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Posted Date: 12 February 2024

doi: 10.20944/preprints202402.0630.v1

Keywords: Species distribution model; rattlesnakes



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Article

Potential Distribution of the Long-Tailed Rattlesnake *Crotalus stejnegeri* Dunn 1919 (Squamata: Viperidae): a Rare and Under-Sampled Species

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Abstract: This study employed the MaxEnt model to assess the potential distribution of the long-tailed rattlesnake, *Crotalus stejnegeri*, a threatened species endemic to Mexico. The results demonstrate a good reliability of the model, achieving an AUC of 0.879. They highlight a potential distribution concentrated in the foothills of the Sierra Madre Occidental, primarily in south-central Sinaloa, southwestern Durango, and northern Nayarit, characterized by tropical dry forest. Temperature during the driest quarter and the seasonality of precipitation are identified as determining factors, while the low suitability in Chihuahua suggests a tropical affinity of the species. The variability in precipitation during the cooler quarter emphasizes the importance of expanding the number of occurrence records for the species through further field exploration within its range. These findings provide valuable information for conservation efforts and underscore key areas for future research.

Introduction

Species distribution refers to the spatial arrangement of various species throughout the world. It is a key concept in ecology and biogeography, and is influenced by a variety of factors, such as climate, topography, resource availability, competition with other species, and the dispersal ability of each organism (Chuine, 2010; Kissling et al., 2018; Bakx et al., 2019). Understanding species distribution is fundamental for biodiversity conservation, as it helps to identify priority areas for ecosystem protection and management (Da Silva et al., 2020; Piccolo et al., 2020; Srinivasulu et al., 2021). Thus, the study of these patterns can provide valuable information on the ecological mechanisms that govern the spatial distribution of threatened species.

Species distribution models (SDM) are tools and approaches used in biodiversity conservation to predict and understand the potential spatial distribution of species as a function of environmental and geographic variables (Peterson and Soberón, 2012; Piccolo et al., 2020; Srinivasulu et al., 2021). These models are based on the idea that the presence or absence of a particular species within a given region is closely linked to specific environmental variables (Phillips and Dudík, 2008). However, acquiring such data can pose logistical and costly challenges for some species. Consequently, MDS allows leveraging existing data, such as observational records, to extrapolate and make inferences about distribution in areas where direct information may be limited (Gaubert et al., 2002; Meza-joya et al., 2018; Da Silva et al., 2020).

The long-tailed rattlesnake *Crotalus stejnegeri* (Dunn, 1919) is a species endemic to Mexico (Figure 1). It is classified as vulnerable (VU) by the IUCN and threatened (A) by the Mexican species protection standard (NOM-059-SEMARNAT-2010). This species is considered rare because it has not been collected since 1976 and has a restricted distribution (Armstrong and Murphy, 1979). Van der Heiden and Flores-Villela (2013) provided a geographic review of *C. stejnegeri* collections to clarify its distribution in Sinaloa and Durango, states where records of the species exist. The authors acknowledge that *C. stejnegeri* is present in southern Sinaloa and southwestern Durango (only in the locality of Ventanas). However, they dispute the record in Durango's Yamoriba area, citing an elevation range (1780 m asl) deemed too high for the species, as noted by Robert Meidinger (pers. comm., 31 July 2011 in Uetz et al., 2023). Interestingly, Van der Heiden and Flores-Villela (2013) did not address the historical records of the species in Nayarit. In the herpetofauna listing of Nayarit,

Woolrich-Piña et al. (2015) omitted *C. stejnegeri* due to a lack of photographic evidence and supporting documentation its presence in the state. It is noteworthy that also failed to mention that the ENCB-IPN 8307 collection record near San Blas is a juvenile *Crotalus basiliscus* (pers. comm., Jesús Alberto Loc Barragán, after examining collection records from Nayarit).



Figure 1. Specimen of long-tailed rattlesnake (*Crotalus stejnegeri*, Dunn 1919) collected by A. Forrer in the town of Ventanas, Durango (NHMUK: 1883.4.16.64). Photograph by herpetological collection of the Natural History Museum, London.

Reyes-Velasco et al. (2010) proposed that the range of *C. stejnegeri* may be much larger than currently known. The authors provide several explanations supporting this assertion, including the existence of illicit operations and the limited availability of passable routes, particularly challenging to traverse during the wet season in these regions. Additionally, anthropogenic factors with the potential to impact its habitat, such as agriculture, livestock grazing, deforestation, and mining, are identified (Castro-Bastidas et al., 2022; Jacobo-González et al., 2023; unpublished data; HACB). The presence of *C. stejnegeri* in southern Sinaloa and the neighboring states of Durango and Nayarit is believed to be probably greatly underestimated (Van der Heiden and Flores-Villela, 2013).

Presently, there is a 70% increase in *C. stejnegeri* records, facilitated by the contributions of citizen science in the state of Sinaloa (45 records from GBIF, 2024, compared to 13 collections in Van der Heiden and Flores-Villela, 2013). Additionally, recent information on the biology and ecology of the species is now available (Van der Heiden, 2019; 2021). Here, we present a SMD for *C. stejnegeri*, a species with limited data, to predict its potential distribution.

Methodology

Data source. Records of *C. stejnegeri* were obtained after a review of records in scientific collection databases (Global Biodiversity Information Facility, Vertnet), citizen science observations (iNaturalist) and literature records (Van de Heiden and Flores-Villela, 2013; Van der Heiden, 2019). Each record underwent verification, and those lacking coordinates were assigned one if a reference locality was provided via Google Earth. Records without coordinates or a reference locality were excluded. To mitigate spatial bias, a nearest neighbor analysis was conducted (expected mean distance 0.145, index 22042.762, and observed mean distance 3209.109). Duplicate records were eliminated because clustering of the data was obtained (Abdelaal et al., 2019). Records from Yamoriba in Durango and San Blas in Nayarit were not considered due to geographic and misidentification concerns associated with these records.

On the other hand, the selection of environmental variables was obtained from the climatological database CHELSA v2.1 (Brun et al., 2022). This database encompasses 19 traditional bioclimatic variables with a 30-second resolution (~1 km), and its data span from 1980 to 2018 (Table 1). These variables were chosen primarily because the majority of *C. stejnegeri* records are post-2000. Additionally, an elevation raster file (Figure 2A) with the same resolution was integrated into the

model generation (INEGI, 2023). Moreover, Mexico's ecoregions at level IV (CONABIO, 2020) served as the geographic boundary for the model. These ecoregions share similar ecological and biogeographic characteristics, including various vegetation types that may influence the distribution of *C. stejnegeri* (Bakx et al., 2019). The raster files were cropped according to the ecoregions that intersected with nearby records of the species: Canyons with tropical dry forest of the Sierra Madre Occidental (SMO), Hills with xerophytic scrub and tropical dry forest of Sinaloa, and Mountains with coniferous, oak, and mixed forests (Figure 2B).

Table 1. Bioclimatic variables from the CHELSEA climatological database and Variance Inflation Factors (VIF) analysis of the best predictor variables for the model. The asterisks show the highly correlated variables in the first analysis.

Code	Unit	Variable	First multicollinearity analysis (VIF)	Second multicollinearity analysis (VIF)
Bio1	C°	mean annual air temperature	Infinite	—
Bio2	C°	mean diurnal air temperature range	Infinite	—
Bio3	C°	isothermality	Infinite	—
Bio4	C°	temperature seasonality	Infinite	—
Bio5	C°	mean daily maximum air temperature of the warmest month	Infinite	—
Bio6	C°	mean daily minimum air temperature of the coldest month	Infinite	—
Bio7	C°	annual range of air temperature	Infinite	—
Bio8	C°	mean daily mean air temperatures of the wettest quarter	Infinite	—
Bio9	C°	mean daily mean air temperatures of the driest quarter	3.002	1.421
Bio10	C°	mean daily mean air temperatures of the warmest quarter	Infinite	—
Bio11	C°	mean daily mean air temperatures of the coldest quarter	6.500*	—
Bio12	mm	annual precipitation amount	Infinite	—
Bio13	mm	precipitation amount of the wettest month	Infinite	—
Bio14	mm	precipitation amount of the driest month	Infinite	2.296
Bio15	mm	precipitation seasonality	6.300*	1.442
Bio16	mm	mean monthly precipitation amount of the wettest quarter	Infinite	—
Bio17	mm	mean monthly precipitation amount of the driest quarter	Infinite	—
Bio18	mm	mean monthly precipitation amount of the warmest quarter	Infinite	—
Bio19	mm	mean monthly precipitation amount of the coldest quarter	1.488	1.462

DEM m snm

Elevation

Infinite

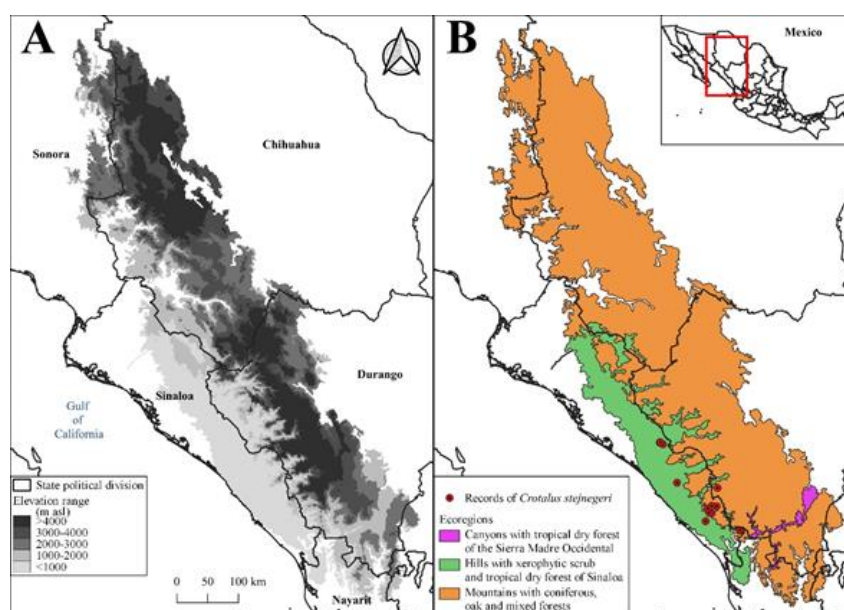


Figure 2. A) Elevation range of the B) selected ecoregions.

Data analysis and model validation. Initially addressed multicollinearity and selected the most relevant predictors demonstrating a higher contribution to the model, the Variance Inflation Factors (VIF) of all environmental variables were tested (Abdalaal et al., 2019). This analysis was performed with the “sdm” package in R where the VIF index was obtained for each variable. A VIF index >5 is considered a high multicollinearity among the variables, therefore, it is recommended to discard these variables for the generation of the model (Abdalaal et al., 2019). Five bioclimatic variables were obtained with a VIF index <10 , Bio9 (3.002), Bio11 (6.500), Bio14 (2.650), Bio15 (6.300) and Bio19 (1.488). However, the variables Bio11 and Bio15 presented a high multicollinearity index (Table 1) and a positive linear correlation coefficient (0.813).

Following a reassessment of multicollinearity, the variable Bio11 was excluded, but Bio15 (Table 1) was retained due to its representation of seasonality data. Despite its high multicollinearity, we decided not to exclude this variable because Sinaloa exhibits pronounced seasonality (Serrano et al., 2014), and it contains the majority of *C. stejnegeri* records. Therefore, it is plausible that this bioclimatic variable plays a role in influencing the species’ distribution. In this second analysis, none of the variables (Bio9, Bio14, Bio15, and Bio19) displayed a significant VIF index (<3), and there was no evidence of a positive linear correlation coefficient ≤ 0.5 between them.

Utilized MaxEnt v3.4.4 software (Phillips et al., 2006) to generate the SMD due to its efficiency in yielding acceptable results even with limited data (Abdalaal et al., 2019; Da Silva et al., 2020). Automation of linear L, quadratic Q, and P product features was implemented to simplify the response curves for ease of interpretation. To enhance model robustness, we employed a bootstrap-type model fit, randomizing 40% of the test records while using the remaining data for training. A total of 27 replicates were generated, corresponding to the number of records of *C. stejnegeri*, with a maximum of 5000 iterations (Dai et al., 2022). The test of equality between sensitivity and specificity served as the threshold rule. Furthermore, the jackknife test, recognized as the best index for small sample sizes (Phillips et al., 2006), was employed to evaluate the percentage contribution of each variable.

To assess the accuracy of the resulting models, we calculated the area under the curve (AUC) of the Receiver Operating Characteristic Curve (ROC). The AUC score stands out as a key metric for measuring model performance, primarily due to its independence from the choice of thresholds (Abdalaal et al., 2019; Dai et al., 2022). A higher AUC value, closer to 1, indicates superior model

performance (Phillips et al., 2006). The AUC plot is generated by plotting true positive predictions (sensitivity) against false positive predictions (1-specificity) (Fielding and Bell, 1997).

Finally, the output from MaxEnt was in logistic format, representing a habitat suitability map for the species with values ranging from 0 (unsuitable) to 1 (optimal). For additional analysis, the MaxEnt results were imported into QGIS 3.34.3, where three classes of potential habitats were defined: low potential (0-0.30), moderate potential (0.31-0.69), and high potential (≥ 0.77 -1).

Results and Discussion

The MaxEnt model with the average value of the replicates showed an AUC of 0.879, with a standard deviation of 0.065. For this reason, the estimation of the environmental suitability of can be considered to have a good degree of reliability (Phillips et al., 2006). Figure 3 shows the potential distribution for *C. stejnegeri*. Low probability zones of species presence are represented by blue shades, while reddish colors indicate high habitat suitability, predominantly concentrated in the foothills of the SMO spanning from Sinaloa to the northern part of Nayarit. These regions exhibit high habitat suitability possibly due to the dominance of tropical dry forest (Serrano et al., 2014; Woolrich-Piña et al., 2015), the prevalent vegetation type where the majority of the species' records have been documented (Figure 2B; GBIF, 2024). In the state of Durango, elevated levels of habitat suitability for *C. stejnegeri* are observed in the SMO, particularly in the municipalities of Tamazula and Otáez, adjacent to the municipality of Cosalá in Sinaloa. This heightened suitability may be attributed to the proximity of these Durango municipalities to Cosalá in Sinaloa, where a significant number of *C. stejnegeri* records have been documented.

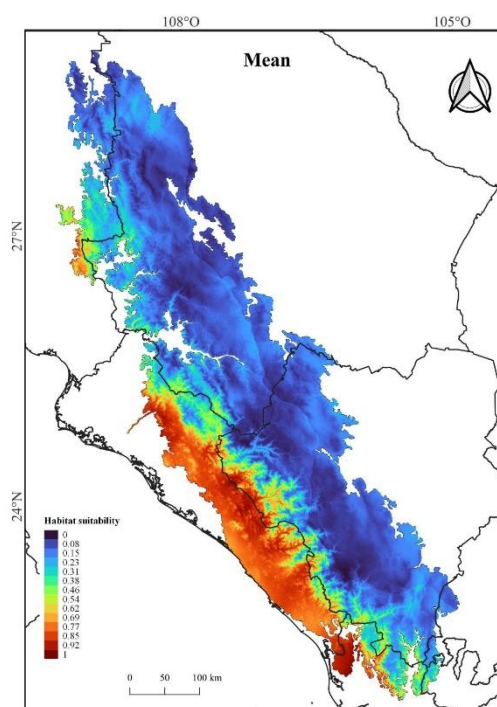


Figure 3. Potential distribution of *C. stejnegeri* showing the mean values of the modeled replicates.

In the same region, particularly in the municipality of San Dimas in Durango, a small area with high habitat suitability for *C. stejnegeri* is depicted in Figure 3. This observation aligns with Robert Meidinger's comment (in Uetz et al., 2023), questioning the altitudinal range of 1780 m asl as being too high for *C. stejnegeri*, as evident by the low habitat suitability around Yamiroba in the municipality of San Dimas, Durango (Figure 2A and 3). On the other hand, Reyes-Velasco et al. (2013) suggested that *C. stejnegeri* could also be found in Nayarit, Sonora and Chihuahua, although Figure 3 shows a high suitability of the habitat for the species in the north of Nayarit and southwest of Sonora, the state of Chihuahua does not present a marked suitability environment for the species. This discrepancy

might be attributed to *C. stejnegeri*'s neotropical biogeographic affinity, asince northeast Sinaloa may be the northernmost limit for neotropical flora and fauna (Gentry, 1946; Morrone et al., 2017; Castro-Bastidas, 2022; Pío-León et al., 2023; Castro-Bastidas et al., 2024). Furthermore, this could also apply to southwest Sonora, although Figure 3 shows an area of high suitability, this result is probably due to the fact that this is a transitional region from the Sonoran desert to the dry forests at the foot of the SMO (Bezy et al., 2017; unpublished data, HACB).

The variables making the most substantial contributions to the habitat suitability model for *C. stejnegeri* are detailed below: Air temperature during the driest quarter (Bio9) (April, May, and June) stands out as the most influential factor in the model, accounting for a significant 74.5%. This high percentage suggests that alterations in this variable exert a noteworthy impact on the potential distribution of *C. stejnegeri*. The precipitation seasonality (Bio15) makes a significant contribution, though to a lesser degree compared to the temperature of the driest quarter, representing 15.3% of the model's influence. This outcome implies that variations in the amount and distribution of precipitation throughout the year play a crucial role in shaping the potential distribution of the species. The amount of reception during the driest month (Bio14) (April) is another relevant factor (9.4%), although its contribution is smaller than the two variables mentioned above. This outcome underscores the significance of water availability during the driest period in the modeling process. The influence of these variables is likely attributed to the fact that most rattlesnakes exhibit heightened activity levels in mid-spring to late summer, corresponding to their reproductive periods (Armstrong and Murphy, 1979; Schuett et al., 2002). This behavior could potentially align with the distribution patterns observed in *C. stejnegeri*. Moreover, the warm and humid conditions in south-central Sinaloa, attributed to the tropical dry forest of this region (Serrano et al., 2014), could also contribute to shaping the distribution of the species. Conversely, monthly precipitation during the coldest quarter (Bio19) (December, January, and February) makes the smallest contribution to the model at 0.8%, possibly due to variations observed between replicates.

For a more comprehensive analysis, Figure 4 illustrates the response curves of the variables with the most substantial contributions. According to these curves, *C. stejnegeri* exhibits a higher probability of occurrence in areas with air temperatures ranging between 29-30°C during the driest quarter (Bio9) (April, May, and June) and precipitation seasonality (Bio15) coefficients between 1000-1200 mm. On the other hand, the species demonstrates probability ranges for occurrence in areas where precipitation during the driest month (Bio14) (April) falls between 25-100 mm. However, there is a low probability of occurrence in areas with monthly precipitation during the coldest quarter (Bio19) (December, January, and February) ranging between 50-150 mm. Notably, this variable exhibits significant variability, evident from the blue standard deviation bands in Figure 4. This indicates that the relationship between *C. stejnegeri* and precipitation during the coldest quarter (Bio19) is less consistent or more variable in specific areas. Therefore, the highlighted variability emphasizes the importance of considering uncertainty in model predictions, potentially indicating areas for future research or improvements in data collection.

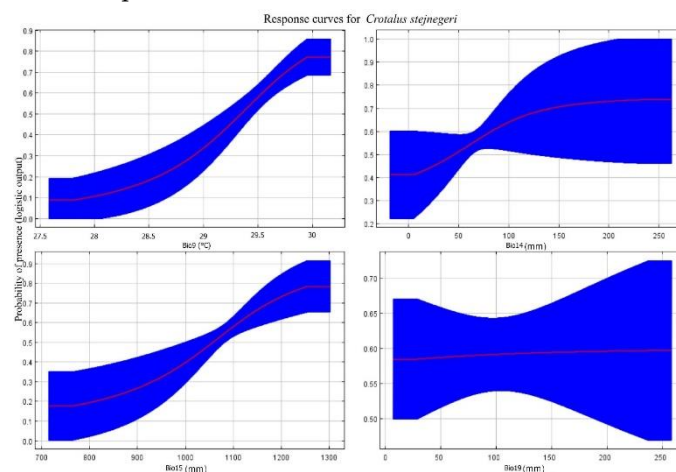


Figure 4. Response curves of *C. stejnegeri*: Bio9 air temperature during the driest quarter, Bio14 amount of precipitation during the driest month, Bio15 seasonality of precipitation and Bio19 monthly precipitation during the coldest quarter. The red line shows the mean values of the model replicates and the blue fringe show their standard deviation.

Conclusions

The MaxEnt model delivers a reliable estimate of habitat suitability for *C. stejnegeri*. The potential distribution of the species is prominently observed in the foothills region of the SMO, particularly in the municipalities of Sinaloa and Durango, characterized by a prevalence of tropical dry forest. These results align with previous observations regarding the species' preference for specific altitudes. The absence of distinct environmental suitability in Chihuahua may be linked to the neotropical biogeographic affinity of the species. Bioclimatic variables, notably the temperature of the driest quarter (April, May, and June) and precipitation seasonality, play crucial roles in the modeling, with water availability during the driest month (April) identified as a key factor. However, the variability highlighted by the blue standard deviation bands in the response curves, particularly in precipitation during the coldest quarter (December, January, and February), underscores the necessity of considering uncertainty in model predictions. Additionally, it directs attention to specific areas that warrant further research and efforts to enhance records of the species' presence.

Acknowledgments: To the curators of the herpetological collection at the Natural History Museum, London for the availability of the photograph of *C. stejnegeri* (NHMUK: 1883.4.16.64). Also, to Jesús Alberto Loc Barragán for providing information on the alleged records of the species in Nayarit, Mexico.

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