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DISTRIBUTION AND CONSERVATION STATUS OF *ANDINOBATES VIROLINENSIS* (DENDROBATIDAE), A THREATENED ANDEAN POISON FROG ENDEMIC TO COLOMBIA

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***Abstract*.—Detailed information of geographic distribution is critical for the conservation and management of endangered and endemic taxa. Such knowledge is limited for the Santander Poison Frog (*Andinobates virolinensis*), a threatened frog endemic to the Cordillera Oriental of the Colombian Andes. Here, we use new and historical data to model the potential distribution of this species and estimate its extent of occurrence. Our model predicted that suitable habitat exists on the western slope of the Cordillera Oriental in Santander, Boyacá, and Cundinamarca departments in Colombia. The occurrence of this species was strongly, positively associated with precipitation of the driest month, and positively, but more weakly related to mean diurnal temperature range and isothermality. Our models suggest the low elevations of the Chicamocha and Sogamoso canyons and the high elevations of the Cordillera Oriental constitute unsuitable habitats for this species. We identified 10,828 km^2 of suitable habitat, of which about 3.5% is inside protected areas. Our findings suggest that *A. virolinensis* should be re-categorized from Endangered to Vulnerable in the Red List of the International Union for the Conservation of Nature. Improving protective measures, collaboration with local farmers, and expanding the network of national protected areas are likely to benefit *A. virolinensis* and other species from this Andean region.**

Key Words.—endemic species; extent of occurrence; geographic distribution; species distribution model

INTRODUCTION

The lack of basic natural history and distribution data represents a challenge for conservation of many amphibian species (Chunco et al. 2013). This holds especially true for rare, threatened, and endemic species, and impedes the assessment of their conservation status (Guisan et al. 2006; Kumar and Stohlgren 2009; Kamino et al. 2012; Groff et al. 2014; Foggi et al. 2015). Species distribution modeling has enormous potential for conservation planning because it can improve the understanding of geographic distribution and habitat suitability for data-poor species (Raxworthy et al. 2003; Gaston and Fuller 2009; Kamino et al. 2012; Khafagi et al. 2012; Fourcade et al. 2014). The extent of occurrence (EOO) and area of occupancy (AOO) are two approaches to determining geographic distribution of species and both are used by the International Union for Conservation of Nature (IUCN) to evaluate conservation status (IUCN 2014). The EOO is the area within the outermost geographic limits of the occurrence of a species, whereas AOO is the area within the EOO where the species is currently known to occur (Gaston and Fuller 2009).

The Santander Poison Frog, *Andinobates virolinensis* (Ruiz-Carranza and Ramírez-Pinilla 1992), is a small dendrobatid (Fig. 1) found on the northwestern slope of the Cordillera Oriental of the Andes in Colombia, with confirmed records in Cundinamarca and Santander departments (Ruiz-Carranza and Ramírez-Pinilla 1992; Stuart et al. 2008; Brown et al. 2011). This diurnal frog inhabits primary and secondary cloud forests and some traditional agroecosystems (Stuart et al. 2008; Meza-Joya et al. 2015; Fig. 2A-C). The species is included in the Andinobates bombetes species group (Brown et al. 2011), a cluster of species threatened by ongoing loss of habitat due to agricultural expansion (Brown et al. 2011; Amézquita et al. 2013; Fig. 2D).

The IUCN Red List of Threatened Species was designed to assess the extinction risk of species (Mace et al. 2008). Following the IUCN Categories and Criteria, *A. virolinensis* is listed as Endangered B1ab(iii) because its estimated EOO is < 5,000 km^2, it was known to occur at no more than five threat-defined locations (i.e., a geographically or ecologically distinct area in which a single threat event will soon affect all individuals of a given taxon; IUCN 2014), and there is a continuing decline in the quality and extent of its

Figure 1. Adult male of Santander Poison Frog (*Andinobates virolinensis*) in Santander Department, Serranía de los Yariguíes, municipality of San Vicente de Chucurí, vereda La Colorada, Colombia. Note one tadpole on back being transported to phytotelmata in bromeliads. (Photographed by Carlos A. Hernández).

natural habitat (Amézquita and Rueda-Almonacid 2004). Most information about the assessment of the species is anecdotal. Consequently, understanding of current conservation status and the nature of threats is incomplete for *A. virolinensis*. This species is known from one national protected area (Santuario de Fauna y Flora Guanentá Alto Río Fonce; Amézquita and Rueda-Almonacid 2004), but the size of its local range in this and other protected areas is unknown.

Herein, we provide new locality records and develop a species distribution model (SDM) for *A. virolinensis*. We use our data and model to estimate the EOO for this species. We also review the representation of the species in protected areas within its distributional range and propose an update to its conservation status following IUCN guidelines. Lastly, we discuss conservation and research priorities that should contribute to the long-term survival of *A. virolinensis*.

Materials and Methods

Surveys.—We surveyed for the presence of *A. virolinensis* in 24 localities in Santander Department (Colombia). We selected these localities to include areas where the species is known to be present, unsurveyed areas within its previously hypothesized range (Amézquita and Rueda-Almonacid 2004), and areas near but beyond its range limits as currently understood. We conducted surveys between January 2013 and March 2016 (8 mo in 2013, 5 mo in 2014, 6 mo in 2015, and 1 mo in 2016), totaling 1,462 sampling hours. We performed diurnal visual encounter surveys (Crump and Scott 1994) and opportunistic observations between 0800 and 1600. We identified specimens based on the original description of the species (Ruiz-Carranza and Ramírez-Pinilla 1992) and comparison with the key provided by Brown et al. (2011). We deposited specimens (UIS-A 5505, UIS-A 5506) in the Colección Herpetológica of Universidad Industrial de Santander.

Distribution data.—We compiled distribution data from our field surveys, published literature, and specimens housed at Colección Herpetológica of Universidad Industrial de Santander, Colombia (UIS); Colección Herpetológica of Grupo de Ecofisiología del Comportamiento y Herpetología of Universidad de Los Andes, Colombia (GECOH); the online catalogue of Instituto de Ciencias Naturales (ICN) of Universidad Nacional de Colombia (http://www.biovirtual.unal.edu.co [Accessed 5 November 2015]); and Colección de Vertebrados of Instituto Alexander von Humboldt, Colombia (IAvH) through the SiB Colombia (http://www.sibcolombia.net [Accessed 5 November 2015]). We assigned latitude/longitude to localities that lacked coordinates based on site descriptions by the collectors and plotted their locations with Global Gazetteer Version 2.3 (http://www.fallingrain.com [Accessed 11 January 2016]) and Google Earth (Google Inc., Mountain View, California, USA; Table 1). Although there is uncertainty around these coordinates, we expect them to fall near or in the correct pixel of the environmental data (pixel size is 30 arc-seconds, or about 1 km^2; see next paragraph). We used the Spatially Rarefy Occurrence analysis (package SDMtoolbox; Brown 2014) to reduce sampling biases via spatial filtering (Anderson and Raza 2010; Boria et al. 2014). This approach reduced our

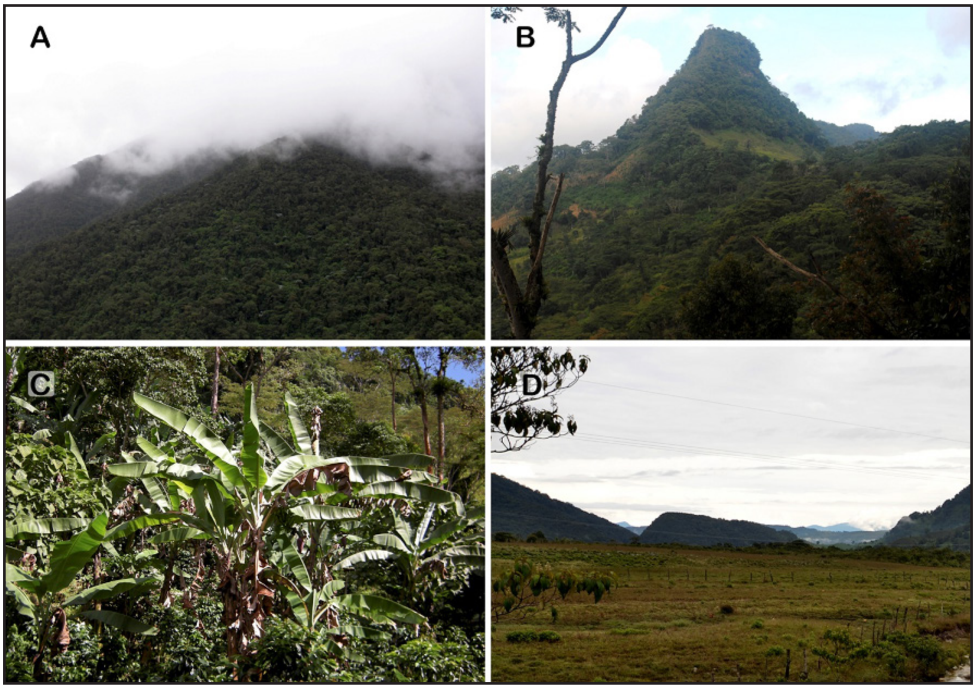

Figure 2. Habitats in the range of Santander Poison Frog (*Andinobates virolinensis*), Colombia. (A) Primary forest at type-locality, municipality of Charalá, corregimiento of Virolín. (B) Secondary forest in municipality of Florián, vereda La Vueltiada. (C) Traditional agroecosystem of mature mixed culture of native-shaded coffee and plantain trees in municipality of San Vicente de Chucurí, vereda La Colorada. (D) Intensively grazed pastures near the type-locality (Santander Department). (Photographed by Carlos A. Hernández).

data to 12 independent occurrence records that were ≥ 10 km away from one another (Table 1). Using higher filtering values (20 km) left too few occurrence points for model building, whereas decreasing filtering values (5 km) increased the effects of sampling bias.

Climate and elevation data for modeling.—We used data for elevation and 19 bioclimatic variables (Appendix A; O'Donnell and Ignizio 2012) from the WorldClim Project for the years 1960–1990 (Hijmans et al. 2005; WorldClim. 2014. WorldClim - Global Climate Data. Free climate data for ecological modeling and GIS. Available at http://www.worldclim.org/. [Accessed 1 December 2015]). We used two methods to define the limits of our study region (Fig. 3A), following Anderson and Raza (2010). In Method 1, we calibrated the model to a rectangular region encompassing the known localities for the species. Method 2 included mainly the Andean Mountains of the study area from Method 1, which is recognized as the habitat of this species (Amézquita and Rueda-Almonacid 2004). The selection of these methods seems appropriate because it excludes large regions where the species is likely absent (i.e., areas where the species has not been collected historically [Brotons et al. 2004], or Inventory Pseudo-absences [Elith and Leathwick 2007]).

Modeling strategy.—We generated SDMs using the software MaxEnt (Phillips et al. 2006) v. 3.3.3k (www.cs.princeton.edu/~schapire/maxent [Accessed 3 February 2016]). To select the variables used in the final models, we followed the process outlined by Warren et al. (2014). We began by running a model including all bioclimatic variables and elevation, and calculated the contribution scores for each variable. To do so, MaxEnt employs two metrics: percentage contribution, which is a heuristic approach to estimate the contribution values of the corresponding variable by the increase in gain (a measure of goodness-of-fit) in the model, and permutation importance, which is a measure that determines the contribution of each variable by randomly permuting each variable among the presence and background training points and measuring the resulting drop in the area under the curve (AUC). To get alternate estimates of which variables are most important in the model, we also ran a jackknife test. This approach generates a series of models in an iterative process, excluding one variable at a time, retaining each variable in isolation, and using all variables in conjunction, to provide information on how important each variable is and how much unique information each variable provides for the model (see online tutorial for MaxEnt at www.cs.princeton.edu/~schapire/maxent [Accessed 18 December 2017]). We calculated the spatial correlations (Pearson coefficient) between variables using ENMTools 1.3 (Warren et al. 2010). We used contribution scores and scores from spatial correlations to reduce predictors from the full model.

Table 1. Locality data (sorted from south to north) for Santander Poison Frog (*Andinobates virolinensis*) from Colombia. Date (month-year) is for surveys conducted during this study. Dates in bold represent sites we did not survey for this study. Locality data (after Spatially Rarefy Occurrence analysis) used in species distribution models are denoted (1). Coordinates inferred from Global Gazetteer and Google Earth are marked (2). Coordinates are in decimal degrees (WGS-84 datum). Type Locality (sensu Ruiz-Carranza and Ramírez-Pinilla 1992) includes coordinates based on subsequent surveys of Valderrama-Vernaza et al. (2010). Acronyms for museum specimens are as in the text and elevation in meters above sea level.

Date	Locality: Department, Municipality, Site	Coordinates	Elevation	Source
10–1995	Cundinamarca, Yacopí, Guadalito, Cabo Verde[1, 2]	5.5553°N, 74.2844°W	1,540	ICN-42926
11–2015	Boyacá, Otanche, La Cunchalita[1, 2]	5.6553°N, 74.1867°W	1,331	GECOH 1111–4
08–2014	Santander, Florián, La Vueltiada[1]	5.8138°N, 73.9817°W	1,746	This study (UIS-A 5505–6)
12–2015	Santander, La Belleza, Buena Vista	5.8456°N, 73.9628°W	1,969	Daniel Mejía, pers. obs.
01–2013	Santander, Gámbita, Bogotacito[1]	6.0146°N, 73.2157°W	2,400	ICN-12744
09–2014	Santander, Charalá, Virolín, El Palmar	6.0604°N, 73,2144°W	1,906	This study (not collected)
09–2014	Santander, Charalá, Virolín, Cerro El Rayo	6.0612°N, 73.1807°W	2,137	ICN-08551
09–2014	Santander, Charalá, Virolín, Costilla de Fara	6.0781°N, 73.2300°W	2,108	UIS-A-03584
06–2013	Santander, Charalá, Virolín, Costilla de Fara	6.0783°N, 73,1964°W	1,785	ICN-05482
09–2013	Santander, Charalá, Virolín[1]	6.0954°N, 73.2006°W	1,807	UIS-A-00108
09–2013	Santander, Charalá, Virolín, El Reloj[1]	6.0983°N, 73.2187°W	1,744	ICN-16101; Type Locality
04–2015	Santander, Charalá, Virolín	6.0989°N, 73.1743°W	1,780	ICN-04588
04–2015	Santander, Charalá, Virolín	6.1651°N, 73,2463°W	1,946	ICN-04256
07–1985	Santander, Ocamonte[1, 2]	6.3411°N, 73.1048°W	1,670	IAvH-Am-1132
07–1996	Santander, Confines, Km 11.2 road Oiba to Socorro[1]	6.3558°N, 73.2567°W	1,650	ICN-52860
Unknown	Santander, Socorro[1, 2]	6.4658°N, 73.2430°W	1,578	Brown et al. (2011)
12–2013	Santander, San Vicente de Chucurí, Pamplona[1]	6.7048°N, 73.4361°W	1,700	ICN-26984
08–2014	Santander, San Vicente de Chucurí, La Colorada[1]	6.7966°N, 73.4785°W	1,450	Meza-Joya et al. (2015)
07–2014	Santander, San Vicente de Chucurí, Cerro de las Tetas	6.8453°N, 73.3812°W	1,803	This study (not collected)
06–2013	Santander, San Vicente de Chucurí, El Centro[1]	6.8669°N, 73.3793°W	1,543	This study (UIS-A-3755)

We eliminated variables with low contribution and permutation importance scores (< 5%) in the full model. We retained environmental variables with the highest jack-knife scores. We deleted variables that were highly correlated with these kept variables (Pearson r > 0.70). This process resulted in three bioclimatic variables for subsequent models (Table 2).

Because of the low number of independent occurrences (12), we generated models using the cross-validated approach, with the minimum training presence (equal to the lowest presence decision threshold) to distinguish suitable from unsuitable areas (Pearson et al. 2007). This threshold identifies pixels predicted to be at least as suitable as those where the species has been recorded (Pearson et al. 2007). This method has previously been used with sample sizes as small as five records (e.g., Pearson et al. 2007; Anderson and Raza 2010; Kamino et al. 2012; Chunco et al. 2013; Shcheglovitova and Anderson 2013). To avoid overparameterization, we used linear plus quadratic (LQ) and hinge (H) features (Shcheglovitova and Anderson 2013; van Proosdij et al. 2016). We assessed three alternative regularization multiplier values (0.5 and 2.0; default setting is 1.0) following Radosavljevic and Anderson (2014). We used recommended default values for convergence threshold (10–5), maximum number of iterations (500), maximum number of background points (104), and default prevalence of the species (0.5). Lastly, we selected the logistic output format, which yields continuous values ranging from 0 to 1 that indicate the probability of suitable environmental conditions for the species (see Phillips and Dudík 2008).

Performance of models.—We evaluated model performance using (1) area under the curve (AUC) of the receiver operating characteristic (ROC) measure provided by MaxEnt, (2) success rate in jack-knife tests using the pValue Compute program from Pearson et al. (2007), and (3) sample size-corrected Akaike information criteria (AICc; Akaike 1974; Burnham and Anderson 2002) using ENMTools 1.3 (Warren et al. 2010). Once we selected the best model (Table 3), its logistic output was transformed to a binary prediction model for the suitable habitat of the species (i.e., a presence/absence map) by applying the minimum training presence threshold value (0.401) obtained by MaxEnt. Then, we evaluated the final binary model by visual examination based on our knowledge of

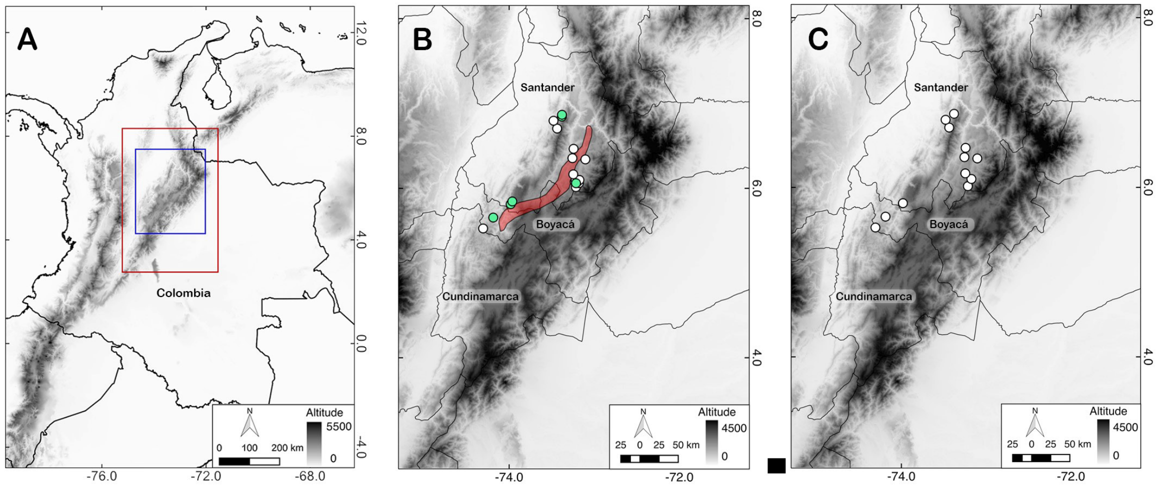

Figure 3. Distribution of Santander Poison Frog (*Andinobates virolinensis*) in the Cordillera Oriental of the Colombian Andes, Colombia. (A) Location of the study area in north of South America. Rectangles represent the two methods used to define the study region for calibrating distribution models of species. Method 1 is red. Method 2 (blue) defines a smaller region mainly in the Andes. Elevation units are meters. (B) Regional map of historical (white circles) and new localities found during this study (green circles). Red polygon indicates the range of the species sensu the International Union for the Conservation of Nature. (C) Spatially filtered localities used to build the species distribution model (white circles). Locality details are in Table 1.

the natural history and geographic distribution of *A. virolinensis*. This examination led us to the exclusion of a few small isolated areas located on the eastern slope of the Cordillera Oriental in Norte de Santander department, a region where no species of this genus is known to occur, and areas on the northwestern slope of the Cordillera Central in Antioquia Department where another species in the bombetes group (Andinobates opisthomelas) occurs (Acosta Galvis, A.R. 2017. Lista de los anfibios de Colombia: Referencia en línea. V.07.2017.0. Electronic database available at http://www.batrachia.com. [Accessed 28 December 2017]). After our evaluation, we calculated the extent of occurrence based on pixels within the binary model.

Minimum convex polygon.—We generated a minimum convex polygon (MCP) using Quantum GIS software (QGIS Development Team. 2016. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. Version 2.8.2. Available at http://qgis.osgeo.org [Accessed 22 January 2016]). We used the Convex Hull function to create the smallest convex polygon enclosing all occurrence sites. We removed pixels identified as unsuitable habitats that were outside the documented altitudinal range of this species (i.e., 1,331–2,400 m; see Results), as defined in the IUCN mapping protocols (https://www.conservationtraining.org [Accessed 16 March 2016]). Lastly, we calculated the area of the range polygon of the species as a proxy for the extent of occurrence of the species by summing the pixels within the final MCP.

Table 2. Contribution percentage and permutation importance of environmental variables used in distribution modeling of Santander Poison Frog (*Andinobates virolinensis*). Variable codes are defined in Appendix A.

Environmental Variable	Code	Contribution percentage	Permutation importance
Precipitation of the Driest Month	BIO14	77.9	64.3
Mean Diurnal Temperature Range	BIO2	17.1	19.7

Table 3. Performance statistics for two methods used to model the potential distribution of Santander Poison Frog (*Andinobates virolinensis*). An asterisk (*) denotes the combination of features with highest performance values. AICc with a dash (--) are models with more parameters than occurrence points (i.e., > 12 parameters). The abbreviation Regul. = Regularization.

Method	Features	Regul.	AUC	Success Rate	AICc	P
1	Linear plus quadratic	0.5	0.928	0.8	251.7	< 0.001
		1	0.914	0.8	260.6	< 0.001
		2	0.884	0.8	260.9	< 0.001
	Hinge	0.5	0.950	0.8	--	< 0.001
		1	0.954	0.8	--	< 0.001
		2	0.955	1.0	257.6	< 0.001
2	Linear plus quadratic	0.5	0.948	0.6	242.1	< 0.001
		1	0.936	0.8	247.8	< 0.001
		2	0.903	0.8	250.1	< 0.001
	Hinge	0.5	0.959	0.8	248.1	< 0.001
		1	0.960	0.8	246.1	< 0.001
		2	0.962*	1.0*	232.1*	< 0.001

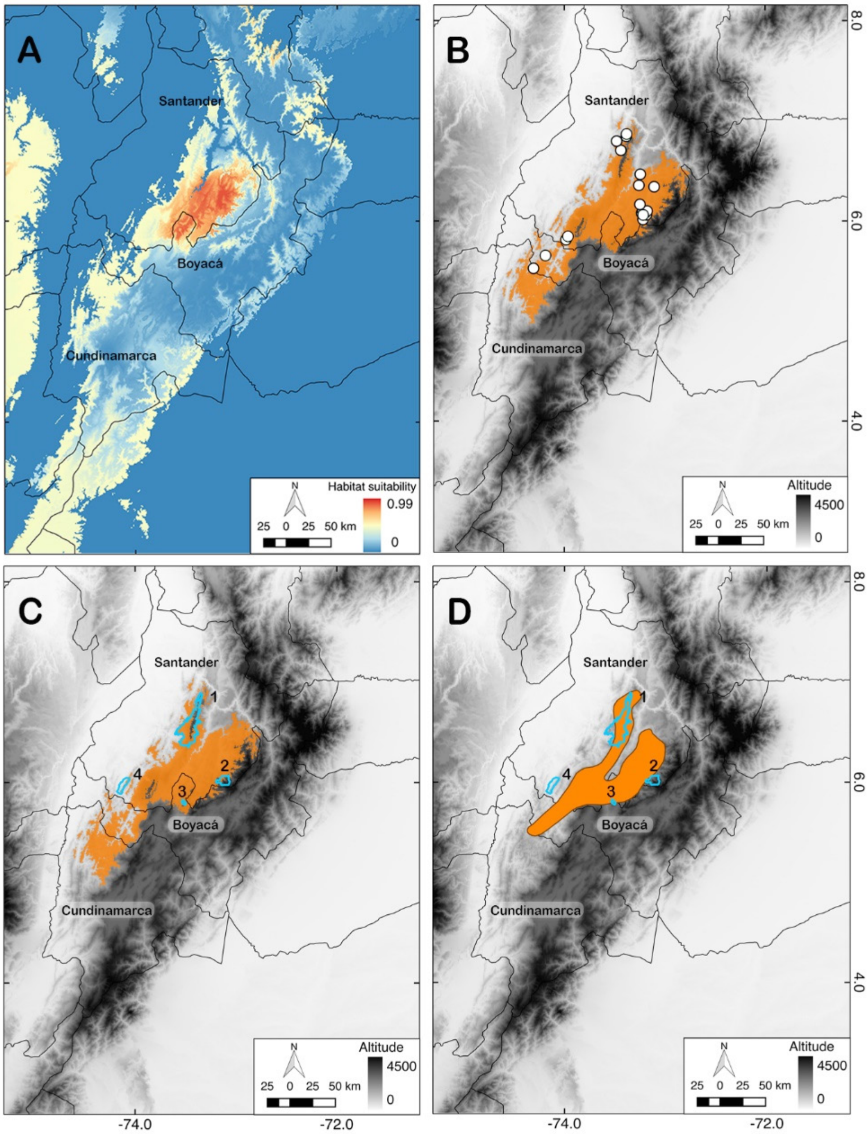

Figure 4. MaxEnt models of the potential geographic distribution of Santander Poison Frog (*Andinobates virolinensis*). (A) Logistic output and (B) binary model (orange) after applying the decision threshold and visual validation. White circles indicate unfiltered presence records (see Table 1). Elevation units are meters. (C) Protected areas (blue) near or in the binary model (orange). (D) Protected areas (blue) near or in the minimum convex polygon (orange). Protected areas are: 1 = Parque Nacional Natural Serranía de los Yariguíes, 2 = Santuario de Fauna y Flora Guanentá Alto Río Fonce, 3 = Reserva Forestal Protectora Sierra El Peligro, and 4 = Reserva Forestal Protectora Cuchilla El Minero.

Results

Distribution data.—Our field surveys detected *A. virolinensis* in 13 localities: four were new and nine were documented in herpetological collections. We did not find the species in 11 of the surveyed localities (Appendix B). We obtained additionally seven locality records of which we were not aware at the outset of the study: two from published literature, four from scientific collections, and one new locality from an unpublished observation (Table 1). Hitherto unpublished specimens in herpetological collections provided first records of *A. virolinensis* from Boyacá Department in the municipality of Otanche (GECOH 1111–4; Fig. 3A), as well as the northernmost locality for the species in northern Serranía de los Yariguíes, Santander Department (UIS-A-3755; municipality of San Vicente de Chucurí, vereda El Centro). Based on our detections and review of historical records, we define the altitudinal range for *A. virolinensis* as from 1,331 m (GECOH 1111–4) to about 2,400 m (ICN-12744). These data extend the distribution of *A. virolinensis* along the western slope of the Cordillera Oriental in Colombia; its range now extends from northern Serranía de los Yariguíes

Table 4. Extent of occurrence (EOO) estimated for Santander Poison Frog (*Andinobates virolinensis*) from the species distribution model (SDM) and the minimum convex polygon (MCP). Protected areas in Colombia are Parque Nacional Natural Serranía de los Yariguíes (SY), Santuario de Fauna y Flora Guanentá Alto Río Fonce (GF), Reserva Forestal Protectora Nacional Cuchilla El Minero (CM), and Reserva Forestal Protectora Nacional Sierra El Peligro (SP).

Method	EOO (km^2)	EOO in protected areas (km^2)				EOO under protection (%)
		SY	GF	CM	SP	
SDM	10,828	311.8	30.6	18.7	15.3	3.47
MCP	6,973	446.9	2.1	-	11.9	6.61

in Santander Department (UIS-A-3755) to northern Cundinamarca Department (ICN-12744; Figs. 3A and 4). This represents an increase of at least 4,482 km^2 over the range reported by the IUCN (2,491 km^2; Amézquita and Rueda-Almonacid 2004).

Species distribution model.—Inclusion of georeferenced localities generated models that better represent the range limits of the species as currently understood. Thus, we included these data in our distribution models. The extent of the study region affected model performance. Models calibrated mainly in the Andean region (Method 2) performed better than models based on the broader region (Method 1). Method 2 yielded a higher success rate than Method 1 (Table 3), indicating low omission rates. Models with the hinge feature and high regularization multipliers (i.e., 2.0) performed better and with less parameterization (Table 3). SDMs generated with Method 2 led to more statistically robust, less parameterized models and fewer predictions in environments where the species is likely absent (Fig. 4A). The final model performed well with an AUC value of 0.957 ± 0.006 SD. The model had a predictive success rate equal to 0.8 ($P < 0.001$), indicating low omission rates. These results indicate that the model is informative for potential suitable habitat for *A. virolinensis*.

Predicted habitat suitability for *A. virolinensis* was strongly associated with precipitation in the driest month (contribution 77.9%) and modestly associated with the mean diurnal temperature range and isothermality (Table 2). Suitability increased sigmoidally with the precipitation of the driest month, mean diurnal temperature range, and isothermality. Suitability for *A. virolinensis* was maximized around 50–60 mm of precipitation in the driest month, 10–12° C for mean diurnal temperature range, and 83–93 for isothermality. The SDM predicted suitable habitat for *A. virolinensis* on the western slope of the Cordillera Oriental in Santander, Boyacá, and Cundinamarca departments (Fig. 4).

Our model yielded very low habitat suitability scores at high elevations (above about 2,400 m) in the Cordillera Oriental and low elevations (below about 1,300 m) in the Chicamocha and Sogamoso canyons. Habitats beyond these unsuitable features were identified by the model as of low suitability and were clipped from the final model based on the threshold value (Fig. 4B; see Methods). We estimated the total EOO for the species to be 10,828 km^2. The SDM showed that most of the predicted occurrence of this species (about 96.5% of EOO) is outside boundaries of protected areas (Fig. 4C; Table 4).

Minimum convex polygon.—The EOO estimated with the MCP was 6,973 km^2. The MCP (Fig. 4D) excludes large regions of Andean forest identified as suitable habitat by the SDM (Fig. 4C). The MCP showed that a small portion of the predicted occurrence of this species (about 6.6% of EOO) is outside boundaries of protected areas (Fig. 4D; Table 4).

DISCUSSION

The new records presented here improve our knowledge of the geographical distribution of *A. virolinensis*, extend the range of the species, and suggest areas for additional surveys where the species could be present. In Santander Department, the known distribution includes the type locality and several additional locations through the western slope of the Cordillera Oriental. Single localities also occur in Boyacá and Cundinamarca departments. The new locality record provided here from Boyacá Department fills the distribution gap between Santander and Cundinamarca departments. There is little or no information about *A. virolinensis* in several areas predicted to be suitable by the models (e.g., southern Santander and northern Boyacá and Cundinamarca). Factors not incorporated in our models (e.g., land-cover, interspecies interactions, diseases) may also limit the presence of *A. virolinensis* in areas identified as suitable.

According to the information available to date, we propose that the current IUCN status for *A. virolinensis* (i.e., Endangered, see Introduction) should be downgraded to Vulnerable (VU), because its extent of occurrence (EOO) is > 5,000 km^2 and < 20,000 km^2 (SDM = 10,828 km^2, MCP = 6,973 km^2). However, this conservation status could change as new information is collected. The destruction of forests represents a major threat for this species, as well as other species in this region of the Andes. This is especially true for Santander and Boyacá departments, where livestock grazing and intensive farming continue to increase (Sánchez-Cuervo et al. 2012). However, reliable data on how rapidly forest destruction is occurring in the study area and how this species responds to forest loss and degradation are lacking. The discovery of a population of *A. virolinensis* on traditional sustainable agricultural systems at relatively high densities (42–73 adult individuals per ha; Meza-Joya et al. 2015) suggests that it may be resilient to some types of land cover change, provided some key features of the native habitats are retained (e.g., large native trees with bromeliads). Estimations of detection probabilities and local abundances are critical to assess occupancy and population trends for *A. virolinensis*.

Precipitation during the driest month was the most important variable explaining the modeled range of *A. virolinensis* (Table 2). Only two other predictors were in our final model (mean diurnal range and isothermality) and these were much less influential. Areas with conditions outside favored range of precipitation during the driest month (50–60 mm), and to a lesser extent, mean diurnal temperature range (10–12° C), likely represent unsuitable conditions for this species. High elevation summits (above 2,400 m elevation) and low elevation canyons (below 1,300 m) may be outside the physiological tolerances and ecological requirements of the species. The Chicamocha and Sogamoso canyons reach depths of 400 m and host dry tropical forest and semi-arid spiny tropical scrubland. High elevations (up to about 2,600 m) support forests and Páramo ecosystems characterized by low temperatures and high solar radiation (Kattan et al. 2004; Navas 2006; Morales et al. 2007). Our inspections of the literature, herpetological collections, and unpublished results from surveys in and around these features have failed to document *A. virolinensis*.

Our modeling suggests that national protected areas currently provide limited refuge for *A. virolinensis*. Through active participation of local communities, economic development could be promoted with sustainable agriculture practices that would facilitate the conservation of *A. virolinensis* (Meza-Joya et al. 2015). Such conservation efforts in agricultural landscapes, however, should be considered as complementary to enforcing the protection and restoration of national protected areas. Further work is needed to reinforce habitat protection both outside and within the existing network of protected areas in Colombia to ensure the long-term survival of this and other organisms in this Andean region.

Our SDM predictions are based on broad climatic variables, but other factors (e.g., biotic interactions, stochastic events) can shape distributions of amphibians (Blank and Blaustein 2012). Further studies that link ecology, phylogeography, and behavior, are required to develop integrated conservation strategies for *A. virolinensis*. Our study presents a regional habitat context for developing management plans and conservation policies aimed at conserving this species. However, some limitations are worth noting, including the limited occurrence data to build models using standard approaches and the absence of information about changes in land use throughout the predicted range of the species. Further surveys in unexplored or under-sampled areas, taking into consideration the detection probabilities for the species, are needed. Such data would help generate more robust SDMs and improve understanding of the extent of occurrence and area of occupancy for this species.

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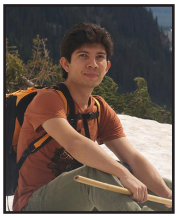

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Appendix A. Environmental variables used in species distribution models. Data are from WorldClim (Hijmans et al. 2005). Units are in brackets.

Variable	Code	Definition
Annual Mean Temperature	BIO1	Annual mean temperature [° C].
Mean Diurnal Temperature Range	BIO2	Mean of monthly (max temp - min temp) [° C].
Isothermality	BIO3	(Mean Diurnal Range)/(Temperature Annual Range)×(100) [%].
Temperature Seasonality	BIO4	(Standard deviation of mean monthly temperatures)×(100) [° C].
Max Temperature of Warmest Month	BIO5	Maximum temperature value across all months within a given year [° C].
Min Temperature of Coldest Month	BIO6	Minimum temperature value across all months within a given year [° C].
Temperature Annual Range	BIO7	(Max Temperature of Warmest Month - Min Temperature of Coldest Month) [° C].
Mean Temperature of Wettest Quarter	BIO8	Mean temperature during the wettest quarter [° C].
Mean Temperature of Driest Quarter	BIO9	Mean temperature during the driest quarter [° C].
Mean Temperature of Warmest Quarter	BIO10	Mean temperature during the warmest quarter [° C].
Mean Temperature of Coldest Quarter	BIO11	Mean temperature during the coldest quarter [° C].
Annual Precipitation	BIO12	Annual total precipitation [mm].
Precipitation of Wettest Month	BIO13	Total precipitation during the wettest month [mm].
Precipitation of Driest Month	BIO14	Total precipitation during the driest month [mm].
Precipitation Seasonality	BIO15	Variation in monthly precipitation totals over the course of the year [%].
Precipitation of Wettest Quarter	BIO16	Total precipitation during the wettest quarter [mm].
Precipitation of Driest Quarter	BIO17	Total precipitation during the driest quarter [mm].
Precipitation of Warmest Quarter	BIO18	Total precipitation during the warmest quarter [mm].
Precipitation of Coldest Quarter	BIO19	Total precipitation during the coldest quarter [mm].

Appendix B. Sampling localities where Santander Poison Frog (*Andinobates virolinensis*) has not been recorded. Data sources are from this study and from additional surveys by the authors (ERP, FLMJ, and CHJ). Coordinates are in decimal degrees (WGS-84 datum). 'Effort' is survey effort in total sampling hours (number of surveys). Date (month and year) is for most recent survey carried out in each locality. Localities are sorted chronologically from older to recent.

Date	Municipality	Department	Locality	Effort	Coordinates	Elevation (m)	Source
01–2011	El Cerrito	Santander	Las Arreviatadas lagoon complex	72 (2)	6.8559°N, 72.5235°W	3,360	FLMJ
04–2011	Lebrija	Santander	Vereda La Girona	16 (1)	7.3234°N, 73.3375°W	202	CHJ
04–2011	Piedecuesta	Santander	Reserva Forestal El Rasgón	432 (8)	7.0438°N, 72.9808°W	2,345	ERP and FLMJ
05–2011	Betulia	Santander	Vereda Sogamoso, site Corintios	24 (1)	6.9966°N, 73.4119°W	658	FLMJ
05–2011	Zapatoca	Santander	Vereda San Javier, stream La Ramera	36 (1)	6.8219°N, 73.3347°W	2,145	FLMJ
01–2012	Bucaramanga	Santander	Barrio La Esperanza II, cañada La esperanza	56 (3)	7.1536°N, 73.1284°W	708	FLMJ and CHJ
03–2012	Floridablanca	Santander	Jardín Botánico Eloy Valenzuela	30 (3)	7.0673°N, 73.0872°W	915	CHJ
01–2013	Tona	Santander	Vereda El Quemado, Reserva Núcleo Arnania	245 (5)	7.2074°N, 73.0072°W	1,993	This study
05–2013	Floridablanca	Santander	Pico de La Judía, Reserva Los Maklenques	68 (2)	7.0874°N, 73.0464°W	1,678	This study
06–2013	Piedecuesta	Santander	Vereda Las Amarillas	64 (2)	6.9973°N, 72.9794°W	2,169	This study
06–2013	Girón	Santander	Vereda Sogamoso, site Linderos	120 (3)	7.1002°N, 73.3875°W	350	CHJ
08–2013	Floridablanca	Santander	Vereda Guarumales, farm El Carajo	104 (2)	7.1469°N, 73.0362°W	2,127	This study
08–2013	Matanza	Santander	Santa Cruz de la Colina, vereda Guayaquil	64 (2)	7.3722°N, 73.1024°W	1,495	FLMJ
10–2013	Los Santos	Santander	Mesa de Los Santos, Hacienda El Roble	134 (3)	6.8617°N, 73.0491°W	1,632	This study
10–2013	Guapotá	Santander	Vereda Las Flores, farm La Chocolatera	87 (2)	6.3905°N, 73.3262°W	1,102	This study
11–2013	Santa Bárbara	Santander	Vereda Esparta, farm Monterey	64 (2)	7.0203°N, 72.9027°W	2,263	FLMJ
04–2014	Barrancabermeja	Santander	Vereda Pozo de Nutria, Quinta Estrella	186 (4)	7.0350°N, 73.6416°W	102	ERP and FLMJ
06–2014	San Gil	Santander	Vereda San José, farm Villa Mandarina	32 (1)	6.5214°N, 73.1075°W	1,584	This study
08–2014	Barrancabermeja	Santander	Universidad de La Paz, Reserva Santa Lucía	196 (4)	7.0818°N, 73.7490°W	104	ERP
11–2014	Guaca	Santander	Vereda Quebradas	32 (1)	6.9146°N, 72.8711°W	2,928	This study
04–2015	Páramo	Santander	Vereda Juan Curí	10 (2)	6.3683°N, 73.1718°W	1,414	CHJ
06–2015	Sabana de Torres	Santander	Reserva Natural El Cabildo Verde	88 (3)	7.3521°N, 73.4992°W	193	This study
07–2015	San Vicente de Chucurí	Santander	Vereda La Lizama, Bioparque El Arboretum	162 (3)	7.0767°N, 73.5383°W	257	This study
09–2015	Ríonegro	Santander	Llano de Palmas, vereda La Honda	72 (4)	7.2458°N, 73.2102°W	845	FLMJ and CHJ
09–2015	El Carmen del Chucurí	Santander	El Centenario, vereda Los Andes	98 (2)	6.6896°N, 73.6154°W	502	This study
10–2015	Charta	Santander	Vereda La Rinconada, stream El Juncal	16 (1)	7.2858°N, 72.9641°W	2,119	FLMJ
11–2015	Matanza	Santander	Vereda Vulcaré, stream Vulcaré	32 (1)	7.3407°N, 72.9932°W	1,597	FLMJ and CHJ
11–2015	Guaduas	Cundinamarca	Vereda Chipauta	24 (1)	5.0654°N, 74.5632°W	1,636	FLMJ
12–2015	El Colegio	Cundinamarca	El Triunfo, Hacienda Misiones	56 (2)	4.5441°N, 74.4375°W	1,508	FLMJ
12–2015	Albán	Cundinamarca	Vereda El Garbanzal, Hacienda Rancho Grande	12 (1)	4.8733°N, 74.4434°W	2,098	FLMJ
12–2015	La Vega	Cundinamarca	Vereda San Juan	24 (1)	4.9791°N, 74.3214°W	1,528	FLMJ
03–2016	Charalá	Santander	Reserva Nuestro Sueño	20 (2)	6.2912°N, 73.1904°W	1,745	CHJ