April 1974 than in other months. There were no differences in quadrat counts among age–sex classes across all months, and the interaction between age–sex class and month was not significant (Table 1c).

The frequency with which individuals were encountered during the study period differed from an even distribution in *E. brandsfordii* only ($\chi^2 = 155.8$, $P < 0.001$). All other species were relatively evenly distributed across the 14 months of the study (Fig. 2). Our data on the distribution of the three age classes across the study period indicated that the observed frequency...
with which juveniles were encountered differed from what would be expected based on an even distribution ($\chi^2 = 125.9, P < 0.001$), but that males and females were evenly distributed throughout the year (Fig. 4).

DISCUSSION

Phenology of individual species

Our data on body size variation indicate that recruitment of juveniles occurred during the dry season at La Selva for four out of six species analysed. Moreria & Lima (1991) interpreted monthly increases in SVL as representing growth in recently metamorphosed individuals of leaf litter frogs in their sample from the Brazilian Amazon. We believe that the small juvenile body size in the dry season, followed by several months of increase in mean SVL represents the emergence and growth of cohorts of juveniles in the four species for which we documented significant temporal differences in juvenile body size. Donnelly (1999) stated that reproduction in *E. brandsfordii* was continuous at La Selva, though she noted that the high abundance of juveniles during the dry season in her sample may indicate some seasonality in reproductive output. We believe that her data in conjunction with ours indicate that the dry season is an important period of juvenile recruitment for many species of litter frogs at this site in northeastern Costa Rica.

The dry season may be an important time for juvenile recruitment among terrestrial species at La Selva and this is indicated by the pattern seen in the microhylid *G. pictiventris*. *Gastrophryne pictiventris* deposit their ova in ephemeral pools during rainy periods where they probably develop over a few weeks (Donnelly, de Sa & Guyer, 1990). Adult *G. pictiventris* breed in water and adult males showed a decrease in testis volume during the dry season, indicating that breeding activity in adults is concentrated during the rainy season in this species. The individuals in our sample probably deposited ova late in the wet season of 1973 (November–December), with juvenile froglets emerging during the dry season and showing the same pattern as most terrestrial-breeding *Eleutherodactylus* in our sample: recruitment and growth of juveniles was concentrated in the dry season.

The recruitment of juveniles during the dry season at La Selva may be tied to the phenology of arthropods, the principal prey items of leaf litter frogs. Several studies have indicated that leaf litter arthropod abundance is higher during the dry season and dry season–wet season transition at sites in Central America (Toft, 1980; Lieberman & Dock, 1982; Levings & Windsor, 1984). At La Selva, the abundance of most litter arthropods, especially ants and orthopterans (important prey items for most of the species included in this study) peaks in April–May, before the onset of the heaviest rains during the summer months (Lieberman & Dock, 1982). At other sites in the Neotropics, including the south-western Amazon and the Caribbean, arthropod abundance peaks during the rainy season (Tanaka & Tanaka, 1982; Pearson & Derr, 1986). We suggest that many litter anurans time their reproduction in such a way that juveniles emerge during the season of peak arthropod abundance. In Central America, this may result in increased recruitment of litter anurans during the dry season. In Amazonia and the Caribbean, arthropods are relatively more abundant in the wet season, which may explain the peaks in reproductive activity and juvenile growth documented from these areas (Aichinger, 1987; Gascon, 1991b; Moreira & Lima, 1991; Ovaska, 1991). Other researchers have tied patterns of juvenile recruitment to food availability among coatis in Central America (Russell, 1982) and saddle-back tamarins in South America (Goldizen et al., 1988). Here we suggest a link between food availability and the timing of reproduction among litter frogs in the tropics. Although predictable cycles of arthropod abundance may influence populations at sites in both Central and South America, seasonal patterns of recruitment differ between the two continents.

Temporal variation in abundance

Our analyses of community phenology indicate that abundance of frogs was higher in the dry season than in the wet season. The most abundant species in our sample, *E. brandsfordii*, is responsible for the significant monthly differences in quadrat counts. When *E. brandsfordii* was removed from the analysis we found no differences in the abundance of species among months. The patterns discussed below, then, are driven largely by variation in the abundance of one common frog at La Selva.

Other researchers have found that litter amphibians and reptiles at La Selva and other sites in Central America are more abundant in the dry season than the
wet season (Toft, 1980; Lieberman, 1986). Guyer (1986) documented a dry-season peak in abundance in *Norops humilis*, a leaf litter anole collected at the same time as the frogs in our sample. He attributed the higher abundance of animals during the late dry season to the high volume of leaf litter, which provides foraging and oviposition substrate for terrestrial amphibians and reptiles. At relatively wet and dry sites in Panama, frogs are also more abundant in the dry season (Toft, 1980; Toft, Rand & Clark, 1982). In contrast, researchers at sites with seasonal patterns of rainfall in the Amazon have found that anuran abundance is lower in the dry season than the wet season (Cuzco Amazonico, Peru; Duellman, 1995; Manaus, Brazil; Allmon, 1991). Of the 14 species included in Allmon’s (1991) sample, only juveniles of *Colostethus marchesianus* were more abundant in the dry season than in the wet season. While total annual rainfall at Cuzco Amazonico, is much lower than La Selva (2387 mm at Cuzco Amazonico vs. 3962 mm at La Selva), rainfall at Cuzco Amazonico is similar to Toft’s (1980) dry site in Panama (which receives 2200 mm of rain/year). However, annual patterns of anuran abundance differ between Panama and Peru, which suggests that the mechanism driving patterns of anuran abundance acts in a fundamentally different manner between Central and South America.

The increase in the abundance of frogs during the dry season is because of the increase in the number of juvenile individuals observed from February–May 1974. As described above, we believe that many anurans time their reproduction so that juveniles emerge during periods of peak prey abundance, which occur during the dry season or dry season–wet season transition in Central America, and during the wet season in much of the Amazon. At first this seems counter-intuitive, given that frog ova, which lack a calcified shell, risk desiccation if they are not kept moist during development (Duellman & Trueb, 1986). However, the dry season in Central America is shorter and wetter than in much of the Amazon basin (Table 2). Furthermore, at La Selva the leaf litter layer, where many of the species included in this study deposit their ova, is deeper in the dry season than in the wet season due to variation in decomposition rate throughout the year (Frankie, Baker & Opter, 1974). We suggest that the dry season in Central America is pronounced enough to trigger seasonal variation in leaf fall and the abundance of arthropods, but not so severe as to prevent some species from depositing terrestrial ova during the dry season.

Table 2. Distribution of precipitation (± 1 sd when data were available) at eight sites in the neotropics

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean annual rainfall (mm)</th>
<th>No. months with rainfall &lt; 200 mm</th>
<th>No. months with rainfall &lt; 100 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central America</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>La Selva, Costa Rica(^a)</td>
<td>3962 ± 723</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Osa Peninsula, Costa Rica(^b)</td>
<td>5296 ± 228</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Barro Colorado Island, Panama(^c,d)</td>
<td>2616 ± 422</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>South America</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Santa Cecilia, Ecuador(^e)</td>
<td>4289</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Panguana, Peru(^f)</td>
<td>2634</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Manu, Peru(^g)</td>
<td>2110</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>Manaus, Brazil(^h)</td>
<td>2379 ± 300</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Belem, Brazil(^h)</td>
<td>3136 ± 382</td>
<td>6</td>
<td>0</td>
</tr>
</tbody>
</table>

\(^a\) Sanford et al. (1994).
\(^b\) L. Gilbert (pers. comm.)
\(^c\) Dietrich, Windsor & Dunne (1982).
\(^d\) Rand & Rand (1982).
\(^e\) Crump (1974).
\(^f\) Aichinger (1987).
\(^g\) Rodriguez (1992).
\(^h\) NOAA.

Although there was no significant interaction between wet season (Toft, 1980; Lieberman, 1986). Guyer (1986) documented a dry-season peak in abundance in *Norops humilis*, a leaf litter anole collected at the same time as the frogs in our sample. He attributed the higher abundance of animals during the late dry season to the high volume of leaf litter, which provides foraging and oviposition substrate for terrestrial amphibians and reptiles. At relatively wet and dry sites in Panama, frogs are also more abundant in the dry season (Toft, 1980; Toft, Rand & Clark, 1982). In contrast, researchers at sites with seasonal patterns of rainfall in the Amazon have found that anuran abundance is lower in the dry season than the wet season (Cuzco Amazonico, Peru; Duellman, 1995; Manaus, Brazil; Allmon, 1991). Of the 14 species included in Allmon’s (1991) sample, only juveniles of *Colostethus marchesianus* were more abundant in the dry season than in the wet season. While total annual rainfall at Cuzco Amazonico, is much lower than La Selva (2387 mm at Cuzco Amazonico vs. 3962 mm at La Selva), rainfall at Cuzco Amazonico is similar to Toft’s (1980) dry site in Panama (which receives 2200 mm of rain/year). However, annual patterns of anuran abundance differ between Panama and Peru, which suggests that the mechanism driving patterns of anuran abundance acts in a fundamentally different manner between Central and South America.

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On Barro Colorado Island, Panama, Andrews, Rand & Guerrero (1982) reported that *N. limifrons* does not generally deposit ova in the litter layer until the beginning of the wet season. We are not aware of any data describing patterns of recruitment or ova deposition among *Eleutherodactylus*, the largest group of terrestrially breeding frogs, from other sites in Central America. At Panguana, Peru, Toft & Duellman (1979) found indirect evidence that *E. peruvianus* and *E. toftae*, bred during the dry season, but Aichinger (1987) categorized the same two species as primarily wet season breeders. In the central Amazon basin, Moreira & Lima (1991) found that juvenile recruitment in the terrestrial breeders *Adenomera andreae* and *Colostethus stepheni* occurred during the rainy season. More data describing reproductive patterns among many species of terrestrial breeders from both Central and South America are necessary to evaluate the hypothesis suggested by the data presented in this study: the dry season in Central American rainforests is not severe enough to limit the ability of some terrestrially breeding species to deposit ova and recruit juveniles during dry periods.

Although there was no significant interaction between...
species and month, indicating that the relative importance of each taxon in the community did not vary temporally, the number of species present in the assemblage was lowest during months when frogs and arthropods were least abundant. It is possible that a reduction in arthropod abundance during rainy months may create a seasonal food shortage for litter frogs. As noted by Wiens (1977), ecological ‘crunches’ may result in the local redistribution of individuals, affecting the ability of short-term censuses using small plots to relate resource abundance to the density of animals. Even if species in our sample do not experience population declines during times of low prey availability, our data indicate that the composition of the litter frog community is influenced either directly (by population declines of some species) or indirectly (by changes in the distribution of frogs in the forest) by seasonal fluctuations in rainfall at La Selva.

We found that the temporal distribution of juveniles varied throughout the year. The differential distribution of juveniles among months may have important implications for the ecological influence of litter frogs given the role of frogs as predators in rainforest habitats (Stewart & Woolbright, 1996). Work at La Selva and in the Brazilian Amazon indicates that the diet of many litter frogs changes ontogenetically (Donnelly, 1991; Lima & Magnnusson, 1998). In *D. pumilio*, for example, sites are more important prey items in juveniles than adults, and adults eat more ants than juveniles (Donnelly, 1991). Lima & Magnnusson (1998) found that the diet of diurnal litter frogs varies as much among size classes within a species as it does among species. If ontogenetic changes in diet occur among many litter frogs at La Selva, then the cumulative effect of frogs as predators in the reserve probably varies throughout the year. At the same time, the availability of frogs as prey items for larger predators (especially snakes, which eliminate relatively small prey items as they grow; Arnold, 1993) also differs (especially snakes, which eliminate relatively small prey items as they grow; Arnold, 1993) and appears to affect the temporal distribution of juveniles in the community.

In conclusion, we found that patterns of abundance and recruitment of juveniles is seasonal for many litter frogs at one site in north-eastern Costa Rica. As noted by Wiens (1977), ecological ‘crunches’ may result in the local redistribution of individuals, affecting the ability of short-term censuses using small plots to relate resource abundance to the density of animals. Even if species in our sample do not experience population declines during times of low prey availability, our data indicate that the composition of the litter frog community is influenced either directly (by population declines of some species) or indirectly (by changes in the distribution of frogs in the forest) by seasonal fluctuations in rainfall at La Selva.

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