



Insights into the natural history of the endemic Harlequin Toad, *Atelopus laetissimus* Ruiz-Carranza, Ardila-Robayo, and Hernández-Camacho, 1994 (Anura: Bufonidae), in the Sierra Nevada de Santa Marta, Colombia

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Abstract.—*Atelopus laetissimus* is a bufonid toad that inhabits the mountainous areas of the Sierra Nevada de Santa Marta (SNSM), Colombia. This species is endemic and endangered, so information about its ecology and distribution are crucial for the conservation of this toad. Here, the relative abundance, habitat and microhabitat uses, and vocalization of *A. laetissimus* are described from the San Lorenzo creek in the SNSM, as well as its potential distribution in the SNSM. To this end, 447 individuals were analyzed during several sampling trips from 2010 to 2012. Against expectations, population density was significantly higher in the stream than in the riparian forest. Overall, *A. laetissimus* used seven different diurnal microhabitats, with a high preference for leaf litter substrates and rocks. The rate of recaptures decreased linearly across the survey nights. Two types of vocalizations related to the advertisement call of *A. laetissimus* were recorded: a series of pulsed calls like a buzz and another short call, lacking pulses or partially pulsed. According to this analysis, the areas with higher habitat suitability for *A. laetissimus* were located principally in the northern and northwestern regions of the SNSM, in agreement with literature. Moreover, the data modeling indicated a significant increase in habitat loss from 2013 to 2017. The information presented here should be considered as a starting point for the conservation of this species.

Keywords. Advertisement call, amphibian decline, conservation, ecology, habitat loss, habitat suitability, home range, microhabitat selection, nocturnal site fidelity

Resumen.—*Atelopus laetissimus* es un sapo de la familia Bufonidae que habita las zonas montañosas de la Sierra Nevada de Santa Marta (SNSM), Colombia. Para esta especie endémica y en peligro, la información ecológica y de distribución es crucial para su conservación. En el presente trabajo describimos la abundancia relativa, usos de hábitat y microhábitat, y las vocalizaciones de *A. laetissimus*, así como su distribución potencial en la SNSM. Para esto, analizamos 477 individuos durante varios muestreos entre 2010 y 2012. Contra las expectativas, la densidad poblacional fue significativamente mayor en el lecho de la quebrada que en el bosque ribereño adyacente. En general, *A. laetissimus* utilizó siete microhábitats diurnos, con una alta preferencia por los sustratos de hojarasca y rocosos. La tasa de capturas decreció linealmente a lo largo de los muestreos nocturnos. Registramos dos tipos de vocalizaciones relacionadas con el llamado de anuncio de *A. laetissimus*. Una serie de llamados pulsados como zumbidos y otros más cortos, con pulsos ausentes o parcialmente pulsados. De acuerdo con nuestros análisis, las áreas con mayor idoneidad de hábitat se localizan en los sectores septentrionales y noroccidentales de la SNSM, lo que es concordante con la literatura. Además, el modelo construido indica un incremento significativo de la pérdida de hábitat entre 2013–2017. Esta información debe ser considerada como punto de partida para la conservación de esta especie.

Palabras clave. Ámbito doméstico (home range), conservación, declive de los anfibios, ecología, fidelidad de percha nocturna, idoneidad de hábitat, llamado de anuncio, pérdida de hábitat, selección de microhábitat

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Introduction

The harlequin toads (Bufonidae: *Atelopus*) are small amphibians (<10 cm) which have aposematic coloration and predominantly diurnal activity periods (Lötters 1996). With a worldwide diversity of 96 described species (Frost 2019), the conservation of these amphibians has been seriously affected during the last decades due to the population decreases detected in a majority of species and the extinction of others, and currently 97.92% of the species of this genus are included in the IUCN Red List of Threatened Species, with one extinct species (Young et al. 2001; La Marca et al. 2005; Gascon et al. 2007; Tapia et al. 2017; IUCN 2019). Among the main risk factors for the decline of these populations are the loss of habitat, the introduction of exotic species which are potential predators and competitors, as well as deaths by pathogens (mainly by the chytrid fungus *Batrachochytrium dendrobatidis* [Bd]) and climate change (Lötters 2007; Catenazzi 2015; Barrio-Amorós and Abarca 2016; Valenzuela-Sanchez et al. 2017).

In general, information about the population biology and ecology of the different *Atelopus* species is relatively scarce. For example, the males of the species *Atelopus cruciger* (Lichtenstein and Martens, 1856) are known to remain longer in the streams than the females (Sexton 1958). But, on the other hand, studies conducted on *Atelopus carbonerensis* (Rivero, 1974 “1972”) in Venezuela, found that they remain almost all year in their habitat, except in the dry season when individuals migrate towards the streams for reproduction (Dole and Durant 1974). In the Variable Harlequin Toad of Costa Rica, *Atelopus varius* (Lichtenstein and Martens, 1856), both males and females are territorial and have fidelity for their reproduction sites. This indicates that even temporary alterations of the aggregation patterns of individuals between dry and rainy seasons, when they are more dispersed due to the increase in humidity (Crump 1988; Pounds and Crump 1989), results in an apparent decrease in detection (González-Maya et al. 2013). In Panama, the Golden Toad, *Atelopus zeteki* (Dunn, 1933) is concentrated in streams at the beginning of the breeding season, which occurs only during the transition between the rainy season and the dry season (Karraker et al. 2006). Another study determined site fidelity, habitat utilization, and range of households in the Suriname Toad, *Atelopus hoogmoedi* (Lescure, 1974) during the rainy season (Luger et al. 2009).

The Sierra Nevada of Santa Marta (SNSM) is a mountain massif located in the Caribbean region of Colombia. The particular conditions of isolation and vegetation of this mountainous system, which is not connected to the Andes, have led to a series of speciation processes in several groups of vertebrates, such as amphibians and reptiles (Ruthven 1922; Bernal-Carlo 1991; Sánchez-Pacheco et al. 2017), mammals (Alberico et al. 2000), and birds (Strewe and Navarro

2004). This applies to the harlequin toads (Bufonidae: *Atelopus* Duméril and Bibron, 1841), whose current diversity includes five endemic species for this region: *Atelopus arsyecue* Rueda-Almonacid, 1994, *Atelopus carrikeri* Ruthven, 1916, *Atelopus laetissimus* Ruiz-Carranza, Ardila-Robayo, and Hernández-Camacho, 1994, *Atelopus nahumae* Ruiz-Carranza, Ardila-Robayo, and Hernández-Camacho, 1994, and *Atelopus walkeri* Rivero, 1963. These species can be found between 800 and 4,500 m asl, and from the tropical moist forests to the páramos of the SNSM (Ruthven 1916; Rueda-Almonacid 1994; Ruiz-Carranza et al. 1994; Rueda-Almonacid et al. 2005).

This study examines some aspects of the natural history and ecology of the Harlequin Toad, *A. laetissimus*. Previous studies have shown that *A. laetissimus* inhabits streams and rivers in the mountainous areas of the northwestern sector of the SNSM (Granda-Rodríguez et al. 2008, 2012; Rueda-Solano et al. 2016a), and it is classified as Endangered (EN) by the IUCN (Granda et al. 2008). A recent study reported individuals infected by the chytrid fungus *Bd* (Flechas et al. 2017), the pathogen that has led to the decline and disappearance of many amphibian populations globally (Young et al. 2001; Catenazzi 2015). This study also includes an estimation of relative abundance, population density, microhabitat preference, spatial dynamics, and vocalization, in a population of *A. laetissimus* in the sector of San Lorenzo, Santa Marta, Colombia. Additionally, the potential distribution and patterns of habitat loss for this species during the 21st century were modeled, recognizing the great influence of habitat loss in recent decades on the extinction of many Neotropical species (Young et al. 2001; Marca et al. 2005; Lötters 2007).

Materials and Methods

Study Area

The study area corresponds to the San Lorenzo creek (11°6'56.21" N, 74°3'0.18" W, 2,100 m asl), an affluent of the upper basin of Gaira river, northwestern sector of the SNSM, Santa Marta district, Magdalena department (= state), Colombian Caribbean. The principal vegetation unit of this area corresponds to lower mountain humid forest (*sensu* Espinal and Montenegro 1963). According to Granda-Rodríguez et al. (2012), the annual averages of rainfall and temperature are 2,622 mm and 13.6 °C, respectively, and the climatic regime is unimodal bi-seasonal, with a dry period from December to March, and a rainy period from April to November.

Estimations of Relative Abundance and Population Density

Relative abundance (RA) was estimated from data collected in seven field campaigns conducted from 2010 to

2012 (October 2010; April, June, and December 2011; January and February 2012). Each fieldtrip had a duration of 12 days, with seven hours of daily work (0800–1200 h, 1800–2100 h). Individuals were detected through Visual Encounter Survey (Crump and Scott 1994), where two observers performed random walks. The sampling effort was 84 h per observer for each field campaign, reaching 558 h per observer in total. Relative abundance was calculated as the number of individuals/(h × observers), or ind/[h × obs] (Lips 1999). Sex was assigned by the size of individuals, assuming that females had a snout-vent length (SVL) > 40 mm and juveniles < 35 mm, and specimens within this range were considered as potential males. Sexual determination also considered the presence of eggs in the corporeal cavity noted through skin, calling behavior, and amplexant couples. Sex was determined in this way because the sexually dimorphic characters typically useful for population studies (La Marca et al. 1990 “1989;” Lampo et al. 2017) have not been established for *A. laetissimus*.

Population density was estimated through 40 permanent transects of 20 × 4 m (Jaeger 1994), with 20 located in the riparian forest and 20 in the stream. These transects were positioned parallel to the stream, separated by at least 20 m. Two observers walked along the transect counting the individuals only once. The medians of density obtained in each riparian forest and stream were compared using the Wilcoxon test for independent samples (*W*).

Habitat Selection and Dispersal Patterns

Testing the microhabitat preferences followed the concept of the third and fourth levels of habitat selection according to Johnson (1980), that indicate which components of the habitat are used and their proportions of use. For diurnal microhabitat, the substrate occupied by each individual was recorded according to the seven categories proposed by Granda-Rodríguez et al. (2008b): (I) rocks, (II) leaf litter, (III) fallen trunks, (IV) ferns, (V) leaves, (VI) bare floor, and (VII) others. The proportion of area for each microhabitat category was measured in 15 random plots of 4 m² located at the side of the stream. A Chi-squared test (χ^2) was performed, where the expected frequency was the number of individuals by substrate (N), while the observed frequency was calculated as the total number of individual (N) per area proportion of the substrate (%). Microhabitat selection was assumed when the proportion of substrate used was different from its availability, following the method of Molina-Zuluaga and Gutiérrez-Cárdenas (2007). To determine which substrates were selected by individuals, this analysis was repeated after deleting the categories most used or those that seemed to be used disproportionately to their availability (Molina-Zuluaga and Gutiérrez-Cárdenas 2007). In cases where significant differences in the second anal-

ysis were not found, the deleted category was considered to be preferred by the species.

To determine the nocturnal site fidelity, 60 specimens were marked with sub-epidermal alphanumeric tags (Visible Implant Alpha Tags, Northwestern Marine Technology Inc., 1.5 × 2.5. mm), and detected at night with a fluorescence lantern (Courtois et al. 2013). During 13 continuous nights (1900–2200 h, 36 h × obs), two observers looked for marked individuals to determine if they stayed in the same sites. The date, hour, location, and distance from the previous capture site were recorded for each recapture. The potential relationship between the number of individuals recaptured and the number of nights of survey was explored using a linear regression.

To describe the patterns of diurnal horizontal movement, each marked and recaptured specimen was spatially located in a Cartesian diagram consisting of a 50 m transect along the stream delimited by a reference point every 5 m (*y* axis), and the perpendicular distance of the specimen to the transect (*x* axis). Then, the distance from diurnal to nocturnal microhabitat was measured when possible. This was carried out in two sampling sessions of three days, with a three-day interval between them. The sampling times on the first day were 0800–1100 h and 1400–1600 h, on the second at 0600–0900 h and 1300–1500 h, and on the third at 0900–1200 h and 1500–1700 h. This sequence was repeated successively. Aggressive behavior observed during the survey was described following the terminology of Crump (1988).

Advertisement Call

On 30 January 2012, 270 seconds (s) of the advertisement call (*sensu* Wells 2007) of a male of *A. laetissimus* was recorded in San Lorenzo creek, at 1732 h, using a Sony (ICD-PX312) digital recorder. Although the advertisement call is not easy to define, we consider that the recorded calls belong to this functional category because they were emitted regularly by a solitary male *in situ* (without manipulation), who had no interactions with individuals of the same sex (which might indicate aggressive calls) or the opposite sex (which might indicate courtship calls). Air temperature and relative humidity at the recording moment were 12.3 °C and 75%, respectively. The traits of advertisement calls were quantified using the software PRAAT 6.0.13 for Windows (Broesma and Weenik 2007). The parameters of the advertisement call measured were: call duration (in seconds: s), number of pulses per call, pulse duration (s), interpulse interval (s), rate of pulses per second (pulses/s), frequency range (Hz), dominant frequency (Hz), and visible harmonics (Hz). Means and standard deviations (SD) were calculated for each call parameter. The terminology proposed and revised by Cocroft et al. (1990) was used for call types and by Köhler et al. (2017) for call parameters. Spectrograms and oscillograms were generated using the Seewave package (Sueur et al. 2008) in R environment (R Core Team 2018).

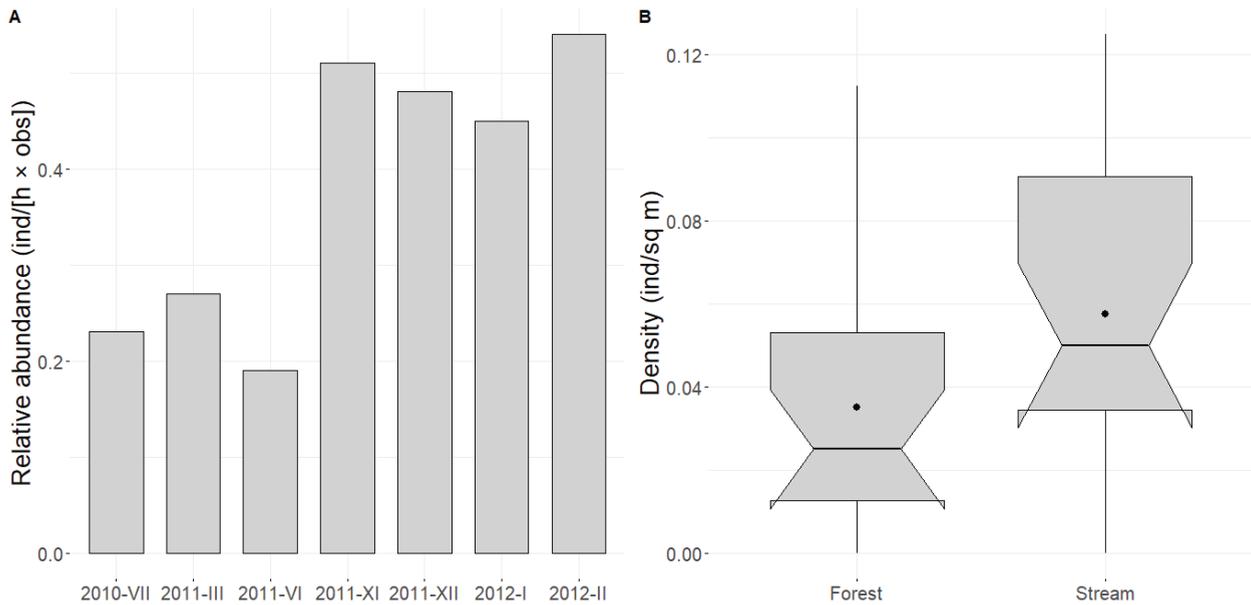


Fig. 1. (A) Temporal variation of relative abundance (ind/[h × obs]). (B) Population density (m²) per habitat of *Atelopus laetissimus*. Roman numerals represent the months of the surveys.

Potential Distribution and Habitat Loss

A species distribution model was performed, which predicts the habitat suitability with predictive algorithms integrated from environmental data and museum records (Phillips et al. 2017). The available records of *A. laetissimus* were compiled from Global Biodiversity Information Facility (GBIF), and the authors’ own data, considering all known records from 1969 to 2017. Nineteen bioclimatic layers from Worldclim 2.0. (Fick and Hijmans 2017) plus altitude, human footprint (Venter et al. 2016), and solar radiation were used as predictor variables. First, data were explored through a preliminary model including all variables, with the technique of maximum entropy (MaxEnt software, 3.4.1, Phillips et al. 2017), considering that this algorithm is not hindered by a minimum number of occurrences. Variables with correlation indexes > 0.7 and lower contributions to the exploratory model were removed. To reduce the overfitting of the model, collinearity was determined with a Spearman correlation test. According to van Proosdij et al. (2016), the size of the background was considered in relation to the prevalence of the species to be modeled (< 25 localities), since this criterion generates acceptable results for species with restricted distributions.

A model of seven-fold bootstrap technique was performed, using 65% of data for training and 35% of data for testing (Puschendorf et al. 2008), considering the small number of locations that could be used (Elith et al. 2011). The average and standard deviation of the predicted suitability were used as a final model, and as a spatially explicit measure of the reliability of the prediction, respectively. The accuracy of the model was estimated using the metric of the area under the curve of the receiver operating characteristic (AUC, Elith et al. 2011).

Additionally, the distribution extent was calculated using the IUCN methodology (2019), based on the area of occupation (AOO) and extent of occurrence (EOO). The AOO was calculated as the intersection of the species occurrence with a square grid of 2 × 2 km, while EOO corresponded to the minimum convex polygon drawn on the peripheral localities of the distribution area. Both AOO and EOO were calculated using only records after 2010.

To determine habitat loss, the resulting map from the distribution model was overlapped with forest cover loss maps from 2000 to 2017. These forest cover loss maps were generated by Hansen et al. (2013), who monitored the changes of forest cover annually with a spatial resolution of 30 m. This product has shown important benefits in terms of its feasibility for evaluating the loss and fragmentation of habitat for forest specialist species (Alaniz et al. 2018; Carvajal et al. 2018). The cumulative and annual habitat losses were calculated for the potential distribution, AOO, and EOO. For the annual habitat loss, fourth order polynomial regressions were performed to test the trends of the multianual habitat loss. The AOO and EOO estimations, and their respective trends, allowed a suggested threat classification based on criterion B of IUCN (2019) Red List of Species.

Results

Relative Abundance and Population Density

A total of 447 individuals of *A. laetissimus* were recorded, distributed potentially among 428 males, 16 females, and three juveniles. The numbers of individuals per survey fluctuated from 32 to 90 (median ± interquartile range, 78 ± 44.5 individuals), with a general RA of 0.38 ind/(h × obs), and 0.21 to 0.54 ind/(h × obs) for each survey (Fig. 1a). *Atelopus laetissimus* showed a population

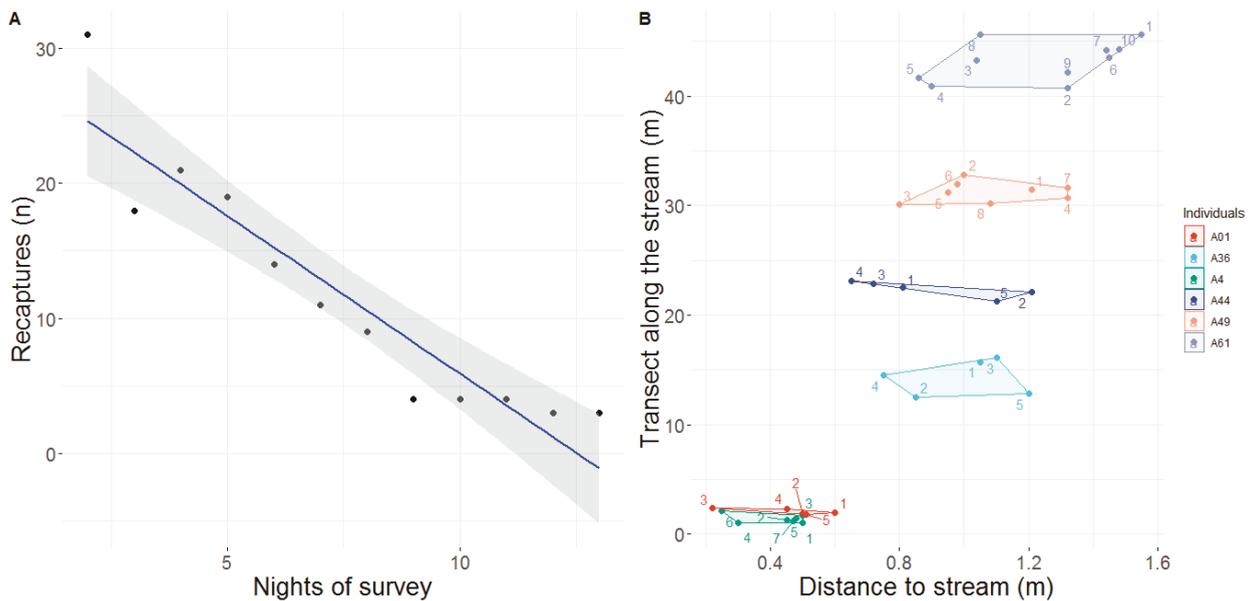


Fig. 2. Temporal variation of the number of recaptures (A) and movement patterns (B) of *Atelopus laetissimus*.

density from 0 to 0.13 ind/m² (0.04 ± 0.06 ind/m²). Population density was significantly higher (Wilcoxon test, $W = 277.5$, $p = 0.036$, Fig. 1b) in the stream (0–0.12 ind/m², 0.05 ± 0.07 ind/m²) than in the riparian forest (0–0.11 ind/m², 0.03 ± 0.05 ind/m²). The corresponding author will provide tables of raw data for individual specimens on request.

Habitat Selection and Dispersal Patterns

Atelopus laetissimus used seven different diurnal microhabitats, which were also used differentially regarding their availability ($\chi^2 = 120.121$, $df = 6$, $p < 0.001$). Although the leaf litter and rocks were the most used substrates (Table 1), significant differences in the use of microhabitat were still evident when these were removed from the analysis ($\chi^2 = 471.991$, $df = 4$, $p < 0.001$), suggesting that there is no preference for these substrates.

From 60 marked specimens, three (5%) to 31 (52%) were recaptured per night of survey. The recapture rate was higher than 30% until the fifth night, while after the ninth night it was reduced to less than 7%, showing a linear decrease across the sampling nights ($r^2 = 0.86$, $F_{1-10} = 69.99$, $p < 0.001$, Fig. 2a). The height of the nocturnal microhabitat ranged between 10 and 168 cm (mean \pm SD, 73.03 ± 48.41 cm). The nocturnal site fidelity of *A. laetissimus* did not appear to be related to its height or to the SVL of specimens. Only six of the 60 tagged individuals were recaptured more than four times. These specimens showed an average home range of 0.35 ± 0.21 m² (0.1–0.59 m², Table 2, Fig. 2b), with an average horizontal displacement of 1.92 ± 0.82 m (0.8–3 m) relative to the nocturnal site. Most of the specimens were separated from each other by at least 5 m, but specimens A1 and A4 were very close to each other, so aggressive behavior between them could be observed. Specimen

A4 pounced and squashed specimen A1, then they began actively “wrestling.” This situation lasted about 120 seconds, until A1 fled. The “winner” male (A4) did not chase the male who left. The males did not emit vocalizations during the event.

Advertisement Call

Two types of vocalizations were recorded in a male *A. laetissimus*. The first call type corresponded to a short series of pulses like a buzz (mean \pm SD, range, N; 27 ± 5.63 pulses, 7–33 pulses, 26 calls, Fig. 3a), with a duration of 0.41 ± 0.112 s (0.111–0.805 s, 26 calls). These pulsed calls showed modulated amplitude, where the amplitude increased along the call and decreased again at the last pulse. The pulse duration was 0.009 ± 0.006 s (0.001–0.099 s, 705 pulses), emitted at a rate of 67.55 ± 9.428 pulses/s (32.298–76.167 pulses/s, 26 calls). In most of these calls, the last pulse had a longer duration. The interpulse interval duration was 0.006 ± 0.004 s (0.0001–0.097 s, 652 interpulse intervals). These calls showed an ascending modulated frequency, although in some cases the frequency decreased notably at the last pulse. The frequency range was 1,287–8,558 Hz, while the dominant frequency was $1,921.433 \pm 114.391$ Hz (1,480.95–2,155.55 Hz, 631 pulses). In addition, the pulsed call of *A. laetissimus* showed three harmonics: first at 2,640.54–4,923 Hz, second at 3,661.56–6,644 Hz, and third at 5,771.95–8,558 Hz. The second type was a short call (Fig. 3b), with a duration of 0.06 ± 0.006 s (0.05–0.07, 12 calls). The short calls showed a variable structure, either unpulsed (Fig. 3b), partially pulsed (Fig. 3c), or pulsed (Fig. 3d). The short calls showed a low dominant frequency ($1,649.59 \pm 32.715$, 1,584.2–1,705.99, 12 calls) and were produced irregularly, from a variable series, and alternated among vocalizations of

Table 1. Microhabitat selection by *Atelopus laetissimus* and χ^2 values for each substrate.

Substrate	Proportion of area	Individuals (n)	Expected frequency (N × proportion of area)	χ^2
Rocks	0.59	49	66.22	4.48
Leaf litter	0.28	28	31.19	0.33
Others	0.03	5	3.55	0.59
Ferns	0.01	3	0.75	6.81
Leaves	0.05	9	5.65	1.99
Bare floor	0.01	12	1.13	104.56
Fallen trunks	0.04	7	4.52	1.36
N	1	113	113	120.12

the first type (Fig. 3e), or within vocalizations of the first type (Fig. 3f).

Potential Distribution and Habitat Loss

The areas with higher habitat suitability for *A. laetissimus* are located mainly in the northern and northwestern sectors of the SNSM, which agrees with the occurrence localities. The model reached an AUC of 0.971 (± 0.011, Fig. 4). The explanatory variables with the highest contributions to the suitability prediction were the average temperature of the coldest trimester (Bio 11), range of annual temperature (Bio 7), elevation, and human footprint. *Atelopus laetissimus* shows a maximum of suitability at 120 mm of rainfall at the coldest trimester; for annual temperature, it shows high suitability at middle ranges, rapidly decreasing at under 12 °C. The suitability shows a Gaussian trend regarding elevation, with a maximum at 2,000–3,000 m asl. Habitat suitability of *A. laetissimus* is inversely related with human footprint (Fig. 4).

The potential distribution area is 1,740.95 km², which corresponds to a continuous area in the northwestern sec-

tor of the SNSM, and a smaller and fragmented area in the northern sector. The AOO calculated by 13 plots was 54 km², while the EOO was 1,074.47 km². The habitat loss from 2000 to 2017 was larger in the southern sector of the SNSM, but was smaller in the northern and northwestern sectors of the massif. *Atelopus laetissimus* lost 1.48% of its habitat based on the potential distribution, 1.16% of its AOO, and 2.51% of its EOO (Fig. 5). A significant increasing trend in habitat loss was detected from 2013 to 2017, where the last year showed the greatest loss of potential habitat for the species. As *A. laetissimus* shows an EOO smaller than 5,000 km² (criteria B1b[i], B1b[ii], and B1b[iii]) and an AOO smaller than 500 km² (criteria B2b[i], B2b[ii], and B2b[iii]), these data reinforce its classification in the Endangered (EN) category.

Discussion

Relative Abundance and Density

The results of these surveys showed that *Atelopus laetissimus* is an easily detectable species in the northwestern

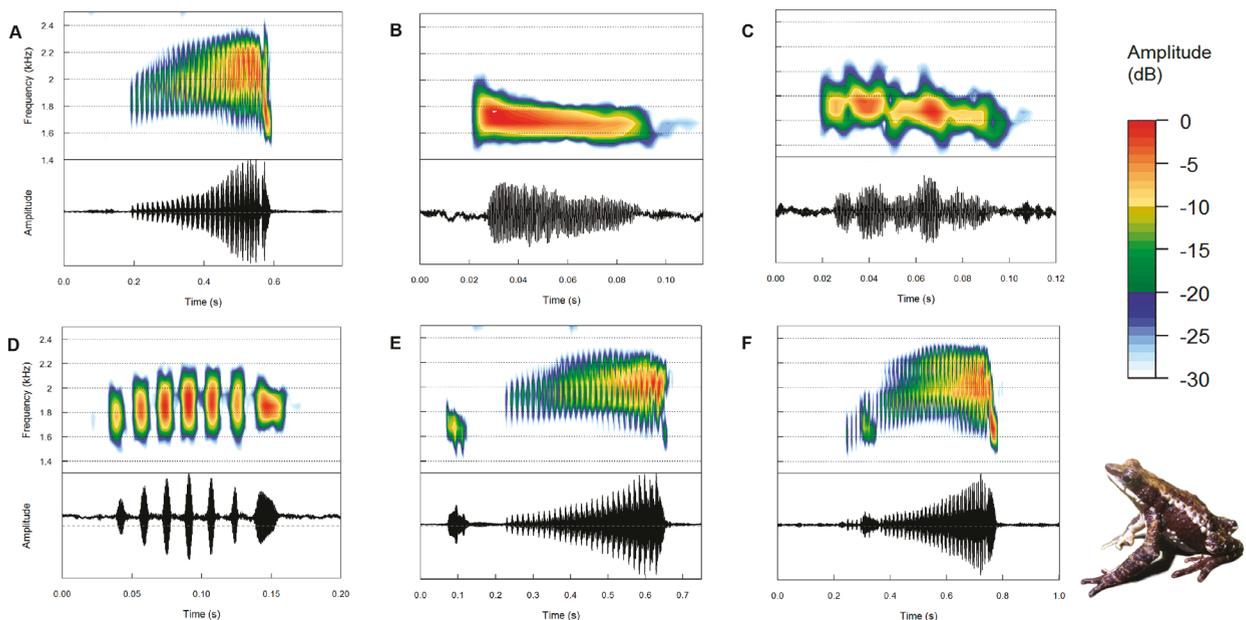


Figure 3. Acoustic repertoire of the advertisement call of *Atelopus laetissimus*. Conventional pulsed call (A), unpulsed short call (B), partially pulsed short call (C), pulsed short call (D), partially pulsed short call before pulsed call (E), and partially pulsed short call within pulsed call (F). The corresponding author will provide tables of raw data for individual specimens on request.

Table 2. Movement patterns of six *Atelopus laetissimus* individuals.

Specimen	Home range (m ²)	Recaptures (n)	Distance to nocturnal sites (m)
A4	0.11	7	2.5
A44	0.47	5	1.2
A49	0.33	8	3
A1	0.54	5	0.8
A61	0.1	10	1.8
A36	0.59	5	2.2
Mean	0.36	6.67	1.92
SE	0.21	2.07	0.82
Minimum	0.1	5	0.8
Maximum	0.59	10	3

sector of the SNSM. Several studies in this zone have reported more than 100 specimens in less than 150 h of survey effort (Granda-Rodríguez et al. 2012; Rocha-Úsuga et al. 2017; Rueda-Solano et al. 2016a). Nevertheless, at less than 2,100 m of elevation, the relative abundances recorded for the species were significantly lower (Car-

vajalino-Fernández et al. 2008, 2013; Granda-Rodríguez et al. 2012). In the model performed in this study, the most suitable habitat was in the altitudinal range between 2,000 and 3,000 m. It is possible that changes in the physical and structural characteristics of the habitat at lower altitudes contribute to the decrease in either the

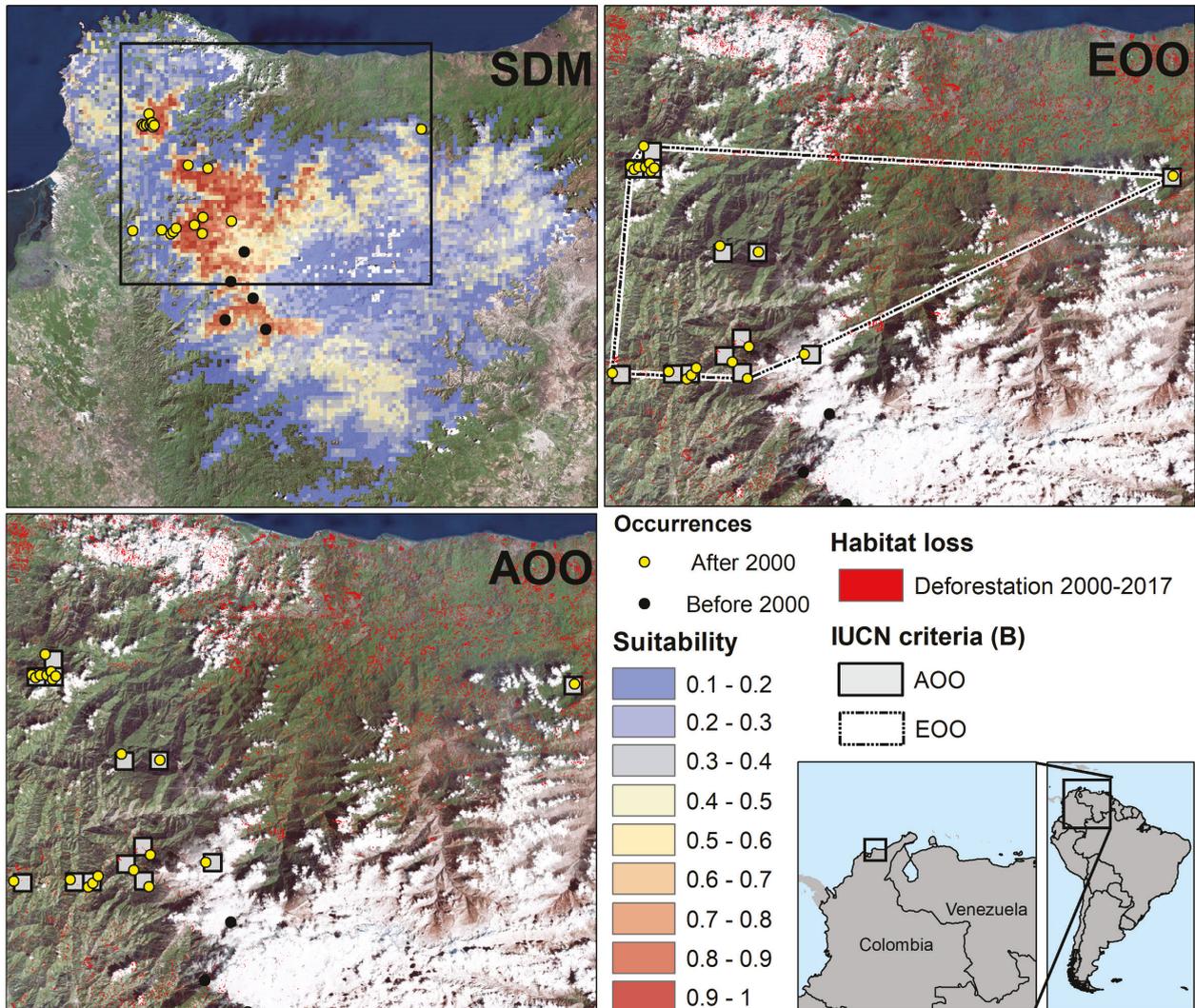


Fig. 4. Habitat suitability estimate (upper left panel), minimum convex polygon of extent of occurrence (EEO, upper right panel), and area of occupation (AOO, lower left panel) of *Atelopus laetissimus*. The total deforested area for the analyzed period and species occurrence locations are provided in red.

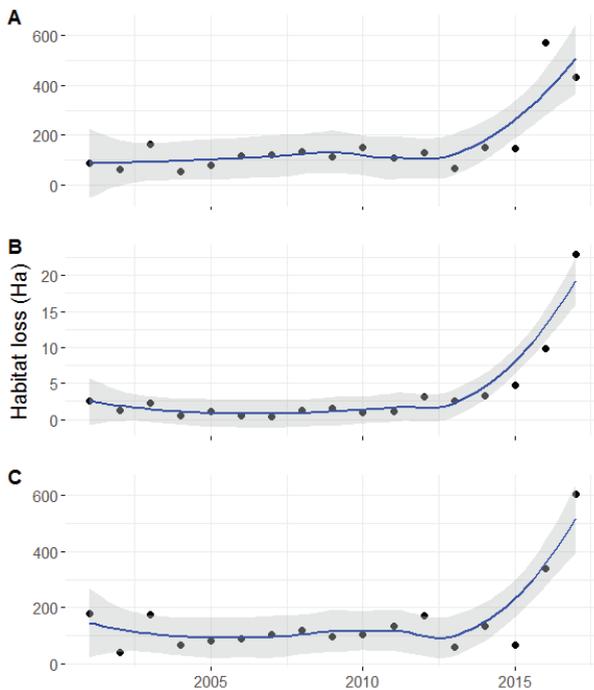


Fig. 5. Estimated annual habitat loss for *Atelopus laetissimus* in the last decade in the potential distribution (A), area of occurrence (AOO, B), and extent of occurrence (EOO, C).

occupation or detection of *A. laetissimus*.

Populations of *A. laetissimus* appear to be highly disproportionate in males. The first publication that mentioned this observation (Rocha-Úsuga et al. 2017) did not describe how the males were differentiated from the females. A sexual proportion that is biased to males can be related to differences in the mortality rate by sex. However, it is also possible that some individuals categorized as males corresponded to small females, especially since the sexuality was assumed based on size (e.g., Gómez-Hoyos et al. 2017). This is an important detail that has been addressed only rarely in population studies of *Atelopus* (Gómez-Hoyos et al. 2014; González-Maya et al. 2018), but it is important due to the conservation interest in the species of this genus.

Regarding population density, there is no previously published information for *A. laetissimus*. Since this study provides the first estimation of this population attribute, it is not possible to estimate variations among different populations of this species. However, comparing the population density of *A. laetissimus* obtained here with lowland species, the densities obtained with distance-based models for *Atelopus spurrelli* Boulenger, 1914 and *Atelopus elegans* (Boulenger, 1882) were slightly lower (0.03 and 0.01 ind/m², respectively, Gómez-Hoyos et al. 2014, 2017). On the other hand, the observed density of *Atelopus hoogmoedi* (0.47 ind/m², Luger et al. 2009) was higher than the mean density of *A. laetissimus* found in this study.

Some species, such as *Atelopus ignescens* (Cornalia, 1849) and *A. varius*, had dense populations before severe population declines, with reports of 0.025–0.75 ind/m²

and 0.065–0.755 ind/m², respectively (Ron et al. 2003; La Marca et al. 2005). *Atelopus cruciger* is one of the few species with information on population density after a decline, which was 0.005–0.057 ind/m² (Lampo et al. 2012). Populations of *A. cruciger* had a high prevalence of chytrid fungus, but remained stable because of the high recruitment rate of healthy individuals in the population (Lampo et al. 2017).

Habitat Selection and Movement Patterns

The differential use of several substrates by *A. laetissimus* has been previously reported, where leaf-litter and rocks were mainly used (Granda-Rodríguez et al. 2008b). The data reported here reinforce these findings, suggesting that this species selects the most available substrates. The structural complexity of the riparian forest occupied by *A. laetissimus* can influence its differential pattern of habitat use, as has been described for some anurans from southeastern Asia (Gillespie et al. 2004). Habitat selection allows organisms to avoid adverse environmental conditions, like extremely low temperatures (Navas 1996). Recently, *A. laetissimus* has been described as a thermoconforming species, showing a direct relationship between the temperature of substrate and the activity temperature (Rueda-Solano et al. 2016b). Therefore, the differential selection of substrates could be associated with some thermoregulatory strategy. The results of these surveys show that *A. laetissimus* exhibits relatively high nocturnal site fidelity, although the recapture rate was decreasing gradually, probably due to the manipulation of the specimens in each recapture. Recently, Rueda-Solano and Warketin (2016) reported that *A. laetissimus* use the nocturnal sites for predatory activities, guided by the vibration of the substrate (leaves and ferns), suggesting that the use of a nocturnal perch is not exclusively for rest.

Regarding the home range of *Atelopus*, some species such as *A. carbonerensis* and *A. hoogmoedi* possess a mean home range much larger than *A. laetissimus* (41 m² and 38.1 ± 17.7 m², respectively; Dole and Durant 1974; Luger et al. 2009), which could be the result of seasonal variation. The results here indicate that individuals of *A. laetissimus* can remain, at least for a short period, near to the stream defending their territories.

Advertisement Call

The pulsed call is the most commonly known vocalization in harlequin toads, being present in at least 17 species (Asquith and Altig 1989; Cocroft et al. 1990; Ibáñez et al. 1995; Jaslow 1979; Lescure 1981; Lötters et al. 1999, 2002; this study). The pulsed call of *A. laetissimus* consists of a short series of pulses (7–33 pulses) emitted rapidly, which is remarkably different from the pulsed calls of *A. barbotini* Lescure, 1981 (41–53 pulses per call, 30.35–33.97 pulses/s, 2,000–3,000 Hz; Lescure 1981),

A. flavescens Duméril and Bibron, 1841 (45–58 pulses per call, 29.76–34.78 pulses/s, 2,500–3,000 Hz; Lescure 1981), *A. franciscus* Lescure, 1974 (31–39 pulses per call, 22.97–23.78 pulses/s, 2,300–3,000 Hz; Lescure 1981), *A. hoogmoedi* (40–42 pulses per call, 33.61–35 pulses/s, 2,300–3,000 Hz; Lescure 1981), *A. spumarius* Cope, 1871 (20–37 pulses per call, 38.55–45.96 pulses/s, 3,600–4,400 Hz; Asquith and Altig 1987; Lescure 1981) or *A. reticulatus* Lötters, Haas, Schick, and Böhme, 2002 (27–32 pulses per call, 75–76 pulses/s, 3,282 Hz; Lötters et al. 2002) by having a higher number of pulses replicated more quickly at a lower dominant frequency. Likewise, it differs from the pulsed call of *A. zeteki* Dunn, 1933 (42–52 pulses per call, 115–146 pulses/s, 1,381–1,510 Hz; Cocroft et al. 1990), by having fewer pulses replicated more quickly at a higher dominant frequency.

Other species such as *A. cruciger* (84–99 pulses per call, 2,400–2,870 Hz; Cocroft et al. 1990), *A. limosus* Ibáñez, Jaramillo, and Solís, 1995 (31–45 pulses per call, 146.4–156.3 pulses/s, 2,600–2,800 Hz; Ibáñez et al. 1995), and *A. varius* (43–56 pulses per call, 119–123 pulses/s, 1,750–1,965 Hz; Cocroft et al. 1990) exhibit pulsed calls with higher numbers of pulses emitted at considerably faster rates than *A. laetissimus*. On the other hand, the structure of pulsed calls of *A. laetissimus* is very similar to the calls of *A. chiriquiensis* Shreve, 1936 (18–33 pulses per call, 59.5–82.3 pulses/s, 2,000–2,700 Hz, Jaslow 1979), *A. exiguus* (Boettger, 1892) [19–21 pulses per call, 2,150–2,700 Hz, Coloma et al. 2000], *A. minutulus* Ruiz-Carranza, Hernández-Camacho, and Ardila-Robayo, 1988, (14–21 pulses per call, 59.5–67.9 pulses/s, 2,700–3,150 Hz, Cocroft et al. 1990), *A. nicefori* Rivero, 1963 (21–24 pulses per call, 53.9–65.7 pulses/s, 2,630–2,871 Hz, Cocroft et al. 1990), *A. senex* Taylor, 1952 (30–34 pulses per call, Cocroft et al. 1990), and *A. tricolor* Boulenger, 1902 (16–19 pulses per call, 2,970–3,450 Hz, Lötters et al. 1999). Pulsed calls of these species also consist of shorter calls emitted at faster rates, but with higher frequencies than *A. laetissimus* in all cases.

The second type of vocalization (short calls) has been described for 12 species (Carvajalino-Fernández et al. 2017; Ibáñez et al. 1995; Jaslow 1979; Lötters et al. 1999, 2002; this study). This call is the more variable of the two in terms of structure, by the definitions proposed by Cocroft et al. (1990), which includes several vocalizations emitted in different social contexts. Both pulsed and short calls of *A. laetissimus* corresponded to the advertisement call context (*sensu* Wells 2007). This is probably the same situation for *A. varius*, whose short calls were obtained in the field, without apparent interaction among individuals (Cocroft et al. 1990). Short calls recorded in captivity for *A. cruciger* and *A. spumarius* also can be related to advertisement calls. This call is also reported in male-female interactions, in an amplexant couple of *A. zeteki*. Wells (2007) described this type of interaction as courtship calls. Encounter calls were re-

corded in a male-male aggressive interaction in *A. chiriquiensis* (Jaslow 1979). Nevertheless, most of the short calls described were release calls obtained at the moment of specimen manipulation (*A. chiriquiensis*, Jaslow 1979; *A. limosus*, Ibáñez et al. 1995; *A. nahumae*, Carvajalino-Fernández et al. 2017; *A. peruensis* and *A. tricolor*, Lötters et al. 1999). In addition, short calls of *A. tricolor* cannot be included in any of these categories, since the context of the recording was not described clearly (Lötters et al. 2002). Previously, the role of vocalizations in the communication of the genus *Atelopus* has been distorted by the absence of several elements of the auditory apparatus (McDiarmid 1971) and the conspicuousness of its visual communication (Jaslow 1979; Crump 1988). Nevertheless, the complexity and diversity of vocalizations described and reviewed here suggests that their roles in communication may be underestimated.

Potential Distribution and Habitat Loss

According to IUCN SSC Amphibian Specialist Group (2014), *A. laetissimus* is a species restricted to the moist low montane forest life zone, at altitudes between 1,500–2,880 and an area of 797 km². In this study, localities are reported between 900 and 2,880 m asl and an EOO of 1,074 km², higher than that reported by IUCN. Despite this increase in the distribution of the species which could be associated with new samplings, we recommend its status of Endangered (EN) be maintained. The niche model of *A. laetissimus* suggests that the potential distribution is restricted to forests in humid zones at the northwestern and northern flanks of the SNSM. The results show that the AOO of the species may not exceed 52 km². The analysis by the model suggested the environmental layers that most influenced the distribution of the species are the average temperature of the coldest quarter, the elevation, and the human footprint. In the case of amphibians, important influences of the climate on their distribution have been described, therefore, factors such as climate change could significantly alter populations of *A. laetissimus*. Among the potential changes are alterations of the precipitation and temperature regimes, resulting in an increase in the annual temperature ranges and thus affecting habitat quality and the availability of specific resources for *A. laetissimus* (Zhang and Yan 2014). On the other hand, human influence generates a very marked negative effect on this type of species in terms of degradation and loss of habitat (Grant et al. 2016).

The model performed here represents the first empirical estimation of the distribution of this species based on distribution modeling, and it also uses the largest compilation of localities. Additionally, recent samples in areas with high suitability predicted by the model support the reliability of the prediction (Rueda and Warkentin 2016). In any case, the predictions of these models should be interpreted with caution and they should be considered as a first approximation to the real distribution of the species,

helping to focus the sampling efforts in order to further adjust and refine the predictions of the distribution of this species in the future.

Although the habitat loss identified does not represent a high percentage in relation to the total habitat of the species, the trends showed a significant increase in loss in recent years (Ribeiro et al. 2018). However, considering that Hansen et al. (2013) does not differentiate between types of vegetation (natural and exotic plantations), the results could vary. This is important since *A. laetissimus* has scarcely been associated with exotic plantations of *Pinus* spp., or in streams associated with this type of coverage in the locality of San Lorenzo (Granda-Rodríguez et al. 2012). In addition, it is also not known how coffee and avocado plantations can affect this species, since in the middle- and upper-part of the distribution large areas of these crops are present (Fundación Pro-Sierra Nevada de Santa Marta 2000). It is necessary to carry out studies at smaller scales in the distribution area of *A. laetissimus*, allowing the identification of the landscape dynamics of forest patch isolations, connectivity, and the different elements that may have negative consequences for this species (Palmeirim et al. 2018). In this sense, remaining remnants of forest become important for the maintenance of *Atelopus laetissimus*, as well as other endemic species of the SNSM. However, in the southern sector of the SNSM there is high fragmentation and habitat degradation; and this site is (was?) inhabited by *A. arsyecue* and *A. walker*, species that have not been seen in the field for more than 20 years, providing possible evidence for the risk of disappearance of this type of toad.

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