

Potential distribution of *Agkistrodon bilineatus* (Squamata: Viperidae) and first records in Central Mexico

Distribución potencial de *Agkistrodon bilineatus* (Squamata: Viperidae) y primeros registros en el Centro de México

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- Received: 06/May/2022
- Accepted: 31/Oct/2023
- Online Publishing: 27/Jan/2024

Citation: Monroy-Vilchis O., González-Desales G.A., Balbuena-Serrano Á., Robles-Rodríguez J. and M.M. Zarco-González. 2024. Potential distribution of *Agkistrodon bilineatus* (Squamata: Viperidae) and first records in Central Mexico. Caldasia 46(2):361-370. doi: <https://doi.org/10.15446/caldasia.v46n2.101348>

ABSTRACT

Agkistrodon bilineatus is a viperid snake with a broad geographic range in Mexico and Central America. Because this species has potent venom and is categorized as Near Threatened on the Red List of Threatened Species of the International Union for Conservation of Nature, understanding its habitat associations and distribution will contribute to both human health and conservation decisions internationally. Based on a comprehensive review of literature and museum records, in addition to our fieldwork, we built the first distribution model for *A. bilineatus*. Our presence-only consensus model exclusively incorporated contemporary records for the species (from 1980 to 2022, n = 36). The variables that contributed most strongly to the consensus model were: (a) distance to deciduous broadleaf forest, (b) human population density, (c) elevation, (d) precipitation of the wettest quarter, and (e) percentage of herbaceous cover. Of the high-probability distribution area for *A. bilineatus* predicted by the model, 72.9 % is in Mexico, 12.7 % in Honduras, 9.1 % in Guatemala and 5.2 % in El Salvador. Of the *A. bilineatus* historical records (those pre-1980), 92.3 % (36/39) were within the high-probability area predicted by the model, indicating either strong model performance or overprediction. Included in our modelling effort were the first two records for *A. bilineatus* from the State of Mexico, which increases the number of reptile species to 102 in this State. We briefly discuss the implications of our work for human medical treatment and improved conservation assessments for this species, which experiences many environmental threats.

Keywords: Cantil, conservation, snakebite, species distribution models, State of Mexico.

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RESUMEN

Agkistrodon bilineatus tiene amplio rango de distribución en México y Centroamérica. Debido a que esta especie es venenosa y está clasificada como Casi Amenazada en la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza, analizar la distribución de su hábitat contribuirá a la salud humana y a su conservación a nivel internacional. Basándonos en una revisión exhaustiva de la literatura, registros de museos y trabajo de campo, construimos el primer modelo de distribución para *A. bilineatus*. Nuestro modelo de solo presencia incorporó exclusivamente registros contemporáneos de la especie (1980 a 2022, n = 36). Las variables que contribuyeron mayormente al modelo fueron: (a) distancia al bosque caducifolio latifoliado, (b) densidad de población humana, (c) elevación, (d) precipitación del trimestre más húmedo y (e) porcentaje de cubertura herbácea. Del área de alta probabilidad de presencia de *A. bilineatus*, el 72,9 % se encuentra en México, 12,7 % en Honduras, 9,1 % en Guatemala y 5,2 % en El Salvador. De los registros históricos de *A. bilineatus* (anteriores a 1980), el 92,3 % (36/39) se ubicaron dentro del área de alta probabilidad predicha por el modelo, lo que indica un desempeño adecuado del modelo o una sobrepredicción. En los registros de *A. bilineatus* utilizados para modelar se incluyeron los dos primeros para el Estado de México, lo que aumenta el número de especies de reptiles a 102. Discutimos brevemente las implicaciones de nuestro trabajo para el tratamiento médico humano y la conservación de especie, que experimenta muchas amenazas ambientales.

Palabras clave: Cantil, conservación, Estado de México, modelos de distribución de especies, mordedura de serpiente.

INTRODUCTION

Effective conservation of species usually requires basic information about their distributions (Franklin 2009, Lewis et al. 2017). Species distribution models (SDM) have been widely used to predict geographic distributions at different scales, and often provide useful results for vertebrate species with uncertain distributions (Peterson et al. 2008, Monroy-Vilchis et al. 2014). Reports of new presence records are also important, because they can better delimit species distributions and their associated ecological patterns (Sánchez-González 2013).

Agkistrodon bilineatus (Günther, 1863) is a snake species for which a SDM and new presence records are likely to produce meaningful advances in scientific knowledge. The species ranges widely along the Pacific Coast of Mexico and Central America, from southwestern Chihuahua and southern Sonora, Mexico, into Guatemala, western Honduras, and El Salvador (Gloyd and Conant 1990, Campbell and Lamar 2004, Lemos-Espinal and Smith 2007, Babb and Dugan 2008, García-Grajales and Buenrostro-Silva 2011, McCranie 2011, Porras et al. 2013). It has also been predicted to occur in the State of Mexico, but this remains

unconfirmed (Lemos-Espinal and Smith 2020). *A. bilineatus* occupies lowland tropical deciduous forest, thorn scrub, and grassland, often in or adjacent to riparian areas (Babb and Dugan 2008, Canseco-Márquez and Nolasco-Vélez 2008, García-Grajales and Buenrostro-Silva 2011). As a member of the family Viperidae, *A. bilineatus* is of substantial medical importance due to its venomous bite, which has been reported to cause serious physical harm including death in humans (Campbell and Frost 2004). The species is categorized as Near Threatened on the Red List of Threatened Species of the International Union for Conservation of Nature, based on an inferred decreasing population trend of close to 30 % over the last fifteen–30 years due to ongoing human activities (Lee and Hammerson 2007, Porras et al. 2013). No published SDM exists for the species, and many aspects of its geographic distribution remain uncertain. The objectives of this study were to: (1) build an SDM to predict the current distribution of *A. bilineatus*, (2) use this SDM to identify the most important habitat features associated with the species' presence, and (3) report the first records for the species in Central Mexico.

MATERIALS AND METHODS

The study area included six biogeographical provinces in Mexico (Sonoran, Pacific Coast, Transverse Neovolcanic Belt, Balsas Depression, Sierra Madre del Sur and Soco-nusco), and three countries in Central America (El Salvador, Guatemala, and Honduras), with a total extent of 834 873 km². We gathered *A. bilineatus* presence records from three sources: (1) scientific literature recovered from querying the ISI Web of Knowledge with search keywords “*Agkistrodon bilineatus*,” “distribution,” “new records,” and “geographic distribution;” (2) the biodiversity data aggregator Global Biodiversity Information Facility (GBIF 2022); and (3) our own field work in Central Mexico.

Ideally, presence records used to calibrate a distribution model should correspond closely to the timeframe in which environmental data incorporated into the modelling effort was generated (Phillips et al. 2006, Zurell and Engler 2019). The environmental variables that we included in our model were based on data generated from 1996–2022, approximately. We therefore filtered our raw database of *A. bilineatus* presence records to include only those records from 1980–2022, selecting 1980 as a threshold due to the rapid regional land use change that occurred from this date (García-Roselló et al. 2014, Espinosa-Martínez et al. 2020). This filtering was intended to exclude presence records representing environmental characteristics that probably no longer exist and which could negatively affect the model’s predictive accuracy.

In addition to this temporal filter, we excluded *A. bilineatus* records that: (1) were obscured on iNaturalist and hence the precise GPS coordinates were unavailable because of the perceived risk of that data being publicly available (Contreras-Díaz et al. 2023); (2) were misidentified and correspond to congeners (e.g., *Agkistrodon russeolus*); and (3) lacked coordinates and had locality descriptors too imprecise for georeferencing (Wieczorek et al. 2004).

We further filtered the remaining records so that only a single presence record existed per pixel (0.25 km²). From this final filtered database, we used the Morans I test to determine the spatial autocorrelation between the records and to verify their distribution pattern. The purpose of this test was to avoid the clustering of the records, because an aggregate distribution pattern may reflect bias due to uneven sampling effort.

We selected the variables used to calibrate of the models according to the ecological requirements of *A. bilineatus* (García-Grajales and Buenrostro-Silva 2011, Porras et al. 2013). We included two climatic variables: mean temperature of the wettest quarter and precipitation of the driest quarter (Fick and Hijmans 2017); three topographic variables: elevation, slope (WorldClim 2022), and distance to water sources (HydroSHEDS 2007); five vegetation variables, three of which were processed as distance maps: distance to deciduous broadleaf forest, distance to evergreen broadleaf forest, distance to herbaceous wetland, percentage of tree cover and percentage of herbaceous cover (Buchhorn et al. 2020); and two anthropic variables: distance to crops (Buchhorn et al. 2020) and human population density of the year 2010 (CIESIN 2005).

Pixel size selection is a key factor in SDM studies. Decreasing grain (pixel) size enhances landscape details, while increasing pixel size can obscure those details. In some cases, using a 1 km² pixel size may be too coarse for studies at small spatial scales (Manzoor et al. 2018). A major limitation in selecting pixel size is the original scale with which the variables were created, and hence we used the finest resolution that the scale allowed (increasing or decreasing the original resolution). We processed the variables in raster format and resampled them to a resolution of 500 m², using ARCGIS 10.4.1 software.

To avoid autocorrelation and collinearity problems, we performed a Pearson correlation test and VIF test using the package “usdm” in R software (Naimi et al. 2014, R Core Team 2020) for all variables (Dormann et al. 2013, Brun et al. 2020). This approach (Pearson + VIF) allows calculation of both the correlation coefficients between variables and the identification of strongly correlated pairs (Dormann et al. 2013).

Because controversy exists about which algorithm is the most accurate for SDMs (Elith et al. 2006, Roura-Pascual et al. 2009), it is often advisable to apply more than one algorithm and generate a consensus model (Marmion et al. 2009a). Using multiple modelling methods to identify congruent predictive areas (Franklin 2009, Marmion et al. 2009a, Roura-Pascual et al. 2009) also incorporates modelling uncertainties and can thus produce more reliable outputs (Marmion et al. 2009a). Therefore, we decided to use several algorithms that have been successfully applied in vertebrate distribution modelling efforts

to generate a consensus model (Marmion *et al.* 2009b, Roura-Pascual *et al.* 2009).

We applied four algorithms. First, the Ecological Niche Factor Analysis (ENFA) in BIOMAPPER 4.0., which compares the distributions of the ecogeographical variables (EGV) between the presence dataset (species distribution) and the whole area (global distribution). Like the Principal Component Analysis, ENFA summarizes many EGV into a few uncorrelated factors that retain most of the information (Hirzel 2008, Hirzel and Le Lay 2008). In ENFA, we used three factors that explain 91 % of the model. Second, we applied Maxent 3.4.2, which compares the locations where a species has been found to all the environments that are available in the study region. It defines these available environments by sampling many points throughout the study area, which are called background points. For Maxent we used the “auto features” configuration, 10 000 background points and a complementary log-log (clog-log) transform to produce an estimate of the probability of occurrence (Phillips *et al.* 2006, 2017). Third, we applied the Genetic Algorithm for Rule Set Production (GARP), which describes environmental conditions under which the species should be able to maintain populations. For input, GARP uses a set of point localities where the species is known to occur and a set of geographic layers representing the environmental parameters that might limit the species’ capabilities to survive (Stockwell 1999). For GARP, we used the “rule types” setting, specified the number of runs as 1 000 and the “convergence limit” as 0.001 to train more fit models. Fourth, we applied Support Vector Machines (SVM) in the OPENMODELLER 1.1.0 software (Sutton *et al.* 2007), which are a set of related supervised learning methods that belong to a family of generalized linear classifiers. A special property of SVM is that they simultaneously minimize the empirical classification error and maximize the geometric margin, and hence they are also known as maximum margin classifiers (Schölkopf *et al.* 2000). We specified the creation of 10 000 background points.

We evaluated the models in IDRISI Selva 17.0 (Clark Labs 2012) through the Area Under the Curve (AUC-ROC; Hernández-Urcera *et al.* 2021, Nguyen and Leung 2022). We carried out two evaluations: one with 75 % of the records used to calibrate the model (internal AUC- training AUC) and the second with 25 % of the records (external AUC- testing AUC), with the records being randomly divided into these two subsets (Guisan and Zimmermann

2000, Zarco-González *et al.* 2013). We assumed that this sample of the original data contains independent observations that can be used in a statistical test (Araújo *et al.* 2005). We used the models that presented external AUC > 0.7 to generate a consensus model (Marmion *et al.* 2009a, Roura-Pascual *et al.* 2009) applying the weighted average. We used the weighted average formula in the IDRISI calculator to get the final consensus model, because this method has the highest predictive performance of all the consensus methods (Marmion *et al.* 2009a, b, Zarco-González *et al.* 2013). We evaluated the final consensus model with AUC and the transformation of AUC into partial-ROC graphics (Peterson *et al.* 2008). We calculated partial-ROC in the software NICHE TOOLBOX (Osorio-Olvera *et al.* 2016). The parameters we used were proportion of omission = 0.05, number of iterations for the bootstrap = 500 and random points percentage = 30 %. We divided the output of the consensus model, which originally had probability values from zero to one, into two categories (Taucare-Ríos *et al.* 2016): low probability (pixels with values from 0–0.5) and high probability (pixels with values > 0.5). Our reasoning in selecting this criterion is that a value greater than 0.5 implies selecting areas where the probability is greater than a random event. By transforming the continuum of values into a binary map, areas with a high probability of the presence of the species can be specifically identified (Schmidt *et al.* 2020). This approach facilitates the application of management and conservation measures, which is particularly important for species of medical importance and/or which are in danger of extinction.

To analyze the performance of the model in identifying historical presence records, we calculated the percentage of records before 1980 that coincided with areas of high probability of presence and those that fell outside the prediction. We used the Maxent algorithm to report the contribution percentage of each variable to the model and the interval of each one in which the probability of the presence of the species increases through the response curves.

To document new records of *A. bilineatus* in Central Mexico, we deposited digital photos in the Colección de Foto-colectas Biológicas, Departamento de Zoología del Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM-CFB). We identified the snakes based on morphological characteristics visible in the photographs as given by Gloyd and Conant (1990) and Porras *et al.* (2013).

We only photographed and did not manipulate the snakes, and thus no government permits were required for the work reported herein.

RESULTS

We gathered a total of 538 records of *A. bilineatus*, with the oldest originating from the year 1828. Our filtering criteria led to the exclusion of 502 of those records: 375 reported before 1980, 98 from iNaturalist, eleven duplicates, nine that represented other *Agkistrodon* species, six that could not be accurately georeferenced, two that presented erroneous coordinates, and one that lacked a catalog number. After this filtering, we used the remaining 36 records to model the potential distribution of *A. bilineatus* (Appendix I). According to the Moran's I test, after filtering the records, we found a dispersion pattern with a tendency to randomness. This implies that no spatial relationship exists between the records, or that the grouping effect of the records due to sampling bias was eliminated by our filtering criteria.

According to the Pearson correlation test and the VIF test, there were no correlation or collinearity problems between the variables, so we included the twelve variables proposed for the calibration of the models. We used all four algorithms to generate the consensus model: GARP (AUC = 0.855), Support Vector Machines (AUC = 0.775), Maxent (AUC = 0.985), and ENFA (AUC = 0.785). The consensus model presented an AUC-ROC value of 0.945 and the partial-ROC bootstrap test showed significant ratio values of empirical AUC over null expectations (ratio = 1.881; P = 0.001). Of the historical (pre-1980) records for *A. bilineatus* that we recovered, 39 had coordinates and

could be compared to areas of high probability of presence (Appendix II). Of these historical records, 92.3 % (n = 36) fell within the high-probability area of the modelled distribution of *A. bilineatus*.

The variables with the highest contribution to the model, according to Maxent, were (a) distance to deciduous broadleaf forest, (b) human population density, (c) elevation, (d) precipitation of the wettest quarter, and (e) percentage of herbaceous cover (Table 1). According to the consensus model, the area of greatest probability of presence of the species covers 191 408 km² (22.9 % of the study zone). In Mexico, most of the high-probability area lies in the Pacific Coast and Balsas Depression biogeographic provinces (Fig. 1). Of the entire high-probability area identified by the model, 72.9 % is located in Mexican territory, 12.7 % in Honduras, 9.1 % in Guatemala, and 5.2 % in El Salvador (Fig. 1); the remaining 0.1 % is due to rounding error.

No previous records exist for *A. bilineatus* from the State of Mexico (Casas-Andreu and Aguilar-Miguel 2005, Aguilar-Miguel and Casas-Andreu 2009), so our two photo-based records from this State (Fig. 2) represent an extension of its verified distribution. The first *A. bilineatus* (IBUNAM-CFB-47228) was found on 18 March 2014 between the towns of Ancón de la Presa and Peña del Órgano, Municipality of Tlatlaya (18°26'8" North, 100°13'51" West, 445 meters above sea level [masl]). This individual was found in an ecotone of tropical deciduous forest and oak forest. The second *A. bilineatus* (IBUNAM-CFB-47229) was found on 27 May 2014 in Palmer Chico, Municipality of Amatepec (18°43'55" North, 100°23'6" West, 685 masl). This individual was found in

Table 1. Details regarding variables used in Maxent modelling of the distribution of *Agkistrodon bilineatus*: percentage of contribution to the model, range within the area of high-probability species occurrence, range within the entire study zone, and influence on the probability of presence.

Variable	Contribution percentage	Highest probability range	Range in the study zone	Influence
Distance to deciduous broadleaf forest	24.8	0–25 km	0–500 km	Negative
Human population density	17.7	0–100 Inhabitants/km ²	0–10 000 Inhabitants/km ²	Negative
Altitude	14.2	0–1 100 masl	0–5 610 masl	Negative
Precipitation of the wettest quarter	13.8	500–2 000	0–2 000 mm	Positive
Percentage of herbaceous cover	8.2	50–100 %	0–100 %	Positive

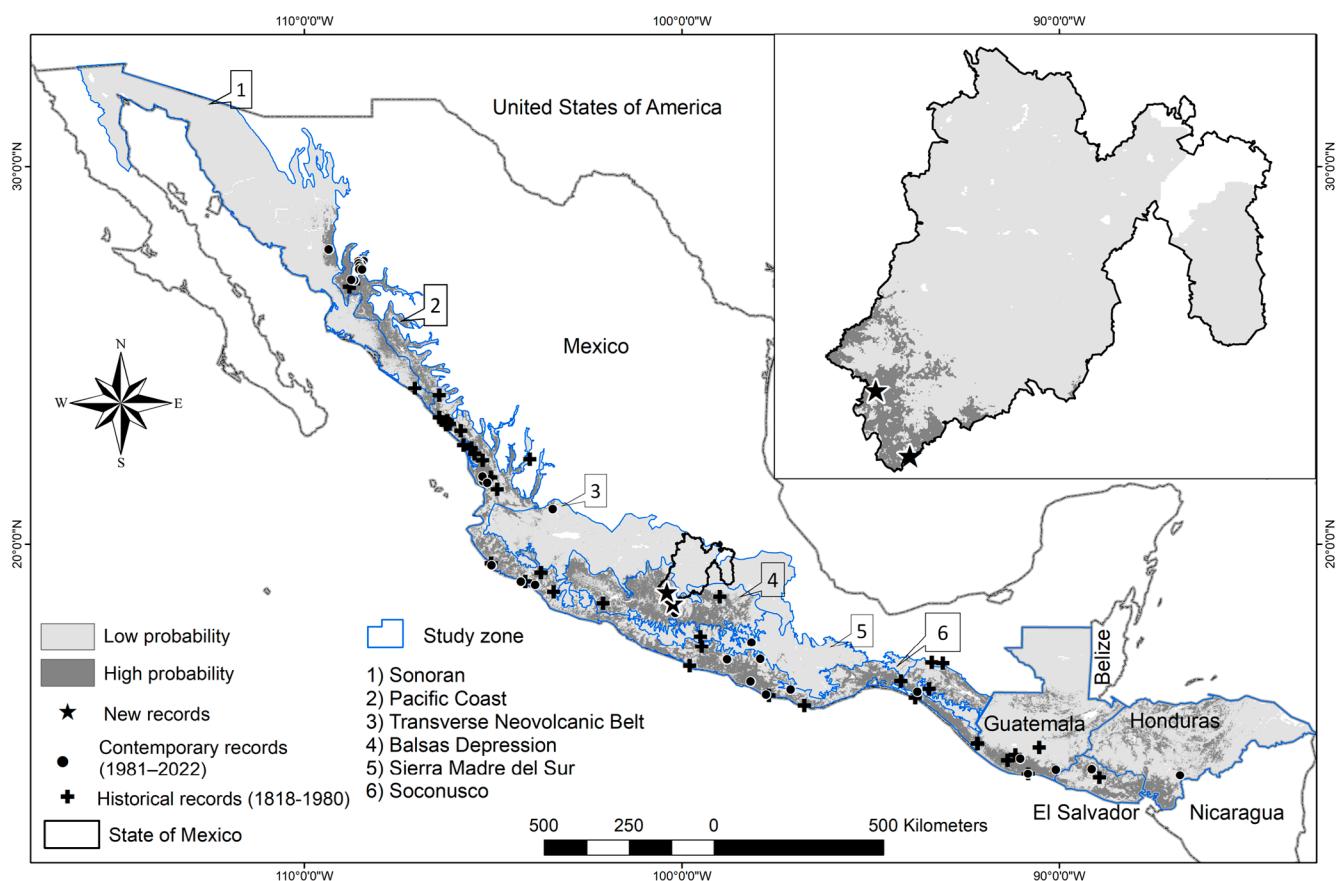


Figure 1. Potential distribution of *A. bilineatus* based on the consensus species distribution model, showing low probability (pale gray) and high probability (dark gray) predicted areas. Blue polygons indicate biogeographic provinces. Inset map provides better resolution of the State of Mexico and our new records therein.

an area of grasslands and croplands, where it was killed after it envenomated a person.

DISCUSSION

This is the first study to explore the potential distribution of *A. bilineatus*. The variables identified by Maxent showed that the species' distribution is most strongly associated with areas close to deciduous broadleaf forest, low elevation areas, and areas with high percentage of herbaceous cover. These variables coincide with habitat characteristics where the species has often been reported (Babb and Dugan 2008, Canseco-Márquez and Nolasco-Vélez 2008, García-Grajales and Buenrostro-Silva 2011). The Maxent model also indicated that human population density was negatively associated with the probability of *A. bilineatus* presence, consistent with Lee and Hammerson (2007).

This study also incorporates the first-ever records for *A. bilineatus* in Central Mexico, representing a 64 km northwest range extension for the species. The nearest previous record was reported in 2007 from Cañada El Naranjo, Municipality of Arcelia in the State of Guerrero (Museo de Zoología “Alfonso L. Herrera” de la Facultad de Ciencias, Universidad Nacional Autónoma de México [MZFC-HE 23953]; Appendix 1). The confirmed presence of *A. bilineatus* in the State of Mexico increases the number of reptile species to 102 (Lemos-Espinal and Smith 2020).

Records from scientific collections provide valuable information on the historical distribution of species. However, historical records are often linked to outdated taxonomies or have incorrect/imprecise locality data (Anderson 2012). Community science platforms like iNaturalist can also provide large numbers of important records, but the geospatial location of these records is often intentionally obscured and hence not easily unattainable by scientists



Figure 2. New records of *Agkistrodon bilineatus* from the State of Mexico, Mexico. (a) Municipality of Tlatlaya (IBUNAM-CFB-47228); (b) Municipality of Amatepec (IBUNAM-CFB-47229). Photos: Jesús Robles-Rodríguez.

(Contreras-Díaz *et al.* 2023). Species occurrence datasets must therefore be carefully vetted prior to inclusion in modelling efforts, as showcased in our study methodology.

Changing environmental conditions also warrant consideration in efforts to build SDM. Species occurrence records with low spatial resolution may cause false results if included in high-resolution SDM, since the environmental conditions at the recording sites might differ from the real ones (Gueta and Carmel 2016, Gábor *et al.* 2023). A similar situation may occur with historical records since the original conditions might differ from the current ones. Therefore, it is often advisable to maintain temporal congruence between the variables and presence records, when possible (Zurell and Engler 2019). In this study, we used contemporary records of *A. bilineatus* (post-1980) to build a consensus model of high-probability distribution of the species, and then we tested the performance of that consensus model by evaluating the proportion of historical records covered by the model's prediction. We found that the predicted high-probability distribution area of

the model contained 92.3 % of the historical records. This high predictive accuracy suggests excellent model performance, but we did not test for overprediction and hence cannot rule out this alternative explanation.

All species in the genus *Agkistrodon* are threatened throughout most of their range due to alteration of deciduous broadleaf forest habitat for agriculture, pasture, and other human activities (Gloyd and Conant 1990, Conant 1992, Greene and Campbell 1993). The deciduous broadleaf forest is, in general, a highly imperiled habitat. From 1990–2005, Latin America lost 69 million hectares of this forest, which is equivalent to 7 % of the forest cover of the entire region (Hansen *et al.* 2013). The area deforested between 2000 and 2012 in Mexico was 23 862 km², in Honduras 4 860 km², in Guatemala 8 863 km², and El Salvador 567 km² (Hansen *et al.* 2013). The implementation of conservation strategies directed toward preserving this forest type is vitally important, not only for *A. bilineatus* but for many other species as well.

Human population density is also directly correlated with habitat loss and fragmentation. This study echoed this reality, with the variable of human population density being negatively correlated with the modeled high-probability presence of *A. bilineatus*. Conversely, in rural areas with low human population density and farmlands, the risk of snakebite is high, and snakes are at risk of intentional killing by humans (Harrison *et al.* 2009, Alirol *et al.* 2010, Chippaux 2012, Yañez-Arenas *et al.* 2014).

Our fieldwork results underscore this potential for conflict between rural human communities and *A. bilineatus*. The new record from the community of Palmar Chico, Municipality of Amatepec (within a rural agricultural farm) involved an *A. bilineatus* that was killed after biting a person. We received reports of four other *A. bilineatus* that were killed by people in this area due to fear of an accident, even though none of these four individuals were responsible for a bite. Because of the medical importance of this species, understanding where it is known to occur and where it is predicted to occur is vital information for pre-hospital treatment in case of a snakebite and decisions regarding where and whether to stockpile antivenom. Furthermore, it is necessary to direct educational efforts to diminish conflict between humans and *A. bilineatus*, by training local people in appropriate methods relocate snakes when they appear in unwanted areas, such as inside houses.

AUTHORS' CONTRIBUTION

OMV: study design, manuscript writing; GAGD: field work, data curation; ÁBS: data curation, species distribution modeling; JRR: field work, data curation; MMZG: study design, manuscript writing.

ACKNOWLEDGEMENTS

We thank Gerardo Rafael Estrada González (Universidad del Valle de Guatemala) for providing some of the presence records and two anonymous reviewers whose feedback improved earlier versions of this manuscript.

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