NOTES

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RELATIVE ABUNDANCE OF LEAF LITTER ANURANS IN PRIMARY FOREST IN THE NUSAGANDI BIOLOGICAL RESERVE, REPUBLIC OF PANAMA

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Recent interest in the decline of amphibian populations has highlighted the importance of surveys of abundance and diversity in the field (Heyer et al. 1994). Amphibian diversity is particularly high in the neotropics, making surveys especially important in this vast region. In this paper I present data from a form of visual encounter survey (Crump and Scott 1994) on leaf litter anurans in tropical moist rainforest at the Nusagandi Biological Reserve, in the Republic of Panama. The surveys were undertaken to provide information on the relative abundance of leaf litter anurans in three plots in primary forest at Nusagandi, to provide a baseline for comparison with future investigations at this site. A previous survey of anuran diversity in this area was carried out by Toft (1980) in forest on the Pacific side of the continental divide. This study provides the first survey of anuran diversity on the Atlantic side of the continental divide in this part of Panama. The results provide data for comparison with the results from similar surveys on nearby and distant sites in the neotropics. This kind of data is particularly valuable given the rapid rates of deforestation in this biologically diverse area.

MATERIALS AND METHODS

The Nusagandi Biological Reserve is near the continental divide in the Central Cordillera along the Carti Road, which runs from the town of El Llano in the Department of Panama to Carti in the Comarca of San Blas, Republic of Panama. The area is characterized by high topographic relief and associated gradients in leaf moisture, with lower moisture levels on ridge tops (Toft 1980). The region receives approximately 3500 mm of rain per year (Pan Canal 1968). Rainfall is seasonal, with a dry season occurring from late December–March. However, sporadic rains occur throughout the dry season.

Relative abundance was assessed in three 10 x 10 m plots along the Ina Igar trail in the Nusagandi Biological Reserve. Surveys were made during the wet season from September–November 1991, and then in May 1992. All three plots were in primary rainforest. The topography of each plot is as follows: Plot 1 was on a slight slope at the base of a hill, and bordered by a dry stream bed (this stream flowed only during heavy rains); Plot 2 was on relatively level ground on a hilltop at the highest point of the Ina Igar trail; Plot 3 was on a slope along the side of a hill. With regard to the trail, Plot 1 was approximately 10 m off the northwest side of the trail, about 20 m from the trailhead leaving from the main road. Plot 2 was at the top of the highest hill on Ina Igar, immediately to the north of the trail (touching the trail in some places). Plot 3 was approximately 100 m further along the trail from Plot 2, about 3 m to the east of the trail.

Each plot was measured using two Suntoo sighting compasses and a 10-m measuring tape. The measuring tape was used to mark straight lines and to place flags. The compasses were used to define the angles of each line and to insure that each corner of the perimeter closely approximated a right angle. Wire-staked plastic flagging was used to mark a grid on each plot. Flags were placed every 2 m within the grid. Observations were made by patrolling the grids so that each 2 x 2 m section of the grid was observed thoroughly before the observer moved on to the next section of the grid. All anurans observed were identified to genus and species if possible, otherwise to genus only. Individuals were also classified as being juveniles or adults. Individuals were captured by hand (if possible), and all captured individuals were marked by toe-clipping. It took approximately 0.5 h to sample each plot. The total time spent observing (time spent recording data on observed or captured specimens was excluded) during each patrol of each grid was recorded. This allows the calculation of the number of frogs seen per unit time, and hence allows for comparison with any technique that yields a rate of observations, such as time constrained searches (Crump and Scott 1994). Simpson's index-bar of diversity was calculated for each plot as $S = 1/Sp_i^2$, where p_i is the proportion of species i.

Observations were made on the plots from 20 September–13 November 1991 during the wet season. Two nocturnal samples were taken on two plots (Plots 1 and 3) in order to compare species compositions between day and night. An additional two samples were taken on the plots during 29–30 May 1992. The same plot was never sampled more than once on the same day, and samples were dispersed over the sampling period. A total of 20 samples were observed on Plot 1, 19 on Plot 2, and 26 on Plot 3. Three different observers made observations on the plots during this project, but each sample was carried out by only a single observer.

Statistical analyses were carried out using the software programs Excel (Microsoft 1993), StatView (Abacus Concepts 1992), and SuperAnova (Abacus Concepts 1989). The data were analyzed to determine whether they met the assumptions of parametric statistical tests, such as normality of the distribution (K-S Normality Test), and homogeneity of variances (Bartlett's Test). Data not meeting these requirements were transformed to fit the assumptions of the parametric tests, or alternative statistical methods were used. Post-hoc comparisons of particular means within ANOVAs were carried out with the Bonferroni Test.

RESULTS

Table 1 shows the numbers of observations of each species seen on the plots, across all plot for both years and for night samples. Sixteen species were observed on all of the plots combined in 1991 and 1992. The relative abundance of those species seen in daylight samples during 1991 is shown in Table 2. Due to non-homogeneity of the samples, a normal parametric ANOVA could not be used to investigate the significance of the variation. However, Welch's Test (a one-way ANOVA that is robust to non-homogeneous variances) showed significant differences among species in relative abundance ($P < 0.0001$). Post-hoc tests are not available for Welch's Test, but *Minyobates minutus* was observed far more frequently than any other species.

There were significant differences among plots in the number of individuals observed per minute (Plot 1: $n = 16$, $\bar{x} = 0.28$, SE = 0.05; Plot 2: $n = 17$, $\bar{x} = 0.14$, SE = 0.03; Plot 3: $n = 21$, $\bar{x} = 0.29$, SE = 0.03; ANOVA, $F = 6.076$, $P < 0.005$). Specifically, a significantly lower number of frogs was seen per minute on the hill-top plot (Plot 2) than on the lower elevation plots (Plot 1 and Plot 3: Bonferroni test, $P < 0.01$ for Plot 1 vs. Plot 2, $P < 0.005$ for Plot 2 vs. Plot 3). The plots also varied in the number of species observed per minute, although the variation was only marginally significant (Plot 1: $n = 16$, $\bar{x} = 0.18$, SE = 0.03; Plot 2: $n = 17$, $\bar{x} = 0.11$, SE = 0.02; Plot 3: $n = 21$, $\bar{x} = 0.15$, SE = 0.01; ANOVA, $F = 3.172$, $P = 0.05$). Post-hoc tests revealed a significant difference only between the hill-top plot (Plot 2) and the plot by the stream bed (Bonferroni test, $P < 0.05$).

Frogs were equally abundant by day and by night (Day: $n = 54$, $\bar{x} = 0.24$, SE = 0.02; Night: $n = 4$, $\bar{x} = 0.31$, SE = 0.05), and similar numbers of frogs were seen in 1991 and 1992 (1992: $n = 6$, $\bar{x} = 0.33$, SE = 0.08). The number of species seen per minute did not differ substantially between diurnal and nocturnal samples in 1991 (Day: $n = 54$, $\bar{x} = 0.15$, SE = 0.01; Night: $n = 4$, $\bar{x} = 0.17$, SE = 0.03), and was the same in 1992 as it was in 1991 ($n = 4$, $\bar{x} = 0.15$, SE = 0.03).

Simpson's indices of diversity, calculated from the day samples in 1991, were as follows: Plot 1 = 5.9, Plot 2 = 6.4, Plot 3 = 4.5, total = 5.6. Diversity indices for the night samples (from Plot 1 and Plot 3 only) were: Plot 1 = 2.6, Plot 3 = 4.9, total = 3.7.

Table 3 shows the proportion of individuals observed that were adults (for day and night samples across all plots, for both 1991 and 1992). This table also shows the proportion of individuals seen that were caught, and the proportion of captures

TABLE 1. Numbers of frogs seen during samples of the plots. Number of samples for each plot is shown in parentheses. Total combines data from day samples in 1991 across plots. *Colostethus* sp. refers to individuals identified to genus only (and for the other genera).

Species	**Plot 1** (16)	**Plot 2** (17)	**Plot 3** (21)	**Total** (54)	**Night** (4)	**1992** (6)
Bufo						
marinus	0	1	0	1	0	2
typhonius	2	3	11	16	0	5
Colostethus						
nubicola	4	3	18	25	0	5
pratti	1	0	0	1	0	0
talamancae	5	2	0	7	4	0
sp.	0	0	3	3	0	0
Eleutherodactylus						
biporcatus	0	0	1	1	0	0
bufoniformis	0	0	0	0	1	0
cerasinus	4	4	8	16	0	3
crassidigitus	1	0	8	9	0	0
fitzingeri	0	0	0	0	0	1
gollmeri	1	1	3	5	3	1
pardalis	1	0	0	1	0	0
talamancae	2	1	10	13	3	0
sp.	0	4	7	11	1	3
Hemiphractus						
fasciatus	0	0	0	0	1	0
Minyobates						
minutus	9	9	50	68	12	20
fulguritus	1	0	0	1	0	1

that were recaptures of marked individuals (for 1991 only).

The amount of rainfall, and the daily maximum temperature, recorded at the Nusagandi Biological Station varied during the course of the study. Nevertheless, scatter plots of the relationship between daily rainfall, max-barimum and mininum daily temperature and the number of frogs seen per minute, species diversity, or the proportion of *Minyobates, Bufo, Colostethus*, or *Eleutherodactylus* observed in the samples indicate that these variables did not have a strong effect on the results of this study. One-way ANOVA's on the relationship between weather (cloudy, partly cloudy, or sunny) and time of day (morning versus afternoon) did not reveal any significant effects on the number of individuals per minute, species diversity, or the proportion of *Minyobates, Bufo*, *Colostethus*, or *Eleutherodactylus* in the samples.

DISCUSSION

Minyobates minutus was clearly the most abundant frog at this site. In terms of generic composition, the genera *Eleutherodacytlus* (21%), *Colostethus* (29%), and *Bufo* (14%) comprised the most dominant genera after *Minyobates* (36%). The dominance of *Eleutherodactylus*, *Colostethus* and *Bufo* is similar to what is seen in lowland sites in central Panama (Ibáñez et al. 1995). The most unusual result of this study in comparison with Ibañez et al. (1995) was the dominance of *Minyobates* caused by the abundance of *M. minutus*.

The reason for the high relative abundance of *M. minutus* in this study is not clear, although it may be associated with high rainfall at Nusagandi, and the consequent presence of abundant epiphytic bromeliads, which provide pools (phytotelmata) that are used by *M. minutus* for tadpole deposition.

TABLE 2. Relative abundances for the species seen on the plots during the day in 1991. Data are combined across plots.

Species	Relative Abundance
Bufo	
marinus	0.01
typhonius	0.08
Colostethus	
nubicola	0.14
pratti	0.01
talamancae	0.10
Eleutherodactylus	
biporcatus	< 0.01
cerasinus	0.12
crassidigitus	0.04
gollmeri	0.03
pardalis	0.02
talamancae	0.07
Minyobates	
fulguritus	0.02
minutus	0.36

Overall, my observations suggest that *Minyobates* is exraordinarily abundant at this site. Nusagandi is an excellent area for research on the ecology and behavior of this species, as well as comparative studies of relative abundance over time.

Analysis of variance detected significant heterogeneity among the plots in terms of individuals and species observed. The plots differed topographically, which may have influenced the amount of moisture available in the leaf litter at each site. Plot 2, which was on the top of a hill, is likely to be more exposed to evaporation, and to have more rapid drainage, than the other two sites. Hence the leaf litter may retain less moisture on that plot. This could have resulted in lower densities of leaf-litter anurans through affects on the availability of arthropods for food or the availability of habitable retreat sites. The results of the comparisons presented here are specific to the three plots sampled, and do not allow a general assessment of the effect of specific topographic features on leaf-litter anuran abundances.

Research on the relative abundance of the leaf litter frogs on the Carti Road near Nusagandi was previously carried out by (Toft 1980), who worked on the Pacific slope of the mountains (whereas the current study was on the Caribbean slope). The relative abundance of species was similar between the two studies, with some notable exceptions. First, *E. vocator* was extremely common in samples taken by Toft (1980), but was never seen on the plots during the visual encounter surveys reported here (it was, however, occasionally seen along the Ina Igar trail during the course of the research). Also, the relative abundance of *M. minutus* was higher in this study than in Toft's (1980). This species was quite common in Toft's (1980) study, but it was by far the most common species of frog found during this study at Nusagandi.

The reason for the differences between this study and Toft (1980) are not known, but could have to do with differences between the Pacific and Caribbean slopes, change over time, or differences

TABLE 3. Percentages of individuals seen (in commonly observed species) that were adults, that were captured, and that were recaptures of marked individuals.

Species	Adult	Captured	Recaptures
Bufo			
typhonius	0.77	0.68	0.68
Colostethus			
nubicola	0.97	0.43	0.60
talamancae	0.95	0.41	0.44
Eleutherodactylus			
cerasinus	0.76	0.44	0.63
crassidigitus	1.00	0.70	0.63
gollmeri	0.78	0.44	0.00
talamancae	1.00	0.71	0.64
Minyobates			
minutus	0.83	0.36	0.60

in sampling methodology. Toft (1980) turned over and examined all leaf litter and other moveable objects during sampling (and each area was searched only once), whereas the leaf litter was not disturbed in this study, and each plot was sampled repeatedly. Species diversity indices were similar between this study and that of Toft (1980).

Colostethus talamancae, *E. crassidigitus* and *E. talamancae* were not seen in the samples in 1992, whereas the other species were seen in approximately the same proportions that they had been seen previously. However, the number of samples was small enough that the chance of missing these three species (which were not among the most abundant in 1991) was probably high.

In addition to the species listed in Table 1, the following 20 species were seen or heard during five months of field work at Nusagandi (not necessarily on the plots): *Dendrobates auratus, Colostethus inguinalis, Hyla rufitela, H. miliaria, Smilisca phaeota, Bufo coniferus, Atelopus varius, Leptodactylus pentadactylus, L. labialis, Glossostoma aterimum, Centrolenella granulosa, Agalychnis callidryas, Physalaemus pustulosus, Eleutherodactylus raniformis, E. bransfordii, E. cruentus, E. diastema, E. gagei, E. ridens, and E. vocator.*

The most surprising result from the nocturnal samples was that *M. minutus*, which is normally considered to be a diurnal species, was also the most abundant species in the samples observed at night. The frogs observed seemed to be active, so it was not merely a case of detecting sleeping frogs in the sample.

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