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POPULATION DECLINES OF MOUNTAIN COQUI (*ELEUTHERODACTYLUS PORTORICENSIS*) IN THE CORDILLERA CENTRAL OF PUERTO RICO

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***Abstract.*—The Mountain Coqui (*Eleutherodactylus portoricensis*) is a frog endemic to montane rainforests in the Cordillera Central and Luquillo Mountains of Puerto Rico. Classified as endangered by the IUCN Red List and as vulnerable by the Department of Natural and Environmental Resources of Puerto Rico, this species has undergone considerable decline in the Luquillo Mountains. To evaluate the population status of *E. portoricensis* across its entire range, we conducted about 87 hours of surveys at 18 historical localities and 25 additional localities that we considered suitable for this species. We generated occupancy models to estimate the probability of occurrence at surveyed sites and to identify geographic and climatic factors affecting site occupancy. We also constructed a suitability map to visualize population status in relation to the presence of land cover at elevations where the species has been documented, and determined the dates when populations were last detected at historical localities. *Eleutherodactylus portoricensis* was detected at 14 of 43 localities, including 10 of 18 historical localities, but it was not detected at any localities west of Aibonito (western Cordillera Central). Occupancy models estimated the probability of occurrence for localities in the western Cordillera Central as zero. Site occupancy was positively associated with montane cloud forest, and negatively associated with the western Cordillera Central, maximum temperature, and precipitation seasonality. The suitability map suggests that declines have occurred despite the presence of suitable habitat. We suggest upgrading the extinction risk of *E. portoricensis* and potentially developing a captive breeding program for this species.**

Key Words.—population status; decline; extirpation; Puerto Rico; Cordillera Central

INTRODUCTION

Puerto Rico is home to 17 species of *Eleutherodactylus* frogs, commonly known as coquis. Of these, three species are presumed extinct (Burrowes et al. 2004) and 13 species are critically endangered, endangered, vulnerable, or near threatened (IUCN Red List, http://www.iucnredlist.org [accessed 20 August 2012]). Documented factors contributing to these declines include climate warming, extended periods of drought, and a potential synergistic interaction between climate and the Amphibian Chytrid Fungus, *Batrachochytrium dendrobatidis* (*Bd*; Joglar and Burrowes 1996; Woolbright 1997; Burrowes et al. 2004; Joglar et al. 2007; Longo and Burrowes 2010). The infectious disease chytridiomycosis, caused by *Bd*, has been implicated in massive and rapid amphibian die-offs world-wide (Berger et al. 1998; Lips et al. 2005; Fisher et al. 2009) and *Bd* has been found in Puerto Rico dating back to 1976 (Burrowes et al. 2004). In light of recent amphibian declines and local extirpations in Puerto Rico, it is imperative to survey historical localities to update and verify the continued persistence of populations or the rediscovery of populations thought to have been extirpated (e.g., Rodríguez-Contreras et al. 2008; Kolby and McCranie 2009; Puschendorf et al. 2011).

The Mountain Coqui, *Eleutherodactylus portoricensis* (Schmidt 1927; Fig. 1), is listed as endangered by the

FIGURE 1. A Mountain Coqui (*Eleutherodactylus portoricensis*) at El Yunque National Forest, Puerto Rico. (Photographed by Alejandro Ríos-Franceschi).

IUCN Red List (IUCN Red List, Available from http://www.iucnredlist.org [Accessed 20 August 2012]) and as vulnerable by the Department of Natural and Environmental Resources of Puerto Rico (Departamento de Estado 2004). A principal occupant of the understory of cool, moist rainforest in Puerto Rico, this frog has been documented at elevations above 180 m in shrubs, palms, herbaceous plants, bromeliads, tree holes, and under rocks, trunks, roots, and leaf litter (Drewry 1970; Drewry and Rand 1983; Schwartz and Henderson 1991; Rivero 1998). The species' range spans the Luquillo Mountains of northeastern Puerto Rico and the Cordillera Central (Schwartz and Thomas 1975; Schwartz and Henderson 1988), which forms the highland "backbone" of Puerto Rico and includes an eastern extension beginning at the city of Cayey (Cayey Mountains; Fig. 2). Documented extirpations of *E. portoricensis* at two low elevation (about 350 m) localities in El Yunque National Forest in the Luquillo Mountains have been attributed to prolonged periods of drought and warm, dry conditions resulting from Hurricane Hugo in 1989 (Stewart 1995; Woolbright 1997). Additionally, a synergistic interaction between climate and *Bd* may explain population declines of *E. portoricensis* at elevations above 600 m (Longo and Burrowes 2010; Longo et al. 2010).

Because of the concern of declining populations and limited geographic distribution, we undertook this study to infer the population status (presence or absence) of *E. portoricensis* across its entire range. We conducted auditory and visual surveys at historical localities and at localities that we deemed suitable for this species based on its documented habitat preferences. Next, we generated occupancy models to estimate the probability of occurrence at surveyed sites and to identify geographic and climatic factors affecting site occupancy. Finally, we constructed a suitability map to visualize population status in relation to the presence of land cover at elevations where this species has been documented, and we determined the dates when populations were last detected at historical localities.

MATERIALS AND METHODS

Auditory and visual surveys.—We conducted auditory and visual surveys at 43 localities in the western Cordillera Central (i.e., west of Aibonito), the Cayey Mountains, and the Luquillo Mountains between April and August of 2007, 2008, and 2010–2013 to infer population status (presence or absence) of *E. portoricensis*. We surveyed 18 historical localities (Table 1) where this species has been documented according to local naturalists (Fernando Bird-Picó, Alberto R. Estrada, Alberto Puente-Rolón, and Richard Thomas, pers. comm.), the scientific literature (Joglar 1998; Villanueva-Rivera 2006), and a database for the Puerto Rico Gap Project (Gould et al. 2008). We also surveyed 25 localities that we deemed suitable for *E. portoricensis* based on its documented habitat preferences (Schwartz and Thomas 1975; Schwartz and Henderson 1988; Joglar 1998; Gould et al. 2008), although we later discovered that six of these localities were located in a habitat identified as being unsuitable for this species by our suitability map (see Results).

We primarily conducted surveys in state and national forests above 600 m. Recent work suggests that *E. portoricensis* has been contracting to elevations above ~600 m in El Yunque National Forest over the past two decades (Stewart 1995; Woolbright 1997; Burrowes et al. 2004; Longo and Burrowes 2010), and to our knowledge there are no published reports of this species occurring below 600 m in the Cordillera Central. Thirty five of the 43 surveyed localities occurred within protected forest remnants corresponding to El Yunque National Forest in the Luquillo Mountains, Carite State Forest, Cerro de la Tabla, and Las Tetas de Cayey in the Cayey Mountains, and Toro Negro State Forest, Los Tres Picachos State Forest, Guilarte State Forest, and Maricao State Forest in the western Cordillera Central (Fig. 2).

We conducted surveys between 1900 and 0100, during the peak calling activity time of *E. portoricensis* (Drewry and Rand 1983; Villanueva-Rivera 2006). With one exception, the localities were georeferenced (< 15 m uncertainty) using a hand-held global positioning system unit (Table 1). We measured temperature, relative humidity, and maximum wind speed using a Kestrel 3000 Pocket Weather Station (Nielsen-Kellerman Company, Boothwyn, Pennsylvania, USA) at the beginning of most of the surveys in 2007 and 2008, but these data were missing for surveys in 2010−2013 due to equipment unavailability. Each survey involved slowly walking on marked trails and/or roadsides listening for the calls of males. The number of observers varied per survey, ranging from one to four persons. All observers knew how to identify *E. portoricensis* by their advertisement call. Each locality was surveyed for a total of ≥ 45 minutes, after which if *E. portoricensis* was detected we captured both male and female frogs to obtain DNA samples for a phylogeographic study of this species (Barker et al. 2011). Thus, the presence of the species was confirmed with acoustic, visual, and genetic data.

Occupancy model.—We used a modeling approach that accounts for imperfect detection (MacKenzie et al. 2002) in Presence 6.1 (Hines 2006; http://www.mbr-pwrc.usgs.gov/software/presence.html [accessed 09 September 2013]) to estimate the probability of occurrence of *E. portoricensis* at surveyed sites and to identify factors that may affect site occupancy. Obtaining an unbiased estimate of site occupancy in

TABLE 1. Results of auditory and visual surveys for Eleutherodactylus portoricensis across its range in Puerto Rico. Locality descriptions, population status (A = not detected; P = detected), coordinates, and dates of surveys are provided. A historical locality (Y = yes; N = no) represents a locality where it has been documented based on museum specimen records, the scientific literature, and/or by reports of local naturalists. The last documented record of E. portoricensis is listed for historical localities where we did not detect this species. Localities and forest names correspond to those depicted in Figure 2. HL = Historical Locality, COR = western Cordillera Central, CAY = Cayey Mountains, and LUQ = Luquillo Mountains.

ID	Mtn. range	Municipality	Locality Name	Historical locality	Status	Elevation (m)	Coordinates	Survey date(s)	Date of last report
1	COR	Adjuntas	Guilarte State Forest, trail beginning at Rd. 131 west of Lago Garzas	N	A	1,148	N 18.142, W 66.769	21-Jul-07	
2	COR	Adjuntas	Guilarte State Forest, near Monte Guilarte	N	A	982	N 18.138, W 66.794	13-Apr-13	
3	COR	Adjuntas	Guilarte State Forest, Río Pellejas	N	A	595	N 18.176, W 66.680	20-Apr-13	
4	COR	Adjuntas	Guilarte State Forest, ~0.4 km west of Lago Garzas	N	A	793	N 18.129, W 66.752	21-Apr-13	
5	COR	Adjuntas	Guilarte State Forest, ~1.4 km southwest of Lago Garzas	N	A	857	N 18.119, W 66.752	4-Apr-13	
6	COR	Ciales	Toro Negro State Forest, Lago el Guineo, mouth of Río Toro Negro	Y	A	961	N 18.160, W 66.531	18-Jul-07 1-Jun-08	2004 Villanueva-Rivera 2006
7	COR	Ciales	Toro Negro State Forest, Lago el Guineo, north of dam	N	A	959	N 18.162, W 66.529	1-Jun-08	
8	COR	Jayuya	Los Tres Picachos State Forest, end of trail from Barrio El Salto entrance	Y	A	979	N 18.211, W 66.539	7-Jun-08	2001 Alberto Puente-Rolón, pers. comm.
9	COR	Jayuya	Los Tres Picachos State Forest, ~0.50 km east of Rd. 144	N	A	798	N 18.205, W 66.549	13-Apr-13	
10	COR	Jayuya	Los Tres Picachos State Forest, ~0.25 km east of Rd. 144	N	A	598	N 18.208, W 66.551	20-Apr-13	
11	COR	Jayuya	Toro Negro State Forest, Cerro Punta	Y	A	1,265	N 18.172, W 66.590	18-Jul-07 31-May-08 2-Jun-08 6-Jun-08 25-Jul-13	2004 Villanueva-Rivera 2006
12	COR	Juana Díaz	Toro Negro State Forest, Cerro Maravillas	N	A	951	N 18.148, W 66.539	17-Jul-07 20-Jul-07 2-Jun-08	
13	COR	Maricao	Maricao State Forest, Monte del Estado	Y	A	693	N 18.161, W 66.998	24-Jul-07	1998 Joglar 1998
14	COR	Orocovis	Lago de Matrullas	N	A	785	N 18.211, W 66.478	20-Jul-07	
15	COR	Orocovis	Toro Negro State Forest, Doña Juana Recreation area	Y	A	840	N 18.176, W 66.493	16-Jul-07 20-Jul-07 2-Jun-08 6-Jun-08	1977 museum record
16	COR	Orocovis	Toro Negro State Forest, el Torre del Bosque Toro Negro	Y	A	1,053	N 18.172, W 66.481	2-Jun-08 18-Jun-10 19-Jun-10 20-Jun-10 10-Jul-11 11-Jul-11 04-Jul-12	1980 Fernando Bird-Picó, unpublished data
17	COR	Orocovis	Toro Negro State Forest, Río Confesora	N	A	-	-	02-Aug-13	
18	COR	Utuado	Cerro Roncador, Utuado	N	A	909	N 18.233, W 66.760	29-May-08 8-Jun-08	
19	CAY	Caguas	Carite State Forest, near Cerro la Santa	N	P	876	N 18.108, W 66.059	30-Jul-07	
20	CAY	Cayey	Carite State Forest, Doppler Radar	N	A	856	N 18.115, W 66.078	23-May-08 27-May-08 24-Jun-07	

Table 1 continued on next page

Presence when sites are only visited once is impossible without auxiliary information about detectability (MacKenzie and Bailey 2004). Due to logistical and financial constraints, we only surveyed 17 of the 43 localities multiple times (range 2–8 times; Table 1), which included seven localities in the western Cordillera Central (localities 6, 11, 12, 13, 15, 16, 18), seven localities in the Cayey Mountains (localities 20, 24–26, 30, 32, 33), and three localities in Luquillo Mountains (localities 38, 40, 42). We analyzed this data subset (excluding localities 6 and 16, which had missing survey-specific covariate data) to explore whether our ability to detect *E. portoricensis* was influenced by survey-specific factors. We followed MacKenzie (2006) suggestion to first model detection while holding occupancy at the most general model. We included temperature, relative humidity, and maximum wind speed as survey-specific covariates because these factors may influence calling activity in the closely related *E. coqui* (Woolbright 1985; Stewart and Rand 1992; Fogarty and Vilella 2001). This analysis estimated the probability of detecting *E. portoricensis* as 1 (SE = 0), and it indicated that including survey-specific covariates did not improve occupancy models. These results suggest that assuming a constant detection probability across surveys [i.e., $p(\cdot)$] is justifiable, so we analyzed the entire detection/non-detection dataset except for locality 17, which had missing site-specific covariate data. Given this high detectability, we also analyzed the entire detection/non-detection dataset with logistic regression models. Logistic models were fit with the glm function (generalized linear model) or lrm (logistic regression model) function in the 'rms' package version 4.2 (Harrel 2014) using R 3.0.2 (R Development Core Team 2013). We attribute the high detection probability of *E. portoricensis* to the loud and distinctive advertisement call of males, which is audible even when a few individuals are calling.

TABLE 1. *continued.*

21	CAY	Cayey	Guayama, ~1 km west of I-15, past Calle La Alturita	N	A	656	N 18.038, W 66.138	26-May-08	
22	CAY	Cayey	La Piedra summit, private plantation	N	A	717	N 18.106, W 66.214	24-May-08	
23	CAY	Cayey	La Plana, private plantation	N	A	605	N 18.087, W 66.211	26-May-08	
24	CAY	Guayama	Cerro de la Tabla, Km. 2.1 on Rd. 7741	N	P	772	N 18.057, W 66.116	22-May-08 23-May-08 26-May-08	
25	CAY	Guayama	Cerro de la Tabla, Km. 3.1 on Rd. 7741	Y	P	786	N 18.052, W 66.122	4-Jul-07 28-Jul-07 22-May-08	
26	CAY	Guayama	Cerro de la Tabla, Km. 4.4 on Rd. 7741	N	P	811	N 18.049, W 66.129	22-May-08 26-May-08 28-May-08	
27	CAY	Guayama	Carite State Forest, south entrance on Rd. 179	N	A	643	N 18.093, W 66.075	25-May-08	
28	CAY	Guayama	Lago Carite, near Casa Carita on Rd. 742	N	A	564	N 18.067, W 66.102	3-Jul-07	
29	CAY	Guayama	Monte el Gato, Rd. 7737	Y	A	809	N 18.084, W 66.180	29-Jul-07	$1980_{\text{museum record}}$
30	CAY	Patillas	Carite State Forest, Km. 20 on Rd. 179	N	P	750	N 18.113, W 66.070	23-May-08 25-May-08 27-May-08	
31	CAY	Salinas	Summit of Las Tetas de Cayey	Y	A	825	N 18.094, W 66.231	24-May-08	$2002_{\text{Gould et al. 2008}}$
32	CAY	San Lorenzo	Carite State Forest, Charco Azul	Y	P	610	N 18.091, W 66.032	2-Jul-07 3-Jul-07 23-May-08	
33	CAY	San Lorenzo	Carite State Forest, Km. 6.1 on Rd. 7740	N	P	715	N 18.101, W 66.028	28-Jul-07 30-Jul-07	
34	LUQ	Río Grande	El Yunque National Forest, El Toro trail, ~1.25 km from Rd. 186	N	A	887	N 18.279, W 65.845	15-Jun-08	
35	LUQ	Río Grande	El Yunque National Forest, El Toro trailhead ~6.5 km from Rd. 186	Y	P	993	N 18.272, W 65.833	15-Jun-08	
36	LUQ	Río Grande	El Yunque National Forest, Pico el Toro	Y	P	1,041	N 18.272, W 65.829	15-Jun-08	
37	LUQ	Río Grande	El Yunque National Forest, Km. 8.8 on Rd. 191	N	A	547	N 18.313, W 65.772	13-Jun-08	
38	LUQ	Río Grande	El Yunque National Forest, El Yunque Rock	Y	P	1,025	N 18.311, W 65.792	23-Jun-07	
39	LUQ	Río Grande	El Yunque National Forest, Forest Service Rd. 10	Y	P	893	N 18.303, W 65.795	23-Jun-07	
40	LUQ	Río Grande	El Yunque National Forest, Km. 12.6 on Rd. 191	Y	P	762	N 18.296, W 65.791	10-Jun-08 11-Jun-08	
41	LUQ	Río Grande	El Yunque National Forest, near Pico del Este	Y	P	758	N 18.292, W 65.783	11-Jun-08	
42	LUQ	Río Grande	El Yunque National Forest, Pico del Este	Y	P	1,021	N 18.269, W 65.758	25-Jul-07 26-Jul-07 11-Jun-08	
43	LUQ	Río Grande	El Yunque National Forest, Tradewinds Trail	Y	P	855	N 18.283, W 65.811	28-Jun-07	

We modeled geographic (region and forest) and climatic (aspects of temperature and precipitation) factors that we hypothesized would affect site occupancy of *E. portoricensis* (Table 2). Region was included as a covariate to test the hypothesis that site occupancy is negatively associated with the western Cordillera Central. We included elevation and the presence/absence of montane cloud forest as site-specific covariates because *E. portoricensis* is reportedly contracting upslope to higher elevation cloud forest in the Luquillo Mountains (Woolbright 1997; Burrowes et al. 2004; Longo and Burrowes 2010). Elevation data were downloaded from the CGIAR-CSI SRTM 90 m Digital Elevation Database (Jarvis et al. 2008). We identified the presence/absence of lower montane wet evergreen cloud forest (tall, mixed palm, and elfin cloud forest) at each site from a map created using recent (1999−2003) satellite imagery (Gould et al. 2008) at a spatial resolution of 15 × 15 m. Lowest precipitation of any monthly minimum precipitation, precipitation seasonality, and highest temperature of any monthly maximum temperature were included as site-specific covariates because prolonged periods of drought have been associated with population extirpations of *E. portoricensis* in the Luquillo Mountains (Stewart 1995; Woolbright 1997), and high temperatures are lethal to this species (Beuchat et al. 1984). High resolution (about 450 m) climatic data were obtained from PRISM climate maps of mean monthly and annual precipitation and minimum and maximum temperature from 1963−1995 (Daly et al. 2003). Precipitation seasonality was calculated using the raster calculator in ArcMap 10.2 (ESRI, Redlands, California, USA) as the standard deviation of the monthly precipitation estimate divided by the mean precipitation estimate per grid cell. We extracted site-specific covariate data for each locality in ArcMap 10.2.

We tested hypothesized relationships between site occupancy and site-specific covariates across the entire range of *E. portoricensis* (i.e., western Cordillera Central, Cayey Mountains, Luquillo Mountains), as well as within the Cayey and Luquillo Mountains. By separately analyzing detection/non-detection data for the Cayey and Luquillo Mountains, we aimed to elucidate factors affecting site-occupancy in regions where *E. portoricensis* is definitively still extant. To improve performance of model-fitting algorithms, we standardized quantitative variables by subtracting the mean and dividing by the standard deviation. We did not include independent variables with correlations greater than 0.5 in the same model to avoid problems with collinearity. In Presence, we used a single-season occupancy model (MacKenzie et al. 2002; MacKenzie 2006), and we assumed that the occupancy state of each site did not change for the duration of the surveying (i.e., there are neither colonizations nor extinctions) and that parameters were constant across sites (MacKenzie et al. 2002). To our knowledge, none of the populations that we surveyed have become extirpated since they were surveyed. Occupancy models in our Presence and logistic regression analysis were ranked and model weights calculated using Akaike's Information Criterion adjusted for small sample size ($\mathrm{AIC_c}$; Akaike 1974; Burnham and Anderson 2002). The $\mathrm{AIC_c}$ weights sum to one for all models in a model set, and the weights measure the appropriateness of a given model relative to other models in a model set.

Suitability map.—We constructed a suitability map for *E. portoricensis* after conducting auditory and visual surveys to visualize population status in relation to the distribution of land cover at elevations where this species has been documented. Using IDRISI Kilimanjaro GIS software (Eastman 2003), we extracted elevation values ≥ 180 m and 16 land cover classes from the land cover map of Gould et al. (2008) where *E. portoricensis* has been documented, which include mature secondary dry and moist serpentine semi-deciduous forest, mature secondary moist limestone evergreen and semi-deciduous forest, mature secondary montane wet alluvial evergreen forest, young secondary montane wet alluvial evergreen forest, montane wet alluvial shrubland and woodland, mature secondary montane wet non-calcareous evergreen forest, mature primary Tabonuco and secondary montane wet non-calcareous evergreen forest, mature primary Palo Colorado forest and secondary montane wet non-calcareous evergreen forest, mature primary sierra palm

TABLE 2. Definitions of site-specific covariates used to model site occupancy for *Eleutherodactylus portoricensis*.

Covariate Category	Variables and definitions
Region	Western Cordillera Central, Cayey Mtns., and Luquillo Mtns.
Montane cloud forest	Lower montane wet evergreen cloud forest (tall, mixed palm, and elfin cloud forest) as defined by Helmer et al. (2002)
Elevation	Elevation (m) at beginning of survey
Prevailing climatic conditions	Lowest precipitation of any monthly minimum precipitation Precipitation seasonality (standard deviation of the monthly precipitation estimate divided by the mean precipitation estimate) Highest temperature of any monthly maximum temperature

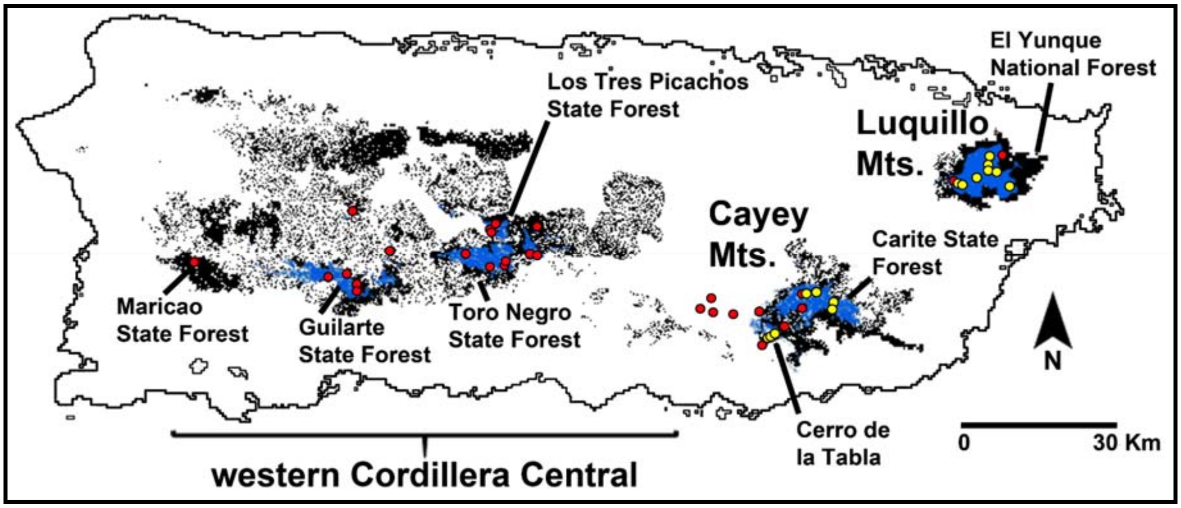

FIGURE 2. A suitability map for *Eleutherodactylus portoricensis* generated in IDRISI Kilimanjaro. Dark areas represent potentially suitable habitat; red circles depict localities that were surveyed during the summers of 2007, 2008, 2010–2013 but *E. portoricensis* was not detected; and yellow circles depict localities where it was detected during the same time period. Blue shading depicts the approximate distribution of montane cloud forest, which was positively associated with site occupancy by *E. portoricensis* (Tables 3 and 4).

and secondary montane wet non-calcareous evergreen forest, mature primary elfin woodland, montane wet non-calcareous evergreen forest, and wet serpentine shrubland and woodland (Schwartz and Thomas 1975; Schwartz and Henderson 1988; Joglar 1998). We merged the two resulting raster layers to show areas where estimates of elevation and land cover were concordant. To visualize the population status of *E. portoricensis* in relation to predicted suitable habitat, we added detection/non-detection data for each surveyed locality to the suitability map in ArcMap 10.2.

Last record at historical localities.**—**We explored historical locality records and museum specimen records to determine when *E. portoricensis* was last detected at historical localities where it was absent according to our auditory and visual surveys. We downloaded museum specimen records from the Museum of Natural History, University of Kansas, Lawrence, accessed through the HerpNET data portal (http://www.herpnet.org) on 3 July 2008, and from the University of Puerto Rico at Mayagüez on 4 June 2008. Because *E. portoricensis* was synonymous with *E. coqui* prior to 1966 (Thomas 1966), we only used specimen records collected after this date.

RESULTS

Auditory and visual surveys.**—**We conducted a grand total of 77 auditory and visual surveys at 43 localities spanning elevations from 547 to 1,265 m in the western Cordillera Central, Cayey Mountains, and Luquillo Mountains. In about 87 h of searching we detected *E. portoricensis* at 15 of the 43 localities (35%), including 10 out of 18 historical localities (56%; Table 1). We conducted auditory and visual surveys at a total of 18 localities in the western Cordillera Central, including six historical localities (Table 1 and Fig. 2). In 46.5 hours of surveys we did not detect a single *E. portoricensis* individual in this region. In addition to these surveys, we drove along PR 143 one evening from Toro Negro State Forest to Barranquitas, south to Orocovis and back, listening for calling males in forest near the roadside. We also listened for calls as we drove along PR 143 from Maricao State Forest to Monte Guilarte. No individuals were heard. We detected *E. antillensis*, *E. coqui*, *E. wightmanae*, and *Leptodactylus albilabris* frequently at surveyed localities in this region.

We conducted auditory and visual surveys at a total of 15 localities in the Cayey Mountains for a total of 24 hours. We detected *E. portoricensis* at six of the 15 localities (40%; Table 1), including two of four historical localities (50%). We did not find this species at the historical localities of Monte el Gato and Las Tetas de Cayey, but there was no protected primary forest at Monte el Gato and both sites were only surveyed once. All detected populations in this region occurred within protected montane rainforest remnants (Carite State Forest and Cerro de la Tabla). The anurans most commonly heard calling with *E. portoricensis* in the Cayey Mountains were *E. wightmanae* and *E. coqui*.

We conducted auditory and visual surveys at 10 localities in the Luquillo Mountains (El Yunque National Forest) for a total of 16.5 hours and detected *E. portoricensis* at eight of the ten localities (80%). As we hiked along El Toro trail, we stopped hearing this species about 1.25 km from the trailhead on Road 186

Table 3. Model structure, number of parameters (K), relative difference in AIC$_c$ values (ΔAIC$_c$), and AIC model weights (w_i) for well-supported occupancy models (ΔAIC$_c$ < 10) for *Eleutherodactylus portoricensis* across its entire range according to Presence and logistic regression. Definitions of site-specific covariates are reported in Table 2.

Model	−2 log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
Presence					
ψ(region, montane cloud forest), $p(\cdot)$	24.79	5	36.46	0.00	0.75
ψ(region, maximum temperature), $p(\cdot)$	27.98	5	39.65	3.19	0.15
ψ(region), $p(\cdot)$	32.95	4	42.03	5.57	0.05
ψ(region, elevation), $p(\cdot)$	31.26	5	42.93	6.47	0.03
ψ(montane cloud forest, precipitation seasonality), $p(\cdot)$	37.08	4	44.16	7.70	0.02
ψ(precipitation seasonality, elevation), $p(\cdot)$	38.46	4	45.54	9.08	0.01
Logistic regression					
ψ(region, montane cloud forest)	21.79	4	33.69	0.00	0.64
ψ(montane cloud forest, precipitation seasonality)	29.52	3	35.79	2.10	0.22
ψ(precipitation seasonality)	32.92	2	39.56	5.87	0.03
ψ(region, maximum temperature)	23.86	4	39.66	5.97	0.03
ψ(precipitation seasonality, maximum temperature)	32.37	3	40.46	6.77	0.02
ψ(region)	30.74	3	40.50	6.81	0.02
ψ(precipitation seasonality, elevation)	32.43	3	41.01	7.32	0.02
ψ(region, elevation)	27.33	4	41.45	7.76	0.01

(887 m; site 34 in Table 1). We also listened for calling males in forest alongside the entire length of Road 186 in El Yunque National Forest, but heard none. The anurans most commonly heard calling with *E. portoricensis* in El Yunque National Forest were *E. coqui* and *E. unicolor*, and *E. locustus* and *E. hedricki* it indicated a significant negative association between site occupancy and the western Cordillera Central (β = temperature of any monthly maximum temperature, and −27.16, SE = 10.00) and highest temperature of any were also heard at some localities. Whereas *E. portoricensis* was sympatric with *E. wightmanae* in the Cayey Mountains, it occurred at higher elevations than this species at our surveyed localities in the Luquillo Mountains.

Occupancy model.—The best-fit occupancy model for *E. portoricensis* across its entire range according to both the Presence (75% of the AIC$_c$ model weight) and logistic regression analysis (64% of the AIC$_c$ model weight) included region and montane cloud forest (Table 3). The Presence analysis revealed a significant positive association between site occupancy and montane cloud forest (β = 3.11, SE = 1.29), and a significant negative association between site occupancy and the western Cordillera Central (β = −136.26, SE = 10.00). According to the logistic regression analysis, the probability of occurrence increased with the presence of montane cloud forest (β = 3.26, SE = 1.28), the Cayey Mountains (β = 10.69, SE = 23.52), and the Luquillo Mountains (β = 10.69, SE = 23.51), but parameter estimates were not significant for either the Cayey Mountains or Luquillo Mountains. The second most highly supported model according to Presence (15% of the AIC$_c$ model weight) accounted for region and highest monthly maximum temperature (β = −4.28, SE = 0.28), and a significant positive association between site occupancy and the Cayey Mountains (β = 39.61, SE = 2.61) and the Luquillo Mountains (β = 37.62, SE = 2.54). In contrast, the second best-fit occupancy according to the logistic regression (22% of the AIC$_c$ model weight) analysis included montane cloud forest and precipitation seasonality, and it indicated that the probability of occurrence significantly increased with the presence of montane cloud forest (parameter estimate = 1.77, SE = 1.02), and significantly decreased with increasing precipitation seasonality (parameter estimate = −16.86, SE = 5.03). Presence estimated the probability of occurrence (ψ) for all localities in the western Cordillera Central as zero (SE = 0.0).

The best-fit occupancy model for *E. portoricensis* in the Cayey and Luquillo Mountains according to both the Presence (74% of the AIC$_c$ model weight) and logistic regression analysis (93% of the AIC$_c$ model weight) included montane cloud forest (Table 4). Presence revealed a significant positive association between site occupancy and montane cloud forest (β = 1.39, SE = 0.65), and the logistic regression indicated that the probability of occurrence significantly increased with the presence of montane cloud forest (parameter estimate = 3.26, SE = 1.10). The second most highly supported occupancy models according to both analyses accounted for < 10% of the AIC$_c$ model weight.

Suitability map.—The suitability map for *E. portoricensis* predicts three disjunct patches of suitable

TABLE 4. Model structure, number of parameters (K), relative difference in AIC$_c$ values (ΔAIC$_c$), and AIC model weights (w_i) for well-supported occupancy models (ΔAIC$_c$ < 10) for *Eleutherodactylus portoricensis* in the Cayey and Luquillo Mountains according to Presence and logistic regression. Definitions of site-specific covariates are reported in Table 2.

Model	−2 log-likelihood	K	AIC$_c$	ΔAIC$_c$	w_i
Presence					
ψ(montane cloud forest), $p(\cdot)$	28.88	3	34.02	0.00	0.74
ψ(minimum precipitation), $p(\cdot)$	33.14	3	38.28	4.26	0.09
$\psi(\cdot)$, $p(\cdot)$	34.30	2	38.85	4.82	0.07
ψ(elevation), $p(\cdot)$	33.89	3	39.03	5.01	0.06
ψ(precipitation seasonality), $p(\cdot)$	34.57	3	39.71	5.69	0.04
Logistic regression					
ψ(montane cloud forest)	21.79	2	27.12	0.00	0.93
ψ(maximum temperature)	24.82	2	32.79	5.67	0.05
ψ(elevation)	27.79	2	36.51	9.40	0.01

habitat in Puerto Rico, which corresponds to the western Cordillera Central, the Cayey Mountains, and the Luquillo Mountains (Fig. 2). With the exception of six localities ~1−10 km west of Cerro de la Tabla, all of the surveyed localities for this study occur in predicted suitable habitat. Thus, *E. portoricensis* is absent from 22/43 (51%) of our surveyed localities despite the presence of historically suitable land cover and elevations. Montane cloud forest, which was positively associated with site occupancy by *E. portoricensis* (Tables 3 and 4), comprises only a fraction of the predicted suitable habitat in our suitability map (Fig. 2).

Last record at historical localities.— *Eleutherodactylus portoricensis* was last documented in the western Cordillera Central in 2004 at Lago el Guineo and Cerro Punta in Toro Negro State Forest (Table 1; Villanueva-Rivera 2006). A museum specimen was collected from the vicinity of Toro Negro Pool in the Doña Juana Recreation Area in 1977, and the species was last detected there and at the nearby el Torre del Bosque Toro Negro in 1980 (Fernando Bird, pers. comm.). *Eleutherodactylus portoricensis* has not been documented in Maricao State Forest or in Los Tres Picachos Forest since 1998 (Joglar 1998) and 2001 (Alberto Puente-Rolón, pers. comm.), respectively. A single specimen was collected from Monte el Gato in the Cayey Mountains in 1980, a locality where we did not detect this species. It was last recorded at Las Tetas de Cayey in 2002 (Gould et al. 2008); however, a population was recently documented in the vicinity of this locality (see Discussion).

DISCUSSION

Our main objective was to provide current information on the distribution and occupancy status of *E. portoricensis* across its entire range in Puerto Rico. Population declines and extirpations of this species have been documented in El Yunque National Forest in the Luquillo Mountains (Woolbright 1997; Burrowes et al. 2004; Longo and Burrowes 2010), and here we report that it may be extirpated from all historical localities west of Aibonito in the Cordillera Central. We did not detect *E. portoricensis* at the 18 localities in the western Cordillera where we conducted auditory and visual surveys, and the Presence analysis estimated the probability of occurrence (ψ) for all localities in the western Cordillera Central as zero (SE = 0.0).

Climatic extremes, weather events, and a synergistic interaction between prolonged droughts and chytridiomycosis are plausible explanations for the possible extirpation of *E. portoricensis* in the western Cordillera Central. Prolonged droughts during the 1980s were likely responsible for initial population declines of *E. portoricensis* at El Verde (~360 m elevation) and Bisley (~355 m elevation) in the Tabonuco forest of El Yunque National Forest, and extirpations from these sites correspond roughly with Hurricane Hugo in 1989, which led to warmer, drier conditions in the forest understory (Woolbright 1991, 1997; Stewart 1995). The effects of drought and hurricanes on *E. portoricensis* populations in the western Cordillera Central are undocumented, but the decline of Richmond's Coqui, *E. richmondi,* in this region following Hurricane Georges in 1999 (Vilella and Fogarty 2005) suggests that hurricanes may have also impacted *E. portoricensis*, because this species has similar ecological requirements (Woolbright 1997). *Batrachochytrium dendrobatidis* has been found above 600 m throughout the Cordillera Central up to Maricao (Burrowes et al. 2008), and this pathogen has contributed to the decline of *E. portoricensis* at elevations above 600 m in El Yunque National Forest (Burrowes et al. 2004; Joglar et al. 2007; Longo and Burrowes 2010; Longo et al. 2010). Whereas a population in the Elfin forest (850 m elevation) of El Yunque National Forest in the Luquillo Mountains recuperated from drastic declines that occurred during the 1990s, those in the Palo Colorado forest (661 m elevation) have been declining since at least 1990

(Burrowes et al. 2004) and are almost extirpated (Longo and Burrowes 2010). *Batrachochytrium dendrobatidis* is prevalent at both study sites, but *Bd* positive frogs may have a lower probability of survival in the Palo Colorado forest because drier conditions there cause more severe infections (Longo and Burrowes 2010; Longo et al. 2010). Given that *Bd* has been in Puerto Rico since at least 1976 and it was detected in *E. portoricensis* at Carite State Forest in the Cayey Mountains (Burrowes et al. 2008), the pathogen probably infected *E. portoricensis* in the western Cordillera Central as well. Our occupancy model for *E. portoricensis* across its entire range based on logistic regression indicated that the probability of occurrence significantly decreased with increasing precipitation seasonality, which suggests that relatively high precipitation seasonality in the western Cordillera Central (data not shown) may have negatively impacted populations by amplifying the effects of chytridiomycosis.

Habitat loss cannot adequately explain extirpations of *E. portoricensis* from historical localities in the western Cordillera Central. All historical localities in this region are in forest remnants (i.e., Los Tres Picachos State Forest, Maricao State Forest, and Toro Negro State Forest) that have been protected over the time period in which populations declined. We found a positive association between site occupancy and montane cloud forest, which suggests that the absence of this species from localities in montane cloud forest in the western Cordillera Central is not due to an absence of highly suitable habitat. Similarly, the presumed extinction of three amphibian species (*Eleutherodactylus karlschmidti*, *E. jasperi*, and *E. eneidae*) and significant declines of six other species of *Eleutherodactylus* above 400 m elevation in Puerto Rico (Burrowes et al. 2004) occurred for reasons other than habitat loss.

It is unlikely that *E. portoricensis* was misidentified or missed during our surveys due to weather conditions. Although the closely related *E. coqui* resembles *E. portoricensis*, it differs slightly in coloration, body size, and timing of the two-note "co-qui" call (Joglar 1998; Rivero 1998). Our ability to correctly discriminate between these two species is supported by mitochondrial and nuclear DNA sequence data (Barker et al. 2011). Puerto Rican frog calling behavior may be affected by temperature, humidity, and sunlight (Drewry 1970), but it is unlikely that seasonality or weather conditions resulted in our inability to detect *E. portoricensis*. First, we conducted our surveys during the wet-warm season, a time period when this species is most active (Joglar 1998). Second, there were several instances in which we detected *E. portoricensis* at localities in the Cayey and Luquillo Mountains within hours or days of surveying localities in the western Cordillera Central where it was not detected. Puerto Rican frog activity is highly influenced by the amount of precipitation (Stewart 1985; Woolbright 1985; Woolbright and Stewart 1987), but unfortunately we did not include survey-specific precipitation covariates into our models because these data were unavailable for most surveyed localities. We suggest that future surveys of *E. portoricensis* should be conducted at both historical and new localities at different times of the year. This species also reproduces during the winter when air temperatures can fall to 15° C, although it may have low activity under desiccating conditions that occur on very cold, rainless evenings (Drewry and Rand 1983; Beuchat et al. 1984). Future surveys should also collect additional site-specific covariate data to improve our understanding of the topographic, land cover, and climatic features that influence site occupancy of this species. For example, ravines may provide moist habitat refugia for *E. portoricensis* (Stewart 1995), but their influence on occupancy dynamics has not been quantified.

Populations of *E. portoricensis* may be patchily distributed (Woolbright 1997), which raises the possibility that this species may be present in an area in the western Cordillera Central that we did not survey. Indeed, a population found at Las Planás in the Cayey Mountains in 2009 (Alberto Puente-Rolón, pers. comm.) is located near Las Tetas de Cayey, a historical locality where we did not find this species in 2008. However, we surveyed most historical localities in the western Cordillera Central (i.e., Cerro Punta, Lago el Guineo, Maricao State Forest, Toro Negro Pool) multiple times, and there have been no published reports of *E. portoricensis* in this region since our surveys. While our data do not provide definitive evidence for the disappearance of this species across the entire western Cordillera, they strongly suggest that it has undergone local extirpations in this region.

Eleutherodactylus portoricensis was last detected in the western Cordillera Central in Toro Negro State Forest in 2004 (Villanueva-Rivera 2006), but assessing the chronological order and dates in which populations disappeared from this region is hindered by a paucity of published survey data, as well as potentially uneven spatial and temporal collection efforts. Estimating the timing of decline based on the number of museum specimens collected per year is complicated by the fact that *E. portoricensis* was synonymous with *E. coqui* prior to 1966 (Thomas 1966), and only three specimens were collected from the western Cordillera Central subsequent to this date. Differentiating between museum specimens of *E. coqui* and *portoricensis* may help with reconstructing the temporal and spatial patterns of decline of *E. portoricensis*.

Natural recolonization of suitable habitat in the western Cordillera Central from sources in the Cayey Mountains is unlikely. Our suitability map and the predicted habitat model for *E. portoricensis* by Gould et al. (2008) both depict an absence of suitable habitat between the Cayey Mountains and the western Cordillera Central. Adults of *E. portoricensis* are highly philopatric (Joglar 1998), and the closely related *E. coqui* rarely disperse horizontal distances more than 6 m during a night unless their home range becomes inhospitable (Woolbright 1985; Stewart and Woolbright 1996). The relatively warm and dry La Plata Basin in the Cayey Mountains is associated with a genetic discontinuity between *E. portoricensis* populations located less than 10 km apart (Barker et al. 2011), which suggests that similar climatic conditions in the upper reaches of the Río Grande de Loíza Basin (Daly et al. 2003), an area where habitat is predicted to be unsuitable, may act as a dispersal barrier.

The simultaneous occurrence of several threats to *E. portoricensis*, including disease and climate change, place the long term survival of this species in grave danger. Montane cloud forest, which is positively associated with site occupancy, is threatened by recent upward shifts in the cloud base and reduced rain fall at high elevations (Comarazamy and González 2011). These data suggest that this prime habitat for *E. portoricensis* will likely become smaller and more isolated. The sensitivity of this frog to small increases in temperature (Beuchat et al. 1984) and desiccating conditions (Woolbright 1997), as well as potentially increased susceptibility to chytridiomycosis during extended periods of drought (Longo et al. 2010), may also make it particularly vulnerable to future climate change. An increase of temperatures between 1 and 4 °C, more intense hurricanes, increased drought frequency, and overall drier conditions are predicted under future climate scenarios for the Caribbean region (Angeles et al. 2007; Cashman et al. 2010; Campbell et al. 2011). We found that site occupancy was negatively associated with highest temperature of any monthly maximum temperature and with precipitation seasonality, which suggests that future climate change may lead to further extirpations.

We suggest that the Department of Natural Resources and Environment of Puerto Rico, the U.S. Fish and Wildlife Service, and the IUCN Red List should elevate the extinction risk status of *E. portoricensis*. Extant populations in the Cayey and Luquillo Mountains should be monitored on a regular basis to gain a better understanding of population dynamic responses to climate change and chytridiomycosis. Continued surveys of historical localities in the western Cordillera Central are needed to verify that there has indeed been local extirpations. We also suggest that agencies that have jurisdiction in the relevant forests consider developing a captive breeding program for *E. portoricensis*. A captive breeding program for the Puerto Rican Crested Toad, *Peltophryne lemur*, was successful in rearing and reintroducing toads to areas where the species had become extirpated (Johnson 1999; Joglar et al. 2007), which suggests that a similarly well-designed program may help re-establish *E. portoricensis* across its historical range. The discovery of unknown populations, continued protection of suitable habitat in national and state forests of Puerto Rico, and development of a captive breeding program will hopefully contribute to the persistence of this species.

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