Caribbean Journal of Science, Vol. 41, No. 1, 157-162, 2005

Diversity and Abundance of Forest Frogs (Anura: Leptodactylidae) before and after Hurricane Georges in the Cordillera Central of Puerto Rico

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ABSTRACT.—Caribbean hurricanes often impact terrestrial vertebrates in forested environments. On 21 September 1998, Hurricane Georges impacted Puerto Rico with sustained winds in excess of 166 km/hr, causing damage to forests of the island's principal mountain range; the Cordillera Central. We estimated forest frog abundance and diversity from call counts conducted along marked transects before and after Hurricane Georges in two forests reserves of the Cordillera Central (Maricao and Guilarte). We used distance sampling to estimate density of *Eleutherodactylus coqui* and recorded counts of other species. After the hurricane, the abundance of *E. coqui* increased in both reserves compared to pre-hurricane levels while abundance of other frog species decreased. In Maricao, relative abundance of *E. richmondi* ($P = 0.013$) and *E. brittoni* ($P = 0.034$) were significantly lower after the hurricane. Moreover, species richness and evenness of the Maricao and Guilarte frog assemblages declined after the hurricane. Our results on abundance patterns of the forest frog assemblages of Maricao and Guilarte Forests were similar to those reported from the Luquillo Experimental Forest after Hurricane Hugo in September 1989. Long-term demographic patterns of the forest frog assemblages in the Cordillera Central may be associated with changes due to the ecological succession in post-hurricane forests.

KEYWORDS.—Call counts, *Eleutherodactylus*, forests, frogs, hurricanes, Puerto Rico

Hurricanes are frequent, large-scale disturbances in the Caribbean which have major effects on plants, soils, animals, and even landforms (Walker et al. 1991). Caribbean hurricanes affect population attributes of animal communities and may influence the community structure, including species composition and relative abundance (Waide 1991). Woolbright (1991) reported populations of *E. coqui* increased markedly in the Luquillo Experimental Forest (LEF) after hurricane Hugo, with some species experiencing moderate increases (e.g., *E. hedricki*), while others declined (e.g., *E. richmondi*).

However, the LEF represents a small portion of the total montane forest in Puerto Rico and how hurricanes affect frog populations in other regions of the island is unknown. Moreover, little is known of the distribution and abundance of amphibian species, or about the ecology of the frog assemblages in the Cordillera Central region (Rivero 1998). Here, we report patterns of diversity and abundance of the frog

ms. received February 4, 2004; re-submitted June 6, 2004; accepted December 22, 2004

assemblages in two forest reserves of the Cordillera Central of Puerto Rico, before and after Hurricane Georges, including detection of short-term changes in species richness and evenness after the hurricane.

Our study was conducted in two forest reserves of the Cordillera Central of Puerto Rico. Maricao Forest (18°08′N, 66°58′W) is a 4,150 ha reserve characterized by steep slopes and dissected drainages with elevations ranging from 150-875 m. The forest comprises 3 life zones (Ewel and Whitmore 1973): Subtropical Moist at lower elevations, Subtropical Wet to 700 m, and Subtropical Lower Montane above 700 m. Mean annual precipitation is 255 cm and mean annual temperature is 21.1 °C. Maricao has some of the greatest plant species diversity of any forest reserve in Puerto Rico with approximately 846 species of vascular plants, including 279 species of trees (Little et al. 1974; Silander et al. 1986).

Guilarte Forest (18°10′N, 66°48′W) is composed of six fragments that together comprise 1,457 ha. Centrally located in the Cordillera Central, Guilarte shares similar topography with Maricao with elevations ranging from 760-1,205 m. Guilarte Forest falls largely in the Subtropical Lower Montane life zone. Mean annual precipitation and temperature are 224.4 cm and 21.1°C. Little et al. (1974) reported 105 tree species from Guilarte Forest. While previous investigations of floral and faunal communities have been conducted in Maricao, practically no research has been done in Guilarte.

We established transects in Maricao and Guilarte Forests either on existing forest trails or alongside streams. Overstories of transects in Maricao were dominated by *Calophyllum brasiliense* (Clusiaceae), *Micropholis chrysophylloides* (Sapotaceae), *Terebraria resinosa* (Rubiaceae), *Linociera dominguensis* (Oleaceae), and *Homalium racemosum* (Flacourtiaceae). Transects in Guilarte were dominated by *Nephelea portoricensis* (Cyatheaceae), *Tabebuia heterophylla* (Bignoniaceae), *Alchornea latifolia* (Euphorbiaceae), and *Prestoea montana* (Arecaceae). We placed seven 250 m transects and one 500 m transect in Maricao Forest. The extreme topography of Maricao Forest restricted all but one transect to 250 m in length. We placed four 500 m transects in Guilarte before the hurricane. However, the transect leading to the summit of Monte Guilarte was lost after Hurricane Georges. Therefore, we used the information collected in the 3 remaining transects for post-hurricane comparisons.

On 21 September 1998, Hurricane Georges passed directly over the Cordillera Central (Fig. 1). We surveyed transects before the hurricane (April-May, 1998) and after the hurricane (May, 1999). We surveyed transects first at dusk to detect species calling primarily at dusk, then a second time to detect those calling during later hours (2100-2300 h) of the night. We counted calls of *E. coqui* within 5 m from centerline of the transect and counted other calling frogs to an untruncated distance. Call counts of *E. coqui* within a 5 m radius of points were correlated with density of calling males (Fogarty and Vilella 2001). Moreover, individuals of *E. coqui* were too highly numerous to effectively count them beyond 5 m from the transects. We conducted 23 surveys before and 30 surveys after hurricane Georges (Maricao and Guilarte Forests combined).

Before each transect survey, we recorded climate data using a portable Weather Monitor II station (Davis Instruments, Hayward, California). The weather station was placed at the forest headquarters (Maricao or Guilarte) to record rainfall, temperature, barometric trends, wind activity, relative humidity, and dew point every 10 minutes. Therefore, every survey had an associated weather recording. We obtained mean (± SE) ambient temperature and relative humidity for every survey because these variables have been related to frog population fluctuations after hurricanes (Woolbright 1991). We pooled weather data for both forests, as climate variables did not differ between Maricao and Guilarte ($P = 0.114$). We used a paired t-test (PROC TTEST SAS 1999) to examine differences in mean temperature and relative humidity before and after the hurricane.

We summarized data by forest, year, and transect, and analyzed total counts and relative abundance for each species. We used a paired t-test (PROC TTEST SAS

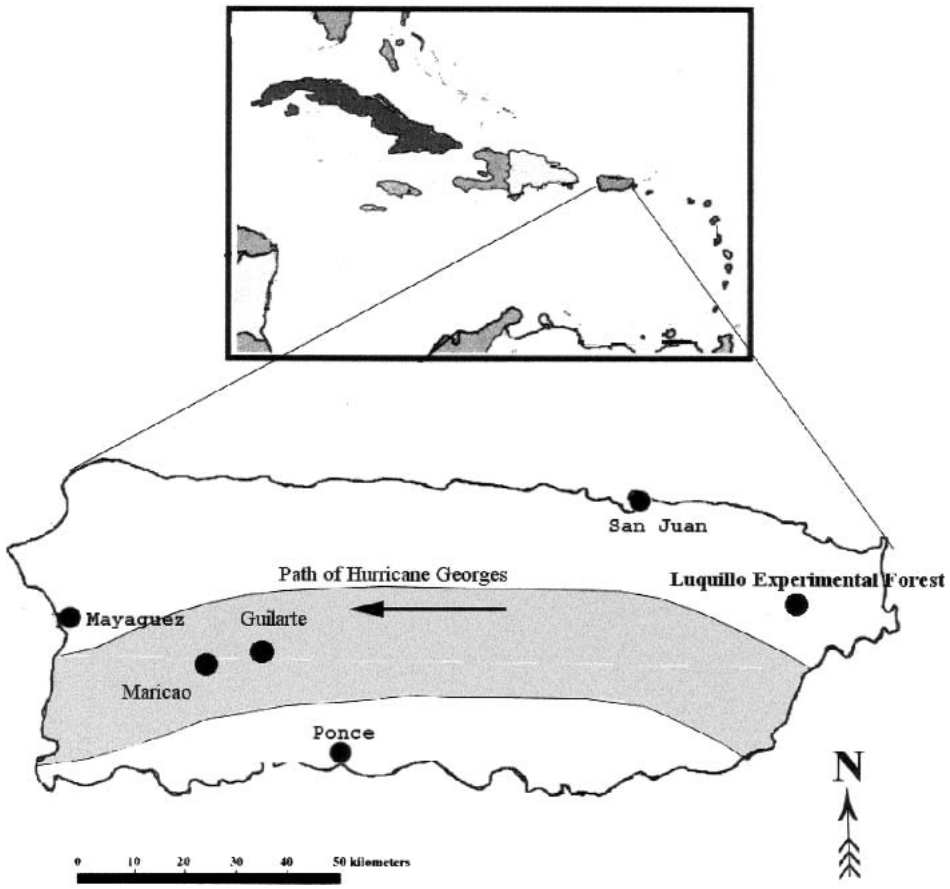

FIG. 1. Map of Puerto Rico indicating locations of the Maricao and Guilarte Forests, and the Luquillo Experimental Forest. Shaded area indicates the path of Hurricane Georges eyewall.

1999) to examine differences in numbers of individuals by species before and after hurricane Georges in Maricao and Guilarte. We used a Type I error of 5% ($\alpha = 0.05$) for all hypotheses tested.

Additionally, we calculated species richness and evenness of the Maricao and Guilarte frog assemblages before and after the hurricane. We used program RAREFACT to calculate expected species richness (± SD) from subsamples of 50 to 100 individuals, and program DIVERS for measures of evenness (Chao 1984; Krebs 1989).

Hurricane Georges' eyewall crossed directly over the Cordillera Central of Puerto Rico causing extensive damage to the region (Fig. 1). Its impact was extensive on both Maricao and Guilarte Forests, with large areas experiencing near total defoliation and >50% of trees suffering major breakage and uprooting. The ambient temperature during pre-hurricane surveys averaged 21.8°C (± 0.29°C) and mean relative humidity 88.7% (± 1.13%). After the hurricane, ambient temperatures during surveys averaged 20.3°C (± 0.33°C) and mean relative humidity 89.3% (± 1.01%). Mean temperature differed between time periods ($t = -3.26$, $df = 51$, $P = 0.002$). However, there was no significant difference in relative humidity before and after the hurricane ($t = 0.40$, $df = 51$, $P = 0.692$).

Our surveys detected 1,193 individuals of 6 abundant to relatively abundant species in transects of the Maricao Forest before the hurricane. Following the storm, we

TABLE 1. Mean ± SE, sample size (N), and relative abundance (%) by species before (1998) and after (1999) hurricane Georges at Maricao Forest, Puerto Rico.

	Abundance		Relative abundance	
Species	1998	1999	1998	1999
Eleutherodactylus coqui	32.5 ± 3.9 (552)	35.8 ± 4.7 (859)	46.3	62.9
Eleutherodactylus antillensis	2.1 ± 1.5 (35)	0.4 ± 0.3 (9)	2.9	0.7
Eleutherodactylus brittoni	4.4 ± 1.5 (75)	1.3 ± 0.5 (31)	6.3	2.3
Eleutherodactylus richmondi	6.7 ± 1.7 (114)	1.0 ± 0.3 (24)	9.5	1.8
Eleutherodactylus wightmanae	22.4 ± 2.5 (380)	17.8 ± 2.4 (426)	31.8	31.2
Leptodactylus albilabris	2.2 ± 1.2 (37)	0.6 ± 0.2 (15)	3.2	1.1

recorded 1,364 individuals of the same 6 species. However, the number of individuals per species varied in the aftermath of the hurricane (Table 1). *Eleutherodactylus coqui* was the only species that increased in abundance following Hurricane Georges, albeit not significantly ($t = -0.88$, $df = 23$, $P = 0.386$). At Maricao we recorded lower numbers for other species after the hurricane (Table 1). The greatest observed decreases in relative abundance included *E. richmondi* (9.5% to 1.8%), *E. antillensis* (2.93% to 0.65%), and *E. brittoni* (6.29% to 2.3%). Abundance of *E. richmondi* ($t = 2.67$, $df = 23$, $P = 0.013$) and *E. brittoni* ($t = 2.25$, $df = 23$, $P = 0.034$) was significantly lower after the hurricane. Similarly, the species richness and evenness (pre-hurricane; $S = 5.98 \pm 0.12$; $J = 0.803$) of the Maricao Forest frog assemblage declined after the storm (post-hurricane; $S = 4.93 \pm 0.27$; $J = 0.606$).

Surveys in the Guilarte Forest detected 453 individuals of 4 abundant to relatively abundant species along 3 of 4 transects before the hurricane. However, it is important to note we recorded 2 individuals of an additional species (*E. hedricki*) during pre-hurricane surveys on the Monte Guilarte transect. Unfortunately, this transect was lost after the storm (Fogarty and Vilella 1999). Following Hurricane Georges, we recorded 704 individuals of the same 4 species. Similar to results in the Maricao Forest, the number of individuals per species in Guilarte varied in the aftermath of the hurricane (Table 2). After the hurricane we recorded increased abundances of *E. coqui* ($t = -1.80$, $df = 5$, $P = 0.131$) and *L. albilabris* ($t = -1.17$, $df = 5$, $P = 0.295$), albeit these increases were not statistically significant. While we recorded decreases in relative abundance in Guilarte following the hurricane, these declines were not as marked as in Maricao (Table 2). Nevertheless, both *E. wightmanae* (15.7% to 13.6%) and *E. brittoni* (6.4% to 3.3%) decreased in relative abundance after the hurricane. Changes in frog assemblage measures were also less marked in Guilarte compared to Maricao. The species richness and evenness (pre-hurricane; $S = 3.33 \pm 0.51$; $J = 0.648$) of the Guilarte Forest frog assemblage was slightly lower after the storm (post-hurricane; $S = 3.00 \pm 0.64$; $J = 0.568$).

We detected an increase in *E. coqui* abundance in the Cordillera Central after Hurricane Georges similar to that reported from the LEF after Hurricane Hugo. Wool-

TABLE 2. Mean ± SE, sample size (N), and relative abundance (%) by species before (1998) and after (1999) hurricane Georges at Guilarte Forest, Puerto Rico.

	Abundance		Relative abundance	
Species	1998	1999	1998	1999
Eleutherodactylus coqui	52.2 ± 6.8 (313)	86.7 ± 19.7 (520)	69.1	73.9
Eleutherodactylus brittoni	4.8 ± 2.1 (29)	3.8 ± 2.2 (23)	6.4	3.3
Eleutherodactylus wightmanae	11.8 ± 3.2 (71)	16.0 ± 7.4 (96)	15.7	13.6
Leptodactylus albilabris	6.7 ± 3.9 (40)	10.8 ± 7.5 (65)	8.8	9.2

bright (1991) reported a fourfold increase in populations of *E. coqui* a year after Hurricane Hugo. Increased abundance of *E. coqui* in the Cordillera Central after Hurricane Georges may have been related to enhanced availability of understory retreat sites from the canopy vegetation debris. Results of mark-recapture experiments in Maricao and Guilarte Forests indicated a close relationship between population densities of *E. coqui* and understory cover (Fogarty and Vilella 2003).

However, we also documented decreases in other relatively abundant frog species in Maricao and Guilarte after the hurricane. Observed population declines for *E. richmondi* in Maricao Forest (79%) were very similar to those reported for the species from the LEF (83%) following Hurricane Hugo (Woolbright 1991). Post-hurricane weather patterns may have contributed to changes in microclimate conditions for species such as *E. richmondi* and *E. antillensis*.

Hurricane Georges greatly modified the vegetation structure of the Maricao and Guilarte Forests and likely affected many basic ecological processes. Microclimate, rainfall patterns, nutrient cycling, and litter fall are among some of the aspects of terrestrial ecosystems disrupted by intense hurricanes (Waide 1991). Following Hurricane Georges the observed changes in diversity and abundance of forest frogs in the Cordillera Central were very similar to those reported for the LEF after Hurricane Hugo (Woolbright 1991). Therefore, we suggest a general pattern may exist for hurricane effects on Puerto Rican forest frog populations. Following a major hurricane, changes in forest structure and composition may promote population increases of habitat generalists (e.g., *E. coqui*), while specialists (e.g., *E. richmondi*) experience declines. *E. richmondi* is a semifossorial species seldom found more than 1 meter aboveground (Rivero 1998).

However, further research is required to confirm the observed patterns of response by frog populations of the principal mountain ranges (i.e., Luquillo Mountains and Cordillera Central) of Puerto Rico, as well as to determine the long-term responses of forest frog populations to hurricanes in the Cordillera Central. Woolbright (1996) reported natural disturbances may influence the long-term demographic patterns of *E. coqui*; thus, we expect forest succession after Hurricane Georges will likely affect frog populations of the Cordillera Central for many years after the storm.

There is a major concern among biologists to collect reliable information on amphibian assemblages in order to monitor and/or validate suspected population declines (Hedges 1993; Young et al. 2001). Our results on short-term responses by forest frog populations after Hurricane Georges provide a clear example why monitoring efforts should be implemented in the Cordillera Central. These efforts may rely on either permanently established grids or points selected along randomly located transects (Fogarty and Vilella 2001). We recommend using available forest trails in Maricao and Guilarte to select locations of survey transects rather than roadside counts, since the latter may be biased by the nonrandom location of roads and the presence of species associated with disturbed habitats and exotic vegetation (Forman and Alexander 1998).

Implementing a monitoring program would provide the framework needed to determine population trends and examine patterns of response to changes in habitat, as well as the long-term responses to natural disturbances (e.g., hurricanes). Moreover, the potential for locating remaining populations of rare species, such as *E. karlschmidti* and *E. eneidae*, is another important justification to implement long-term monitoring programs for the forest frogs of the Cordillera Central.

Acknowledgments.—Funding was provided by the Caribbean Field Office of the U.S. Fish and Wildlife Service. The Forestry Division of the Puerto Rico Department of Natural and Environmental Resources (DNER) provided access to Maricao and Guilarte Forests. Field procedures were conducted under the auspices of DNER permit 97-IC-68. We are grateful to A. Muñiz, DNER Management Officer at Maricao Forest for providing housing facilities. The manuscript was greatly im-

proved by comments from two anonymous reviewers.

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