

The Natural History, Distribution, and Conservation of Lonely Rainfrogs, *Pristimantis eremitus*

CARL R. HUTTER¹, VICTORIA LIU², TIMOTHY KELL², JANE A. LYONS², AND JUAN M. GUAYASAMIN³

Biodiversity Institute and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045-7561, USA

ABSTRACT: Natural history and behavioral information for species of the genus *Pristimantis* is scarce. We conducted an extensive study of *Pristimantis eremitus*, a vulnerable species for which there is scant biological information. We monitored 17 individuals for movements and intraspecific interactions for 13 mo. We describe the species' variation in dorsal color and pattern, which we used to uniquely identify individuals during the study. We also present results on the habitat utilization and home range of this species, providing evidence that this species shows a preference toward the bromeliad microhabitat when compared with other microhabitat types. We also describe the advertisement call and associated behaviors of the species. We update the known distribution of the species. Our data provide a baseline for future researchers to survey and identify individuals of *P. eremitus*, and which could be applied comparatively to other species where little of their natural history is known. We also show how an in-depth in situ study can provide useful information for species conservation.

Key words: Advertisement call; Ecuador; Frog; Habitat usage; Niche model; Species distribution model; Terrarana

THE NEOTROPICS are the center of one of the most diverse assemblages of amphibians in the world, as exemplified by the direct-developing clade Terrarana, or Brachycephaloidea, having more than 900 species (Hedges et al. 2008; Padial et al. 2014). All of the species are known (or presumed) to deposit their eggs in terrestrial habitats, bypassing the tadpole stage, and undergoing direct development into froglets (Duellman and Trueb 1994). This life-history strategy has presumably led to extensive evolutionary radiations, as species are able to colonize habitats distant from moving or standing water (Duellman 1999; Hedges et al. 2008).

Within the family Craugastoridae lies the genus *Pristimantis*, containing >50% of the known species of Brachycephaloidea (currently at 482 species; Frost 2015). The greatest species richness of *Pristimantis* is centered in the tropical Andes Mountains of northwestern South America (i.e., Colombia, Ecuador, and Peru). Their distribution includes the lowland rainforests and extends to elevations of about 4000 m (Lynch and Duellman 1997). Many new species of *Pristimantis* are described each year (e.g., Reyes-Puig et al. 2014; Guayasamin et al. 2015; Hutter and Guayasamin 2015; Kaiser et al. 2015). Despite these efforts, little is reported on their behavior, ecology, and natural history (Hedges et al. 2008; AmphibiaWeb 2015).

In Ecuador, few studies have reported basic natural history and behavioral information for amphibians, especially *Pristimantis* (but see Duellman and Lynch 1988; Guayasamin and Funk 2009; Arteaga et al. 2013; Hutter et al. 2013a; Guayasamin et al. 2015). Herein, we present the results of a 13-mo study examining Lonely Rainfrogs, *Pristimantis eremitus* Lynch 1980, from Reserva Las Galarias, a private reserve located in Andean cloud forest on the western slopes of the Cordillera Occidental in Ecuador. *Pristimantis eremitus*

is a member of the monophyletic *lacrimosus* group (Hedges et al. 2008) and has a conservation status of “Vulnerable” (Castro et al. 2004). We document intraspecific and ontogenetic color variation within this species. Additionally, we present details on the behavior, natural history, vocalizations, habitat utilization, and home range of *P. eremitus*. Furthermore, using georeferenced locality data for this species, we construct a species distribution model and predict the potential range of this species. Finally, we reassess the conservation status of this species given this new information.

MATERIALS AND METHODS

Study Site and Terminology

Fieldwork was conducted at Reserva Las Galarias, a 431-ha ecological reserve on the western slopes of the Cordillera Occidental of the Andes, in the province of Pichincha, Ecuador, from 16 September 2011 to 13 October 2012. The field station was the main location of the study (2065 m above sea level [asl]; 0°0'38"S, 78°43'48"W; datum = WGS84 for all coordinate values). We monitored a transect 86 m long and 3 m wide (258 m²), located in an area that contains a garden planted with a mix of nonnative and native cloud forest vegetation, and that was located 200 m from primary forest. Buildings and human activity were present in the study area. As part of the postconstruction landscaping associated with the field station (conducted during 2004–2010), numerous fallen bromeliads were rescued from trails and planted around the buildings. Bromeliad species present include *Mezobromelia capituligera*, *Tillandsia truncata*, and *Guzmania xanthobracteata*.

We used five terms to describe the spatial scales that this species, and individuals representing it, might occupy (generally following Wells 2010): (1) “Distribution” refers to the known geographic localities where individuals have been documented. (2) “Extent of occurrence” is the area outlined by a minimum convex polygon that encompasses all known localities of the species, and assumes that the species occurs within the bounds of the observed locations (International Union for Conservation of Nature [IUCN] 2012). (3) “Predicted distribution” is estimated from a species

¹ CORRESPONDENCE: e-mail, carl.hutter@gmail.com

² PRESENT ADDRESS: Reserva Las Galarias, Av. Brasil N45-213 y Zamora, Quito, Ecuador

³ PRESENT ADDRESS: Centro de Investigación en Biodiversidad y Cambio Climático (BioCamb), Ingeniería en Biodiversidad y Recursos Genéticos, Facultad de Ciencias de Medio Ambiente, Universidad Tecnológica Indoamérica, Av. Machala y Sabanilla, Quito, Ecuador

distribution model constructed from climatic data of the known localities of individuals representing the species. This describes the realized climatic-niche of the species and includes areas predicted to be suitable for the species; however, other biotic and abiotic factors may further limit this distribution. (4) “Home range” is defined as the area within which an individual lives and moved about (Wells 2010). (5) “Home bromeliad” is the location of a bromeliad within its home range where an individual resides exclusively.

Advertisement Call

We recorded vocalizations of six male *P. eremitus* between 30 September 2011 and 12 November 2011 at the study site. Vocalizations were recorded with an Olympus LS-11 Linear PCM Recorder and Sennheiser ME66–K6 directional microphone at a sampling rate of 44 Hz. All vocalizations were recorded in the field 50–300 cm from the calling male. Air temperature was noted after each recording and all readings ranged from 15.4° to 17°C. Call data were not adjusted for temperature effects because there was no variation beyond 3° (Brown et al. 2006). Recordings were processed using Cornell Lab of Ornithology’s Raven Pro v1.4 Interactive sound analysis software on Mac OS X. Fast Fourier Transformation size was 512 samples and the spectral analysis had a frequency grid resolution of 172 Hz. We analyzed oscillograms and spectrograms for various temporal and spectral components.

Call parameter definitions followed Hutter et al. (2013a) and references therein. We defined a call as the collection of signals emitted in rapid succession. Additionally, we defined a note as an individual subunit of a call distinguished by a short and consistent return to the background noise. The following 13 variables were measured: (1) number of notes per call; (2) call duration (s); (3) interval between calls (s); (4) note duration (s); (5) interval between notes within a call (s); (6) note repetition rate per minute ($[\text{number of notes} - 1]/\text{time from beginning of first note to beginning of last note within a call}$); (7) note shape, a unit-less variable that describes the distribution of the amplitude envelope of a note, allowing comparison between notes of differing lengths (note rise time/note duration); (8) pulse rate (pulses/s); (9) dominant frequency at the maximum amplitude of the note; (10) upper frequency of the fundamental frequency (Hz); (11) lower frequency of the fundamental frequency (Hz); (12) frequency modulation (Hz; change in frequency over the note duration) was measured as the dominant frequency of 0.010 s from the end of the note minus the dominant frequency of 0.010 s from the beginning of the note; and, (13) median frequency of first harmonic (Hz). We measured temporal features using the oscillogram and spectral features using the spectrogram. When measuring temporal and spectral features, we restricted our measurement to areas that were conspicuously different from the background noise (see fig. 3 of Hutter and Guayasamin 2012 for details).

Notes were separated into pulsed and tonal notes. Pulsed notes were defined as having amplitude modulation, with visible increases and decreases in amplitude on the oscillogram throughout the note. Tonal notes were defined as having no clear amplitude modulation. All digital recordings are available upon request and have been deposited at the Centro de Investigación de la Biodiversidad y Cambio Climático, Universidad Tecnológica Indoamérica, Quito, Ecuador (MZUTI).

Activity and Habitat Use

We monitored the study transect from 30 September 2011 to 13 October 2012 for 267 survey nights across 392 d starting at dusk (~1900 h). We conducted acoustic and visual surveys to locate individuals of *P. eremitus*. If an individual was heard calling, the information was recorded, and the area was searched to locate the individual. We visually scanned for individuals present on leaves and searched all bromeliads for presence or absence of individuals within these transects. The intraspecific color variation of *P. eremitus* allowed us to unambiguously identify each individual without applying any marks (Fig. 1). In addition, we recorded the individual’s snout–vent length and whether it had moved to a new position since last being located. If the individual was in a new location, the distance travelled was measured.

We assessed the relationships between either calling activity (present vs. absent) or the number of individuals observed and values for precipitation and temperature (minimum, mean, and maximum). We used Generalized Linear Models (GLM) in the R statistical application (R Core Team 2014) to model the response variables to error distributions other than normal. We used a binomial error distribution for calling activity and a Poisson error distribution for number of individuals recorded. Weather data for each date was collected from an on-site weather station, located ~100 m from the study transect.

To characterize bromeliads used by *P. eremitus*, we measured the following characteristics for all bromeliads along the transect (± 1 cm): (1) height of first bract from the base of the bromeliad; (2) diameter of bromeliad, measured out to widest leaves; (3) height of base of bromeliad from the ground; (4) height from ground to highest leaf tip of the bromeliad; and, (5) height from ground to lowest leaf tip. To detect differences in habitat preference (i.e., bromeliad vs. nonbromeliad habitat), we used an Exact Binomial test with binary coding for bromeliad occupancy (individual presence or absence).

For home range analyses, we constructed a distance matrix for each individual by compiling the measured distance between each location and every other location for the same individual. The columns and rows of the matrix represented each location, where each cell in the matrix represented the measured distance between those two points. We used the `cmdscale` function within the R application to convert the distance matrix to Cartesian coordinates and Euclidean distances. A minimum convex hull polygon of each individual’s home range was constructed, and the area was calculated using the R package `GEOMETRY` (Barber et al. 2012). A minimum convex hull polygon is defined as the smallest polygon that contains all the measured location points, where no internal angles exceed 180° (IUCN 2012).

We acknowledge that these methods might be biased by our search methodology. We could not acquire data from any individual that moved to an inaccessible location (>2 m above ground level). Additionally, the number of locations recorded for an individual might have influenced home range size (problematic if an individual moved frequently to locations where it was difficult to detect). We feel that the low number of observations for some individuals did not

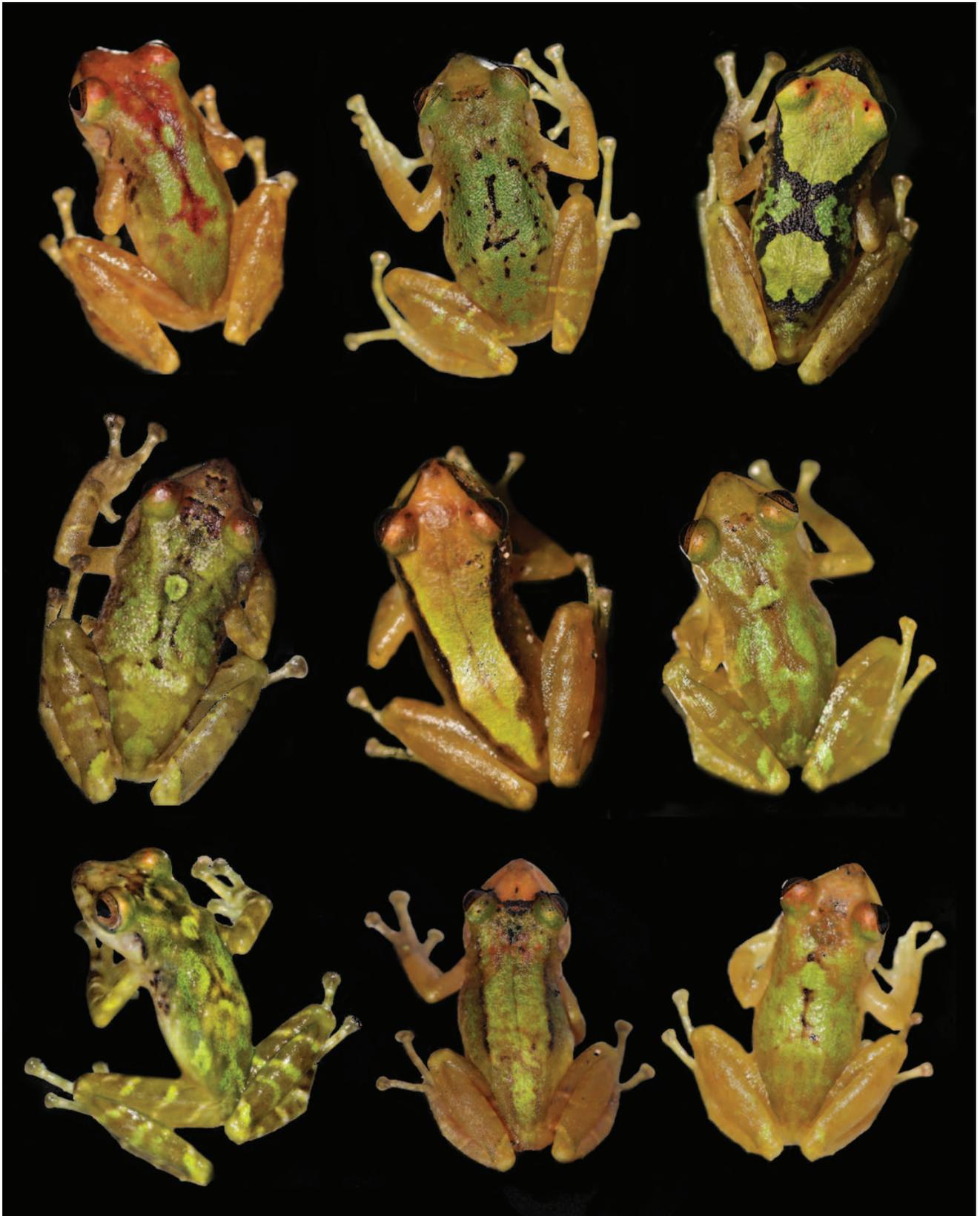


FIG. 1.—Color and pattern variation in *Pristimantis eremitus* observed from September 2011 to October 2012 along a transect at Reserva Las Galarias, Pichincha, Ecuador. The uniqueness of each pattern can be used to identify individuals. A color version of this figure is available online.

TABLE 1.—Bioclimatic variables obtained from the WORLD-CLIM database (<http://www.worldclim.org/bioclim>) for use in predicting geographic distribution of *Pristimantis eremitus*. Also shown is the analysis of bioclimatic variable contributions using a jackknife procedure, obtained from the Maxent output.

Bioclimatic variable	% contribution	Permutation importance
Bio4: Temperature seasonality (SD \times 100)	54.3	73.4
Bio5: Max. temperature of warmest month	18.7	0.1
Bio18: Precipitation of warmest quarter	12.5	0.6
Bio15: Precipitation seasonality (coefficient of variation)	10.1	0.3
Bio19: Precipitation of coldest quarter	2.9	25.7
Bio14: Precipitation of driest month	1.5	0
Bio2: Mean diurnal range (mean of monthly max. temperature – min. temperature)	0.1	0
Bio13: Precipitation of wettest month	0	0

affect our results because home range size was not correlated with the number of recaptures for each individual ($n = 17$, $\rho = -0.339$, $P = 0.18$). This test indicates that frogs that move more frequently are not likely to have larger home ranges.

Distribution

We acquired locality data from various sources: Museo de Zoología of the Universidad Tecnológica Indoamérica (MZUTI), Museo de Zoología of the Pontificia Universidad Católica del Ecuador (QCAZ) database (available at <http://zoologia.puce.edu.ec/vertebrados/>), and through the literature (Lynch 1980; Lynch and Burrows 1990). We also used photographic data, where we were able to confidently assign the species based on the photograph. Locality data were georeferenced using GEOLocate (Rios and Bart 2010) or acquired through a Garmin Global Positioning System, and overlaid on the predicted distribution map (see below) using QGIS (Quantum GIS Development Team 2012). See Appendix for museum specimens and other documented localities.

Based on 21 georeferenced localities (Appendix), we used the program Maxent (Phillips et al. 2006) to calculate the probable distribution of *P. eremitus*. Maxent estimates habitat suitability using the environmental data from known occurrences, and is a robust method of estimating species distribution modeling even when the occurrence data are limited (Phillips et al. 2006). We used the default modeling parameters as recommended by Phillips et al. (2006). The Maximum Entropy Species Distribution Modeling v3.3.3 program was used through the R package DISMO (Hijmans et al. 2012).

We developed a climatic-niche model using climatic data obtained from the WORLD-CLIM data set (Hijmans et al. 2005). A raster coverage with $\sim 1\text{-km}^2$ grid resolution was used and clipped to include only northwestern South America (eastern limit, -65° ; southern limit, -5°). We assessed the 19 bioclimatic variables for multicollinearity by constructing a Pearson-product correlation matrix from climatic data extracted from the 21 occurrence records and 500 randomly sampled background points. Each variable selected represents one variable from a group of strongly correlated variables (i.e., an arbitrary $\rho > 0.75$), and were selected for biological relevance (Table 1; Kozak and Wiens 2006). We excluded differences in yearly mean temperature

or precipitation because variables that describe climatic extremes may be more likely to set the range limits of amphibians (Petranka and Starnes 2001; Kozak and Wiens 2006).

In the creation of the distribution model, Maxent assigns an index of relative suitability for each grid cell of the study area. Because our goal was to model the potential distribution of *P. eremitus*, we set the threshold of presence or absence as the lowest predicted probability of known occurrences. This assumes species presence is restricted to localities equally or more suitable than what is currently known (Phillips et al. 2006; Pearson et al. 2007). We extracted the cumulative probability of presence for each known occurrence record of the species. Next, we took the minimum probability of these known occurrences, and classified each grid cell in the study area as a predicted presence or absence. Receiver operating curve (ROC) analysis was used to assess model quality, where the area under the ROC curve (AUC) was measured. Values approaching 1.0 indicate a good model while values < 0.5 are considered no better than random (Phillips et al. 2006). We plotted these results onto a map using QGIS, which provided a visual representation of the potential distribution of the species. For these analyses we used the following R packages: DISMO, RASTER (Hijmans and van Etten 2012), and RGDAL (Keitt et al. 2012).

Conservation Status Evaluation

Based on the analyses described above, we reevaluated the conservation status of *P. eremitus*, last presented by Castro et al. (2004). We applied the IUCN criteria and guidelines to categorize the conservation status of this species (IUCN 2012). Based on our model of potential distribution, we calculated the area (km^2) in which we predict this species to occur. For comparison, we calculated a minimum convex hull polygon using the coordinates of geographic locality data. These calculations were done in the R packages RASTER and FOSSIL (Vavrek 2011).

RESULTS

Color Variation

Pristimantis eremitus has a dorsal background coloration that varies from yellowish-green to lime green, with various colored markings. These colored markings are highly variable between individuals and include variously shaped patches of red, orange, black, and green (Fig. 1). The uniqueness of the patterns allowed us to identify individuals in absence of standard marking practices. The venter varies from yellowish-white to white. Iris coloration is orange-red to dark copper, with black reticulation. Individuals can adjust their background coloration to a darker shade (also noted in Lynch 1980), but this did not affect the unique dorsal patches we used for identification.

Advertisement Call

We recorded 22 calls that included 112 notes from 6 males of *P. eremitus* (Table 2). Males called from the central core and on the fronds of bromeliads. On rare occasions ($n = 2$), males called from the top of leaves of nonbromeliad plant species, although they were within 1 m of a bromeliad.

TABLE 2.—Acoustic characteristics of advertisement calls of six male *Pristimantis eremitus* recorded along a transect at Reserva Las Galarias, Pichincha, Ecuador. Values are reported as means \pm 1 SD, with the range in parentheses. Single values are attributed to a single sample. The Summary column reports pooled values for all recorded calls (n of 6 males) in the preceding columns.

Acoustic measure	Individual						Summary
	Male 1	Male 2	Male 3	Male 4	Male 5	Male 6	
n notes (calls)	30 (8)	9 (1)	28 (4)	31 (5)	5 (1)	9 (3)	112 (22)
Snout–vent length (mm)	19.8	21.4	21.5	18.3			20.7 \pm 0.842 (19.8–21.5)
Notes/call	3.8 \pm 0.707 (2.0–4.0)	9.0	7.7 \pm 1.5 (6.0–9.0)	6.8 \pm 2.6 (3.0–9.0)	5.0	3.0	5.2 \pm 2.3 (2.0–9.0)
Call duration (s)	0.721 \pm 0.170 (0.302–0.803)	0.508 \pm 0.015 (0.493–0.522)	1.7 \pm 0.331 (1.4–2.0)	1.3 \pm 0.738 (0.482–2.0)	1.6	0.508 \pm 0.015 (0.493–0.522)	1.1 \pm 0.623 (0.302–2.2)
Call interval (s)	19.7 \pm 5.6 (11.6–28.2)	1 call	12.3 \pm 4.2 (9.2–18.5)	6.3 \pm 0.862 (5.6–7.4)	5.7	15.7 \pm 9.1 (9.7–26.2)	14.2 \pm 7.4 (5.6–28.2)
Note duration (s)	0.096 \pm 0.010 (0.084–0.119)	0.084 \pm 0.010 (0.061–0.093)	0.099 \pm 0.011 (0.075–0.114)	0.076 \pm 0.011 (0.063–0.099)	0.133 \pm 0.009 (0.123–0.148)	0.083 \pm 0.008 (0.072–0.095)	0.091 \pm 0.016 (0.061–0.148)
Note interval (s)	0.131 \pm 0.018 (0.109–0.168)	0.225 \pm 0.027 (0.207–0.284)	0.153 \pm 0.037 (0.099–0.250)	0.176 \pm 0.046 (0.104–0.274)	0.223 \pm 0.022 (0.204–0.254)	0.126 \pm 0.014 (0.112–0.143)	0.161 \pm 0.045 (0.099–0.284)
Note rate/m	10.3	1 call	26.0	46.8	27.6	9.6	24.1 \pm 15.3 (9.6–46.8)
Call shape	0.293 \pm 0.290 (0.042–0.892)	0.034 \pm 0.016 (0.012–0.066)	0.159 \pm 0.157 (0.021–0.732)	0.059 \pm 0.032 (0.014–0.152)	0.079 \pm 0.124 (0.015–0.301)	0.114 \pm 0.153 (0.026–0.513)	0.151 \pm 0.200 (0.012–0.892)
Pulse rate/s	26.0 \pm 8.7 (16.8–46.5)	25.7 \pm 5.7 (21.5–36.6)	24.1 \pm 6.6 (17.5–39.5)	26.6 \pm 4.1 (13.7–31.7)	18.2 \pm 5.0 (13.5–24.4)	36.8 \pm 10.7 (21.1–55.6)	26.2 \pm 7.7 (13.5–55.6)
Dominant frequency (Hz)	5133.5 \pm 70.1 (4995.7–5168.0)	4565.1 \pm 92.1 (4478.9–4651.2)	5069.5 \pm 86.8 (4995.7–5168.0)	4756.7 \pm 106.0 (4478.9–4995.7)	4582.3 \pm 94.4 (4478.9–4651.2)	4766.0 \pm 121.8 (4651.2–4995.7)	4916.6 \pm 223.8 (4048.9–5168.0)
Lower fundamental frequency (Hz)	4919.8 \pm 62.3 (4751.8–4996.7)	4133.4 \pm 105.8 (4021.0–4306.0)	4864.9 \pm 66.8 (4754.0–4961.0)	4536.7 \pm 74.3 (4413.0–4751.4)	4103.4 \pm 195.3 (3845.7–4349.0)	4518.6 \pm 89.6 (4379.8–4658.8)	4673.0 \pm 274.6 (3845.7–4996.7)
Higher fundamental frequency (Hz)	5503.7 \pm 67.7 (5303.1–5585.0)	5111.4 \pm 138.8 (4823.4–5227.0)	5351.2 \pm 79.6 (5225.1–5460.0)	5153.3 \pm 116.7 (4900.0–5409.0)	4940.5 \pm 153.1 (4823.4–5185.0)	5178.3 \pm 83.3 (5027.0–5283.7)	5287.3 \pm 191.4 (4823.4–5585.0)
Frequency modulation (Hz)	346.9 \pm 79.5 (172.3–516.8)	496.0 \pm 233.5 (173.2–689.7)	158.9 \pm 62.3 (0–316.0)	116.7 \pm 93.2 (0–344.5)	413.5 \pm 313.0 (0–689.1)	134.0 \pm 76.0 (0–172.3)	231.7 \pm 168.8 (0–689.7)
First harmonic (Hz)	—	—	—	—	9129.9 \pm 243.5 (8785.5–9302.0)	—	9129.9 \pm 243.5 (8785.5–9302.0)

During call recording, the temperature ranged from 15.4° to 17.0°C, with relative humidity from 78% to 94%. To the ear, the call sounds like a loud, high-pitched squeal, similar to a bird chirp. A call consisted of 2–9 notes (mean \pm 1 SD = 5.2 \pm 2.3 notes) emitted in rapid succession (Fig. 2). Calls had a duration of 0.302–2.20 s (1.10 \pm 0.62 s) and an interval of 5.6–28.2 s (14.2 \pm 7.4 s) between calls. Note duration was 0.061–0.148 s (0.091 \pm 0.016 s) with an interval of 0.099–0.284 s (0.161 \pm 0.045 s) between notes within a call. Notes were weakly pulsed, with 1–4 pulses/note (2.3 \pm 0.6 pulses/note) and a pulse rate of 13.5–55.6 pulses/s (26.2 \pm 7.7 pulses/s). The notes had a shape of 0.012–0.892 (0.151 \pm 0.200) because the maximum amplitude was reached early in the production of the note (Fig. 2).

The dominant frequency of *P. eremitus* calls coincided with the fundamental frequency. The dominant frequency of a note is modulated up to 689.7 Hz (231.7 \pm 168.8 Hz). The lower fundamental frequency ranged from 3845.7 to 4996.7 Hz (4673.0 \pm 274.6 Hz) and the higher fundamental frequency ranged from 4823.4 to 5585.0 Hz (5287.3 \pm 191.4 Hz). A single harmonic frequency was recorded in one individual and was 8785.5–9302.0 Hz (9129.9 \pm 243.5 Hz; Table 2).

Activity and Habitat Use

We identified and monitored 17 individuals (11 males, 6 females) of *P. eremitus*. We recaptured individuals 2–106 times (mean = 31.6 \pm 34.3). Subjects were found more often in bromeliads than any other microhabitat type (exact

binomial test: $P < 0.001$). We did not detect a relationship between the number of individuals observed or calling with the measured temperatures (GLM: $n = 135$, $F \leq 1.28$, $P \geq 0.101$). However, we found a positive relationship between the number of calling males and rainfall (GLM: $n = 135$, $F = 1.66$, $P = 0.01$).

Along the study transect, we recorded 58 bromeliads, 31 of which were occupied at least once by an individual *P. eremitus*. Subjects preferred larger bromeliads that were higher off the ground (Table 3). When not found on bromeliads, individuals were recorded on vegetation near a bromeliad at a height of 160.0 \pm 97.6 cm (range = 57.0–425.0 cm; total $n = 29$, including 2 calling males). Other species of *Pristimantis* were observed along the transect (e.g., *P. achatinus*, *P. calcarulatus*, *P. eugeniae*, *P. parvillus*, *P. w-nigrum*), and only three individuals of these other species were observed on bromeliads during our study (two *P. eugeniae*; one *P. w-nigrum*).

We recorded ≥ 3 locations for 15 individuals (2 individuals had 1 location), which enabled the calculation of a home range size. The home range size (i.e., area of a minimum convex polygon encompassing all recapture locations) of an individual frog was a mean 26.14 \pm 28.35 m² (range = 0–108.10 m²). We measured 239 individual movements, with a distance of a mean 4.53 \pm 0.52 m (range = 0.28–36.09 m). Additionally, individuals were recaptured from the same bromeliad more frequently than they were encountered at another bromeliad (exact binomial test: $P < 0.001$).

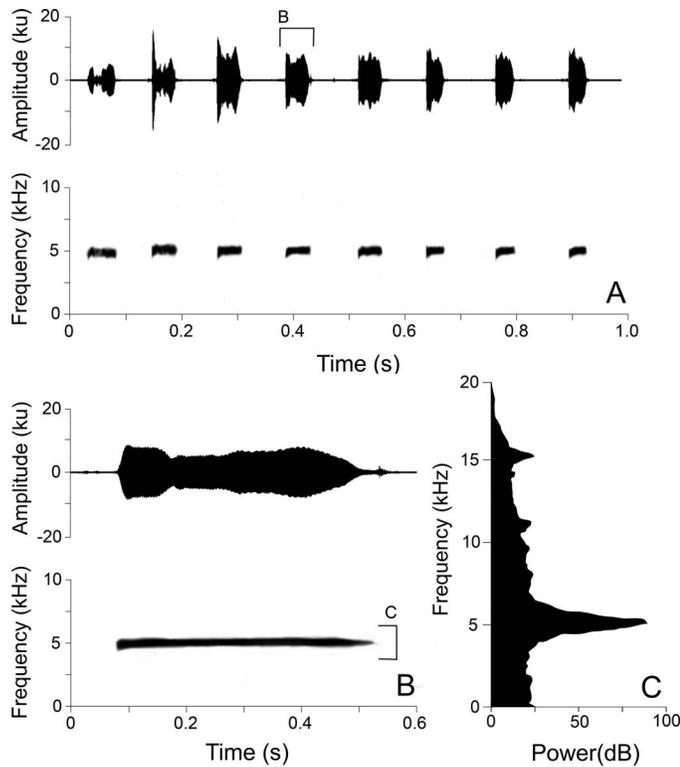


FIG. 2.—Oscillogram, spectrogram, and power spectra of the advertisement call of *Pristimantis eremitus* recorded along a transect at Reserva Las Galarias, Pichincha, Ecuador (air temperature = 15.4–17°C). A is the entire call; B is a single note within the call of A; and C is the power spectra of B.

We made two observations of a male in axillary amplexus with a female on 6–7 November 2011 and 23 June 2012. The weather on both occasions included a light rain. The first pair was observed in amplexus at 1612 h within the central core of a bromeliad, facing upward (Fig. 3A). At 1842 h on the same day and at 1230 h the following day, the pair was still in amplexus. At 1630 h of that second day, the pair could not be found and no eggs masses were observed. The second pair was found in amplexus in the central core of a bromeliad at 1852 h. The pair quickly separated and the female backed down into the core of the bromeliad while the male remained stationary. At 2053 h, the same two individuals were found in amplexus, ~150 cm above the ground on a leaf of a young *Clusia* sp. tree (Fig. 3B), <1 m from their original location. An unsuccessful search was conducted for eggs the following day.

We observed two female *P. eremitus* occupying the same bromeliad for long periods of time. The first female had occupied a single bromeliad continuously from 1 October

2011 until 13 October 2012. The second female joined the first in the same bromeliad 1 December 2011, and was observed in association with the first until 13 October 2012. Furthermore, we observed the same two subjects in this bromeliad on 15 April 2013.

Behavioral responses of *P. eremitus* to the presence of an observer were varied. When an individual was positioned in or near the central core of a bromeliad, it would withdraw into the water and toward the base, often in a backward motion. In these cases, it was difficult to observe the individual because it was concealed within the central core (usually within water) of the bromeliad. When near the leaf edge or tip, however, the subject would instead crouch and press its body against the bromeliad frond. Individuals in this position remained completely still except when there was large disturbance (e.g., accidental knock of the leaf or a nearby branch), which would cause an individual to jump and flee.

Distribution

Observations along our study transect and elsewhere within the species' range, along with new museum records, provide several new localities for *P. eremitus*: (1) El Pahuma Orchid Reserve, Pichincha Province, Ecuador (0°1'39.7"N, 78°38'6.9"W; 1900 m asl); (2–5) Reserva Las Galarias, Pichincha Province, Ecuador: near the researcher cabins (0°0'38.6"S, 78°43'48.8"W; 2100 m asl), MZUTI 426; a calling male at Lucy's Creek, (0°0'17.2"N, 78°44'17.6"W; 1820–1960 m asl), MZUTI 476; Kathy's Creek, (0°0'57.6"S, 78°43'55.2"W; 2040–2066 m asl); and the "Waterfall Trail" (0°0'43.2"S, 78°43'29.9"W; 1900–2100 m asl); and, (6) Lovett School's Siempre Verde Reserve (0°22'18"N, 78°25'18"W; 2470 m asl), Pichincha Province, Ecuador. All new localities are within the current extent of the species' geographic range. The Siempre Verde locality represents an elevational increase of the species by 340 m asl.

The predicted distribution of *P. eremitus* from Maxent shows that the most suitable areas are mainly restricted to the western slope of the Cordillera Occidental of the Andes in Ecuador, with some suitable areas occurring in southern Colombia (Fig. 4). The model AUC was 0.981, which indicated high model fit. The bioclimatic variables of Bio4 (temperature seasonality), Bio5 (max. temperature of warmest month), Bio18 (precipitation of warmest quarter), Bio15 (precipitation seasonality), and Bio19 (precipitation of coldest quarter) were shown to be important predictors for the distribution of *P. eremitus*. Using a jackknife procedure of leaving each variable out and assessing the drop-in model fit, Bio4 and Bio19 were shown to cause the highest drop in model fit (Table 1).

TABLE 3.—Measurements (cm) of bromeliads along a transect at Reserva Las Galarias, Pichincha, Ecuador, as a function of individual *Pristimantis eremitus* being present or absent. Values are reported as means \pm 1 SD; differences in bromeliad characteristics were compared using independent two-tailed *t*-tests.

Measurement	Frogs present	Frogs absent	P-value (confidence interval)
Height of first bract from base of bromeliad	61.4 \pm 57.1 (0–174)	17.7 \pm 34.2 (0–120)	0.001 (0.183–0.692)
Diameter of bromeliad	107.6 \pm 25.3 (55.0–151)	62.3 \pm 31.1 (11.0–125)	<0.001 (0.301–0.609)
Height of base of bromeliad from ground	9.9 \pm 28.5 (0–130)	4.0 \pm 15.3 (0–72)	0.34 (–0.065–0.183)
Height from ground to highest leaf tip of bromeliad	74.1 \pm 32.0 (34.0–172)	46.4 \pm 21.3 (11.0–107)	<0.001 (0.130–0.434)
Height from ground to lowest leaf tip of bromeliad	6.1 \pm 21.5 (0–110)	4.0 \pm 9.3 (0–33)	0.65 (–0.060–0.110)

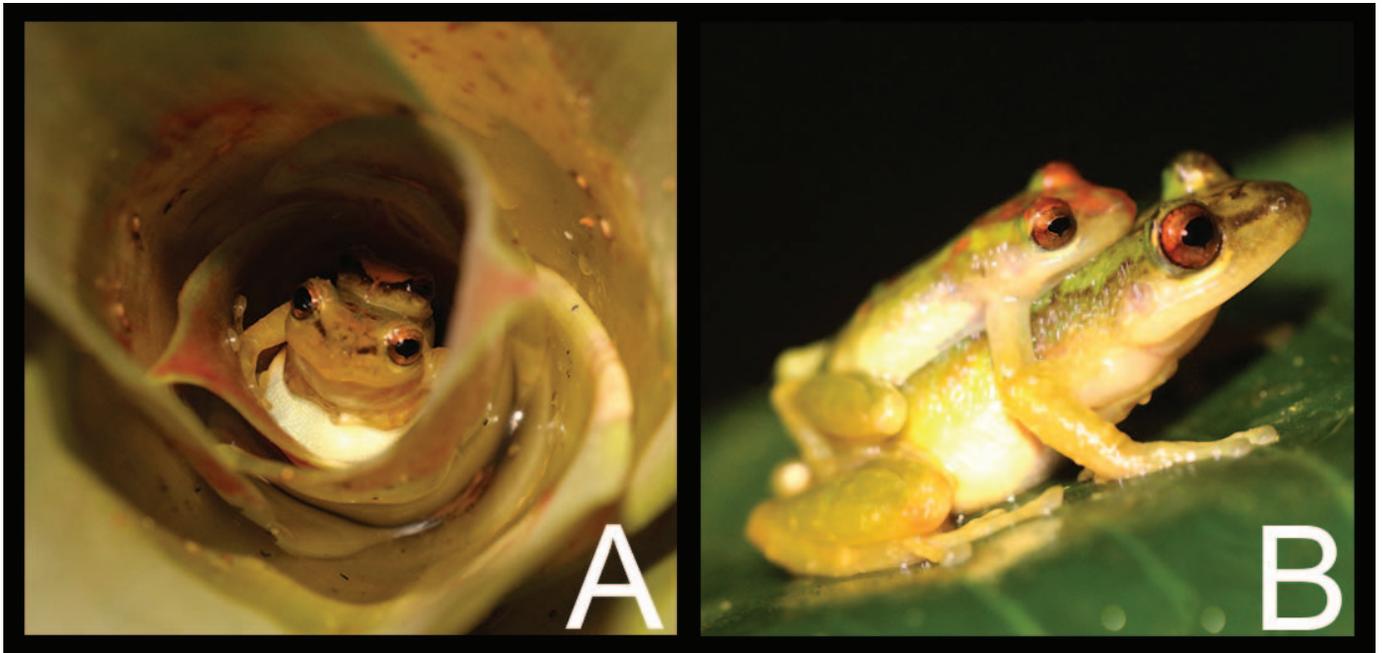


FIG. 3.—Amplexus in *Pristimantis eremitus* within a bromeliad core (A) and on a bromeliad frond (B), as observed along a transect at Reserva Las Galarias, Pichincha, Ecuador. A color version of this figure is available online.

Conservation Status Evaluation

The previous evaluation by Castro et al. (2004) considered *P. eremitus* to be “Vulnerable” (B1ab [iii]; IUCN Red List categories and criteria). The extent of occurrence calculated

from the minimum convex polygon of this species’ known occurrences is $\sim 2502 \text{ km}^2$, whereas the extent of occurrence calculated from the species’ predicted distribution is $\sim 6884 \text{ km}^2$. Despite having a relatively small area of occurrence, the species has been reported from several protected areas within its extent of occurrence: Reserva Las Galarias, El Pahuma Orchid Reserve, Bosque Protector Río Guajalito, from Pichincha Province, Ecuador; Siempre Verde from Imabura Province, Ecuador; and Reserva La Planada from Narino, Colombia (Appendix). All reported new localities herein are within the species’ extent of occurrence.

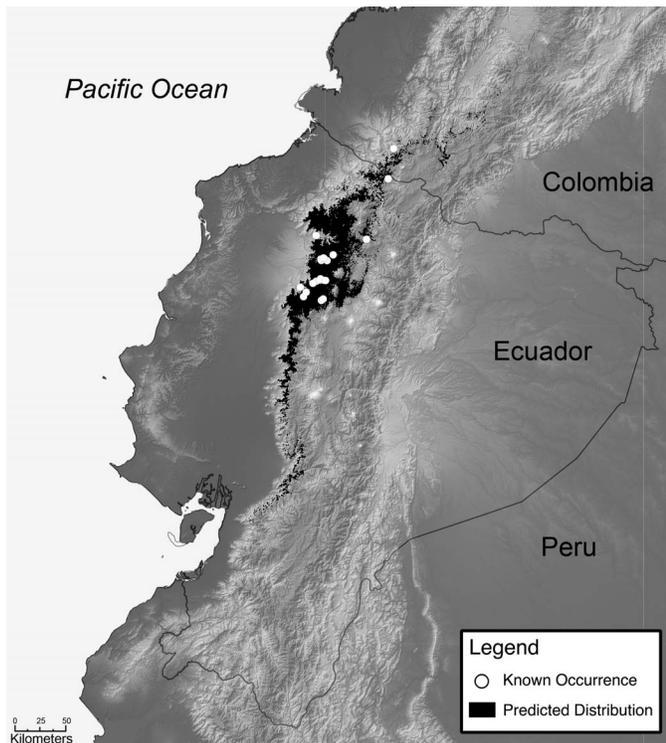


FIG. 4.—Predicted distribution of *Pristimantis eremitus* in the tropical Andes of South America from the Maxent modeling software. Areas in black are the predicted range while the white dots represent the known occurrences.

DISCUSSION

The advertisement call of male *P. eremitus* is similar to those of *P. aureolineatus* (Guayasamin et al. 2006) and *P. zimmermanae* (Heyer and Hardy 1991; McCracken and Forstner 2006). All three calls have a similar sounding chirp noise to the ear. All three species also share overlapping dominant frequencies. The calls differ somewhat in their pulses, with *P. aureolineatus* having a similar number of pulses to that of *P. eremitus* (and *P. zimmermanae* having several more). The most apparent difference between the calls of the three species, however, is that the note duration is nonoverlapping among them, with *P. eremitus* having the longest note duration.

Pristimantis eremitus prefers to inhabit bromeliads and appears to have high site specificity to their home bromeliad. Bromeliad preference is a niche-specific association that has been reported to define the *P. lacrimosus* species group. For example, McCracken and Forstner (2006) reported a preference of *P. aureolineatus* to inhabit bromeliads, with the physical position of those plants being in the upper strata of the rainforest canopy, 19–50 m high. In this study, we observed individuals to occupy bromeliads 0–4 m in height, although these observations are biased because we did not

perform searches in higher vegetation. We did observe males vocalizing from positions higher in the canopy (~6 m; JMG, personal observation). As is typical for most anuran species, reproductive activity (i.e., calling males) is related to the occurrence of precipitation.

It is apparent that this species requires bromeliads, but the reasons for this requirement are unclear. We observed males calling predominantly from bromeliads (and occasionally from similarly structured plants (e.g., *Hedychium coronarium*; Zingiberaceae), and found two amplexant pairs in the central core of a bromeliad. We did not locate an oviposition site, however, and such data are lacking for many species in this group. In the related species *P. aureolineatus*, *P. tayrona*, and *P. zimmermanae*, observations from the literature show that the main site of egg deposition is on the leaves of the bromeliads (*P. tayrona*), within or on top of the leaf litter (*P. zimmermanae*, *P. aureolineatus*), or at the base of a bromeliad (*P. aureolineatus*; Lynch and Ruíz-Carranza 1985; Castro et al. 2004; McCracken and Forstner 2006). It is possible that *P. eremitus* deposits their eggs in a similar manner.

Pristimantis eremitus is known from 21 different localities, and might occur more widely than reported. New locality records for this species are infrequent, however, and much of its occurrence remains uncertain. The predictions from the climatic-niche model expand the range of the species and offer suggestions to future workers conducting amphibian surveys, especially when assessing the distribution of this species. We also show that Bio4 (temperature seasonality) and Bio5 (max. temperature of the warmest month) models provide the best climatic predictors of this species' distribution (Table 1). In particular, Bio5 is likely relevant because warmer temperatures at lower elevations might physiologically limit the dispersal of this species to lower elevations. This model assumes that climatic factors determine the extent of this species, however, and if this species is an obligate bromeliad specialist, then its range might be restricted by the distribution of certain bromeliad species to accommodate the frogs. Furthermore, despite being climatically suitable, the predictive models might not identify suitable habitat in many locations. Thus, caution should be taken when interpreting the model output reported here because other evolutionary and ecological factors might influence this species' distribution.

The amount of suitable forest habitat available to support *P. eremitus* continues to decline throughout the Ecuadorian and Colombian Andes, and that which remains is severely fragmented. The species is abundant both at Reserva Las Galarias and within forested habitat that borders the field station (CRH, personal observation). Our study site is adjacent to areas within the reserve that experience frequent use by tourists and researchers. Most of the bromeliads occurring within the surveyed transect were transplanted to the study area, indicating that suitable areas can be established for this species within highly disturbed habitats. We note, however, that *P. eremitus* appears to be dependent on native bromeliads that are associated with areas of primary and secondary forest. These forested areas are rapidly disappearing, and thus suitable habitat for this species may be affected.

Considering the fragmented extent of occurrence and the predicted importance of temperature on the species, *P. eremitus* might not be able to disperse upward in elevation to

cope with an increase in temperature from global climate change. Given this study, we recommend that the conservation status of this species be revised to "Endangered" B.1.a.b(iii). The criteria met are as follows: (B1) its extent of occurrence is less than ~5000 km²; (a) its distribution is severely and increasingly fragmented; and, (b[iii]) its extent and quality of habitat have been decreasing (IUCN 2012).

The *lacrimosus* species group is widely distributed throughout South America, occurring in many different habitat types that encompass a wide range of climatic-niches (Lynch and Duellman 1997). Niche conservatism predicts that the climatic-niches of closely related taxa would be conserved (Wiens and Graham 2005; Wiens et al. 2010). Members of this monophyletic group are found in lowland tropical forests, however, as well as montane cloud forest, which indicates some degree of diversity in climatic-niche occupancy. Similar results have been suggested for some groups of Andean amphibians (e.g., salamanders, Wiens et al. 2007; glassfrogs; Hutter et al. 2013b). The species within the *lacrimosus* group have a shared preference for the bromeliad microhabitat (conserved in this group), which offers an interesting opportunity to study microhabitat and niche evolution once a complete phylogeny is available.

Acknowledgments.—We thank the Editor and two reviewers for improving the quality of earlier versions of this manuscript. We thank A. Kay for providing additional locality information for this species. This project was supported by Reserva Las Galarias and the Universidad Tecnológica Indoamérica through the project "Estado de Conservación de los Anfibios de los Andes del Ecuador," and by the IUCN Save Our Species program through the project "Conservation of endangered species in the Chocó biogeographic zone: Integrating habitat management, biodiversity monitoring, and community outreach." We thank El Pahuma Orchid Reserve, the Lima family, and C. Woodward and J. Meisel for access and assistance at field sites. We also thank T. and B. Nunnery from Pacha Quindi Nature Refuge for allowing access to their property.

LITERATURE CITED

- AmphibiaWeb. 2015. AmphibiaWeb: Information on amphibian biology and conservation. Regents of the University of California, USA. Available at <http://amphibiaweb.org>. Archived by WebCite at <http://www.webcitation.org/6cDMrt9k> on 11 October 2015.
- Arteaga, A., L. Bustamante, and J.M. Guayasamin. 2013. The Amphibians and Reptiles of Mindo: Life in the Cloudforest. Universidad Tecnológica Indoamérica, Ecuador.
- Barber, C.B., K. Habel, R. Grasman, R.B. Gramacy, A. Stahel, and D.C. Sterratt. 2012. R package Geometry: Mesh generation and surface tessellation. R Package Version 0.3-2. Available at <http://CRAN.R-project.org/package=geometry>. Archived by WebCite at <http://www.webcitation.org/6dxmEv3o> on 22 December 2015.
- Brown, R.M., S.J. Richards, J. Sukumaran, and J. Foufopoulous. 2006. A new morphologically cryptic species of forest frog (genus *Platymantis*) from New Britain Island, Bismarck Archipelago. *Zootaxa* 1334:45–68.
- Castro, F., M.I. Herrera, S. Ron, L.A. Coloma, D.F. Cisneros-Heredia, J.D. Lynch, and M. Yáñez-Muñoz. 2004. *Pristimantis eremitus*. In IUCN redlist of threatened species, version 2014.2. Available at <http://www.iucnredlist.org/amphibians>. Archived by WebCite at <http://www.webcitation.org/6cDOIb2Lj> on 11 October 2015.
- Duellman, W.E. 1999. Distribution Patterns of Amphibians in South America. Johns Hopkins University Press, USA.
- Duellman, W.E., and J.D. Lynch. 1988. Anuran amphibians from the Cordillera de Cutucú, Ecuador. *Proceedings of the Academy of Natural Sciences of Philadelphia* 140:125–142.
- Duellman, W.E., and L. Trueb. 1994. *Biology of Amphibians*. Johns Hopkins University Press, USA.
- Frost, D.R. 2015. Amphibian species of the world: An online reference. American Museum of Natural History, USA. Available at <http://research.amnh.org/herpetology/amphibia/index.html>. Archived by WebCite at <http://www.webcitation.org/6cDN19JKD> on 11 October 2015.

- Guayasamin, J.M., and W.C. Funk. 2009. The amphibian community at Yanayacu Biological Station, Ecuador, with a comparison of vertical microhabitat use among *Pristimantis* species and the description of a new species of the *Pristimantis myersi* group. *Zootaxa* 2220:41–66.
- Guayasamin, J.M., S.R. Ron, D.F. Cisneros-Heredia, W. Lamar, and S.F. McCracken. 2006. A new species of frog of the *Eleutherodactylus lacrimosus* assemblage (Leptodactylidae) from the western Amazon Basin, with comments on the utility of canopy surveys in lowland rainforest. *Herpetologica* 62:191–202.
- Guayasamin, J.M., T. Krynak, K. Krynak, J. Garcia, and C.R. Hutter. 2015. Phenotypic plasticity raises questions for taxonomically important traits: A remarkable new Andean rainfrog (*Pristimantis*) with the ability to change skin texture. *Zoological Journal of the Linnaean Society* 173:913–928.
- Hedges, S.B., W.E. Duellman, and M.P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): Molecular phylogeny, classification, biogeography, and conservation. *Zootaxa* 1737:1–182.
- Heyer, W.R., and L.M. Hardy. 1991. A new species of frog of the *Eleutherodactylus lacrimosus* assembly from Amazonia, South America (Amphibia: Anura: Leptodactylidae) from the northwestern lowlands of Ecuador. *Proceedings of the Biological Society of Washington* 104:436–447.
- Hijmans, R.J., and J. van Etten. 2012. R package Raster: Geographic analysis and modeling with raster data. R Package Version 2.0-12. Available at <http://CRAN.R-project.org/package=raster>. Archived by WebCite at <http://www.webcitation.org/6xxr7pLs> on 22 December 2015.
- Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965–1978.
- Hijmans, R.J., S. Phillips, J. Leathwick, and J. Elith. 2012. R package Dismo: Species distribution modeling. Available at <http://cran.r-project.org/web/packages/dismo/index.html>. Archived by WebCite at <http://www.webcitation.org/6dxxtPiFw> on 22 December 2015.
- Hutter, C.R., and J.M. Guayasamin. 2012. A new cryptic species of Glassfrog (Centrolenidae: *Nymphargus*) from Reserva Las Gralarias, Ecuador. *Zootaxa* 3257:1–21.
- Hutter, C.R., and J.M. Guayasamin. 2015. Cryptic diversity concealed in the Andean cloud forests: Two new species of rainfrogs (*Pristimantis*) uncovered by molecular and bioacoustic data. *Neotropical Biodiversity* 1:36–59. DOI: 10.1080/23766808.2015.1100376.
- Hutter, C.R., S. Escobar-Lasso, J.A. Rojas-Morales, P.A. Gutiérrez-Cárdenas, H. Imba, and J.M. Guayasamin. 2013a. The territoriality, vocalizations and aggressive interactions of the Red-spotted Glassfrog, *Nymphargus grandisonae*, Cochran & Goin 1970 (Anura: Centrolenidae). *Journal of Natural History* 47:3011–3032.
- Hutter, C.R., J.M. Guayasamin, and J.J. Wiens. 2013b. Explaining Andean megadiversity: The evolutionary and ecological causes of glassfrog elevational richness patterns. *Ecology Letters* 16:1135–1144.
- International Union for Conservation of Nature [IUCN]. 2012. IUCN Red List Categories and Criteria, version 3.1, 2nd edition. IUCN, Switzerland.
- Kaiser, H., C.L. Barrio-Amoros, G.A. Rivas, C. Steinlein, and M. Schmid. 2015. Five new species of *Pristimantis* (Anura: Strabomantidae) from the coastal cloud forest of the Peninsula de Paria, Venezuela. *Journal of Threatened Taxa* 7:7047–7088.
- Keitt, T.H., R. Bivand, E. Pebesma, and B. Rowlingson. 2012. R package Rgdal: Bindings for the geospatial data abstraction library. Available at <http://cran.r-project.org/web/packages/rgdal/index.html>. Archived by WebCite at <http://www.webcitation.org/6dxvxC3T> on 22 December 2015.
- Kozak, K.H., and J.J. Wiens. 2006. Does niche conservatism drive speciation? A case study in North American salamanders. *Evolution* 60:2604–2621.
- Lynch, J.D. 1980. *Eleutherodactylus eremitus*, a new trans-Andean species of the *Lacrimosus* assembly from Ecuador (Amphibia, Leptodactylidae). *Museum of Comparative Zoology. Breviora* 462:1–7.
- Lynch, J.D., and P.A. Burrowes. 1990. The frogs of the genus *Eleutherodactylus* (Family Leptodactylidae) at the La Planada Reserve in southwestern Colombia with descriptions of eight new species. *Occasional Papers of the Museum of Natural History of the University of Kansas* 136:1–31.
- Lynch, J.D., and W.E. Duellman. 1997. Frogs of the genus *Eleutherodactylus* in western Ecuador. *Systematics, ecology, and biogeography*. Special Publications of the Natural History Museum, University of Kansas, Lawrence 23:1–236.
- Lynch, J.D., and P.M. Ruiz-Carranza. 1985. A synopsis of the frogs of the genus *Eleutherodactylus* from the Sierra Nevada de Santa Marta, Colombia. *Occasional Papers of the Museum of Zoology, University of Michigan* 711:1–59.
- McCracken, S.F., and M.R.J. Forstner. 2006. Reproductive ecology and behavior of *Eleutherodactylus aureolineatus* (Anura, Brachycephalidae) in the canopy of the Upper Amazon Basin, Ecuador. *Phyllomedusa* 5:135–143.
- Padial, J.M., T. Grant, and D. Frost. 2014. Molecular systematics of terraranas (Anura: Brachycephaloidea) with an assessment of the effects of alignment and optimality criteria. *Zootaxa* 3825:1–132.
- Pearson, R.G., C.J. Raxworthy, M. Nakamura, and A.T. Peterson. 2007. Predicting species' distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *Journal of Biogeography* 34:102–107.
- Petranka, J.W., and S.S. Starnes. 2001. Effectiveness of removal sampling for determining salamander density and biomass: A case study in an Appalachian streamside community. *Journal of Herpetology* 35:36–44.
- Phillips, S.J., R.P. Anderson, and R.E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modeling* 190:231–259.
- Quantum GIS Development Team. 2012. Program Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Available at <http://qgis.osgeo.org>. Archived by WebCite at <http://www.webcitation.org/6dxy0gE4> on 22 December 2015.
- R Core Team. 2014. Program R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Austria.
- Reyes-Puig, J.P., C. Reyes-Puig, S.R. Ramirez-Jaramillo, M.B. Perez, and M.H. Yanez-Munoz. 2014. Three new species of terrestrial frogs *Pristimantis* (Anura: Craugastoridae) from the upper basin of the Pastaza River, Ecuador. *Avances en Ciencias e Ingenierias* 6:B51–B62.
- Rios, N.E., and H.L. Bart. 2010. Program GEOLocate, version 3.22. Tulane University Museum of Natural History, USA.
- Vavrek, M.J. 2011. R package Fossil: Palaeoecological and palaeogeographical analysis tools. *Palaeontologia Electronica* 14:1T.
- Wells, K.D. 2010. *The Ecology and Behavior of Amphibians*. University of Chicago Press, USA.
- Wiens, J.J., and C.H. Graham. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics* 36:519–539.
- Wiens, J.J., G. Parra-Olea, M. Garcia-Paris, and D.B. Wake. 2007. Phylogenetic history underlies elevational patterns of biodiversity in tropical salamanders. *Proceedings of the Royal Society London B* 274:919–928.
- Wiens, J.J., D.D. Ackerly, A.P. Allen, ... and P.R. Stephens. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* 13:1310–1324.

APPENDIX.—Specimens or photographs examined, and localities used for this predicting biogeographic distribution of *Pristimantis eremitus*.

Source	Locality	Accession #	Elevation (m)	Coordinates
Lynch and Duellman 1997	Las Pampas, Cotopaxi, Ecuador	KU 221685-86	1818	00°22'11.32"S, 78°46'12.11"W
Lynch and Duellman 1997	Palo Quemado, Cotopaxi, Ecuador	MHNG 18739	1919	00°31'11.95"S, 78°49'25.02"W
Lynch and Duellman 1997	6.2 km E Tandapi, Pichincha, Ecuador	MCZ 92105, 94723	1889	00°27'30.61"S, 78°45'17.76"W
Lynch and Duellman 1997	Chiriboga, ~8 km W of, Km 58 on Quito-Santo Domingo de Los Colorados Road, Pichincha, Ecuador	USNM 211209	2065	00°15'10"S, 78°48'56"W
Lynch and Duellman 1997	Quebrada Zapadores, 5 km ESE Chiriboga, Pichincha, Ecuador	KU 179085-86	1972	00°12'46.36"S, 78°46'16.44"W
Lynch and Duellman 1997	0.6 km SE of Zapadores, Pichincha, Ecuador	USNM 285924	1793	00°13'36"S, 78°46'12"W
Lynch and Duellman 1997	8.6 km SE Tandayapa, Pichincha, Ecuador	MCZ 98189	1981	00°04'02.41"S, 78°42'42.44"W
Lynch and Duellman 1997	3.5 km NE Mindo, Pichincha, Ecuador	KU165884	1555	00°01'56"S, 78°45'41"W
Lynch and Duellman 1997	Tandayapa, Pichincha, Ecuador	USNM 211208	1657	00°01'00"S, 78°46'00"W
This study	Siempre Verde, Imabura, Ecuador	Photograph	2456	00°22'18"N, 78°25'18.60"W
L. Reyes and A. Esteban	Bosque Protector Río Guajalito, Pichincha, Ecuador	Personal communication	1841	00°13'00.57"S, 78°50'18.69"W
Lynch and Duellman 1997	9.9 km E Maldonado, ca. Maldonado-Tulcán, Carchi, Ecuador	QCAZ 2796	1897	00°53'21.07"S, 78°02'36.07"W
Lynch and Duellman 1997	2 km W Campamento Silante, La Palma-Aloag road, Pichincha, Ecuador	KU 140878	2072	00°26'27.10"S, 78°44'28.42"W
Lynch 1980	18 km NE La Palma, Hwy 28, Pichincha, Ecuador	MCZ 92103-92104	1829	00°16'29.53"S, 78°51'01.15"W
This study	25.7 km NE de La Palma, Pichincha, Ecuador	QCAZ	1624	00°08'01.96"S, 78°44'16.79"W
This study	Reserva Las Galarias, Field Station, Pichincha, Ecuador	MZUTI 476	2052	00°00'38.59"S, 78°43'48.79"W
This study	Reserva Las Galarias, Puma trail, Pichincha, Ecuador	MZUTI 426	1950	00°00'20.05"S, 78°44'17.59"W
This study	1 km up Jane's Road, Reserva Las Galarias, Pichincha, Ecuador	Observation/Call	2090	00°01'15"S, 78°43'35"W
This study	El Pahuma Orchid Reserve, Pichincha, Ecuador	Photograph	1912	00°01'39.72"N, 78°38'06.91"W
This study	Hotel Tinalandia cerca a Alluriquín, Santo Domingo, Ecuador	QCAZ 50012	1667	00°22'20.62"S, 78°50'26.40"W
Lynch and Burrowes 1990	Planada, Cauca, Colombia	Observation	1780	01°09'20.88"N, 77°59'36.60"W