Predicting the potential distribution of the beaded lizard and identification of priority areas for conservation

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A B S T R A C T

The beaded lizard (Heloderma horridum) is listed as a threatened species in Mexico. Scientific research has been limited to two sites within its range (Chamela and Valle Motagua) outside of these two regions there have not been adequate surveys to define range limits or measure environmental correlates for defining suitable habitat. We constructed an ensemble model (EM) for the distribution of suitable habitat for H. horridum in both Mexico and Guatemala and then used that model to identify potential areas to focus conservation. We used nine presence-only modeling methods, and selected three to generate our EM. We used the EM to evaluate the efficacy of the existing Protected Natural Areas (PNAs) in Mexico and Guatemala for H. horridum. Also we used the best individual predictive model (Maxent) to obtain the most important factors for H. horridum presence and used them to analyse the habitat use; finally we used our predictive model to calculate niche breadth for the species. The estimated potential distribution of H. horridum is 370,474 km²; within this area we identified nine zones based on continuity and natural barriers. About 1.5% of the species distribution is under protection in the PNAs. The five most important factors for the presence of this species explained 78.2% of the generated model and are related to seasonality and soil cover, and these are used selectively. This species is closely associated with tropical deciduous forests, one of the most threatened ecosystems worldwide and is inadequately protected in both Mexico and Guatemala. Our results clearly show the necessity of a protection plan for this species.

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Introduction

It is estimated that the main threats to species persistence are anthropogenic, and primarily loss and fragmentation of habitat (Beck 2005; Brown & Carmony 1999; Casas-Andreu 2000). Heloderma horridum (beaded lizard) is listed as threatened in Mexico (SEMBARNAT 2008). While in the international arena is considered a species of least concern (IUCN 2010) also found in Appendix II of CITES (CITES 2007). Beaded lizards range along the Pacific slope of North America, from southern Sonora, Mexico to Guatemala (Beck 2005). H. horridum is found primarily in tropical deciduous forests, but have also been recorded in foothill thornscrub habitats, and in high elevation pine-oak woodlands (Bogert & Martín del Campo 1956; Lemos-Espinal et al. 2003; Monroy-Vilchis et al. 2005).

Mexico, potential habitats include parts of the Sierra Madre Oriental, the Sierra Madre del Sur and trans-Mexican volcanic belt, three of the Mexico’s mountain ranges with the highest levels of biodiversity (Conservancy 2007). In Guatemala, beaded lizards are thought to be restricted to the Motagua Valley in the southeast (Campbell & Vannini 1988), which is one of eight highest priority conservation areas in northern Mesoamerica (Ariano-Sánchez 2003; Ariano-Sánchez & Coti 2007).

The distribution of H. horridum has previously been estimated from records collected from 1577 to present day (Beck 2005; Bogert & Martín del Campo 1956), however, most reports have consisted of casual or unverified sightings. Thus, there is a high likelihood that many important areas in the occurrence of the species have yet to be identified. As a result, it is unknown whether the known distribution accurately reflects the current distribution, and how environmental features may potentially restrict the distribution of H. horridum.

Habitat suitability models are commonly used to predict the potential distribution of species based on the inter-relationships

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between habitat variables (Guisan & Thuiller 2005; Guisan & Zimmermann 2000; Hernandez et al. 2006; McPherson & Jetz 2007; Rodríguez-Soto et al. 2011; Rushton et al. 2004). We developed spatial models of habitat suitability for H. horridum in its range (Mexico and Guatemala) using geographic, biological, and climatic habitat attributes (Elith et al. 2006; Hirzel & Arlettaz 2003; Marmion et al. 2008a; Papes & Gaubert 2007; Phillips et al. 2005; Segurado & Araújo 2004). The objectives of this study are to: (1) use habitat suitability models to determine the potential current distribution of H. horridum; (2) determine the most important habitat features for predicting the presence of H. horridum, in order to estimate habitat use and spatial niche breadth; and, (3) to compare the predicted distribution with the current system of protected natural areas in Mexico and Guatemala.

Methods

Mexico is a large (~2 million km²) and biologically diverse country with a varied geological composition, topography and climate (Conabio 1998). Mexico is considered one of the seven most biologically diverse countries in the world and ranks third in importance for conservation because it is home to between 8 and 12% of the world’s species (Challenger 1998). Mexico further stands out as having the world’s greatest richness of herpetofauna (Flores-Villela 1993; Llorente-Bousquets & Oceguera 2008). In Guatemala, the mountains from the north and south are separated by the Motagua valley, characterised by thorn scrub vegetation (Ariano-Sánchez 2003). The Motagua valley is one of the driest areas of Central America (Hastenrath 1967) and structurally resembles the tropical deciduous forests in Mexico. Because of its location and biogeography, Guatemala is also recognised as a global area of importance for biodiversity (Loening & Markussen 2003; Nations et al. 1988).

We obtained specific locality information for H. horridum in two ways: (1) by reviewing databases of herpetological collections and published scientific literature; and, (2) by field surveys at five locations in Mexico and one in Guatemala. Field locations included: Los Alamos (Sonora), the Chamelá-Cuixmala Biosphere Reserve (Jalisco), Arcelia (Guerrero), the Sierra Nanchitala Nature Reserve (Mexico), Malinloc (Mexico), and the Motagua valley (Guatemala). Fieldwork was conducted in different years (1998–2009) at the different sites, but all work involved visual encounter surveys to locate H. horridum while they were active above-ground. Activity of H. horridum throughout the foraging and breeding season is primarily crepuscular (Beck & Lowe 1991), and we typically hiked foot trails in search of active lizards between 07:00 and 10:00 h, and again between 17:00 and 21:00 h. When lizards were observed, we recorded general habitat notes, date, location, and geographical coordinates (GPS). Because there were significant changes in land use and vegetation cover in Mexico between 1970 and 1990 (FAO 2001), we only used the historic records from databases and published literature from the years 1990 to 2010.

Data for environmental variables used to predict habitat suitability were obtained through online databases of elevation, topography, temperature, precipitation, and vegetation cover (Global Land Cover Facility, Hydro1k and WorldClim). We chose 15 biologically relevant habitat and climate variables (Table 1) to generate models, and processed digital coverage at a resolution of 1 km² using ArcView 3.2, Arc GIS, and Idrisi Andes. Considering the scope of the study area (Mexico and Guatemala), and the space that is typically used by individual lizards (mean home range = 0.216 km²) according to Beck and Lowe (1991), a 1 km² resolution is appropriate to examine the effect of selected habitat variables on the potential distribution of H. horridum.

We applied nine different modeling techniques that have been widely used to delimit the potential distribution of several species of terrestrial vertebrates (Carpenter et al. 1993; Elith et al. 2006; Engler et al. 2004; Ficetola et al. 2007; García 2006; Guisan & Thuiller 2005; Guisan & Zimmermann 2000; Hernandez et al. 2006; Hirzel & Arlettaz 2003; Ochoa & Flores-Villela 2006; Papes & Gaubert 2007; Peterson et al. 2003; Raxworthy et al. 2003; Segurado & Araújo 2004; Thorn et al. 2009; Urbina-Cardona & Flores-Villela 2010). We used: (1) Artificial neural networks; (2) Bioclim; (3) Climate model space; (4) Ecological niche factor analysis (ENFA); (5) Envelope scores; (6) Environmental distance; (7) GARP; (8) Maxent; and, (9) Support vector machines. These models were implemented in three software packages: Open modeller 1.0.8 (Sutton et al. 2007); Biomapper 4.0 (Hirzel & Le Lay 2008); and, Maxent 3.3 (Phillips et al. 2005).

Locality records were randomly divided so that 75% of observations were used to generate predictive habitat models and 25% were used for model evaluation. Evaluation of the nine models was performed using receiver operating characteristic (ROC) plots and area under the curve (AUC) calculations, which have been shown to be robust indicators of model performance (Fielding & Bell 1997; Jiménez-Valverde & Lobo 2007). We performed several ensemble models using between two to nine individual models. We began with the two better models and aggregated the others consecutively according to their rank on the validation test. Then we used the ensemble where the AUC value was the highest (three models). We used the AUC as a weight for each model, as recommended by Marmion et al. (2009b). By combining the weighted single-models, the predictive uncertainty of the consensus model is lower than when considering the models individually (Araújo et al. 2005; Marmion et al. 2009b; Rodríguez-Soto et al. 2011).

The weighted average (WA) ensemble model was generated using Idrisi Andes and the formula:

$$W_A = \frac{\sum (AUC_{mj} \times m_j)}{\sum AUC_{mj}}$$

where $m_j$ is the probability of occurrence for H. horridum in a grid cell in the jth individual model. The ensemble model was considered the best estimate of the potential distribution of H. horridum. To facilitate interpretation of the final model, we reclassified the predictions from continuous probabilities (where probabilities of occurrence ranged from 0 to 1) into two suitability classes: low suitability (value less than the weighted mean probability of 0.332) and high suitability (values above the mean; Jiménez-Valverde & Lobo 2007; Liu et al. 2005). To evaluate the extent that current reserve systems contribute to the protection and conservation of the species, the reclassified ensemble model output was superimposed on the Protected Natural Areas (PNAs) in Mexico and

Table 1 Environmental variables included in the ensemble model of Heloderma horridum (variables 1–9; from WorldClim, Hydro1k and Global Land Cover Facility, 10–15, derived from temperature and precipitation).

<table>
<thead>
<tr>
<th>Number</th>
<th>Variable</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Elevation (DEM)</td>
</tr>
<tr>
<td>2</td>
<td>Slope</td>
</tr>
<tr>
<td>3</td>
<td>Tree cover (%)</td>
</tr>
<tr>
<td>4</td>
<td>Herbaceous cover (%)</td>
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<tr>
<td>5</td>
<td>Conifer cover (%)</td>
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<tr>
<td>6</td>
<td>Hardwood cover (%)</td>
</tr>
<tr>
<td>7</td>
<td>Perennial plant cover (%)</td>
</tr>
<tr>
<td>8</td>
<td>Deciduous cover (%)</td>
</tr>
<tr>
<td>9</td>
<td>Bare soil (%)</td>
</tr>
<tr>
<td>10</td>
<td>Annual rainy season precipitation (%)</td>
</tr>
<tr>
<td>11</td>
<td>Annual dry season precipitation (%)</td>
</tr>
<tr>
<td>12</td>
<td>Maximum precipitation (dry season)</td>
</tr>
<tr>
<td>13</td>
<td>Minimum precipitation (rainy season)</td>
</tr>
<tr>
<td>14</td>
<td>Annual maximum temperature</td>
</tr>
<tr>
<td>15</td>
<td>Annual minimum temperature</td>
</tr>
</tbody>
</table>

Guatemala. Then an estimation of protected area was performed using Idrisi Andes.

We identified the habitat and climate variables that were most important in predicting the distribution of H. horridum using the best performing (highest AUC) single-technique model. Using the potential distribution, we then divided the range of each habitat and climate variable into ten classes considering the greatest possible value for each. Then all records were assigned to one of the categories of each of the evaluated variables. The method suggested by Neu et al. (1974) was followed to determine which habitat types were used more or less frequently than expected. This method compares the frequency of the observed with the expected (Poisson distribution) values in each habitat type. The Neu’s method usually includes a chi-square statistic. In the present study, the likelihood ratio test (G-test) was used since the test is recommended for comparison of more than two classes (e.g. categories of habitat types) by Sokal and Rohlf (2001). The frequency expected was based on habitat type availability as suggested by Krebs (1999). Finally, all values subtracted of each category were added and the habitat use index (HUI) for each variable was obtained.

In order to quantify the specialisation of H. horridum, we applied an analysis of niche breadth. The niche breadth is measured by observing the distribution of individual organisms within a set of resources states. We reclassified the ensemble model into four habitat suitability classes based on the probability of occurrence of the species: (1) unsuitable; (2) low suitability; (3) medium suitability; and, (4) high suitability. These habitat types were considered for analysis and were applied using Hurlbert’s niche breadth index (Krebs 1999). This index were used as it allows for the fact that some resources (in this case habitat suitability classes) are more abundant than others.

**Results**

We obtained 288 locality records for H. horridum (all years), and retained 101 records collected between 1990 and 2010 to develop models (Fig. 1). The three models used to generate our ensemble model (highest AUC) were: Maxent; Support vector machines; and, Environmental distance. Subsequently, we evaluated the ensemble model and the results showed that it had greater predictive ability than the individual models (Table 2).

The potential distribution of H. horridum is 370,474 km² and the species is limited in Mexico to the states of Sonora, Chihuahua, Sinaloa, Durango, Nayarit, Jalisco, Colima, Zacatecas, Aguascalientes, Guanajuato, Michoacan, Guerrero, Mexico, Morelos, Puebla, Oaxaca and Chiapas. In Guatemala, the potential distribution includes Huehuetenango in the east and Quiché, Chimaltenango, Baja Verapaz, Guatemala, Progreso, Jalapa, Zacapa, Chiiquimula and Jutiapa in the southeast (Fig. 2).

The distribution of H. horridum occurs in several zones with differing degrees of fragmentation. Based on this fragmentation and the presence of geographic barriers (mountains), we identified the following areas of importance in the distribution of this species. In northern Mexico there is a continuous area extending south along the west slope of the Sierra Madre Occidental from Sonora to northern Nayarit (1). In southern Nayarit habitats are substantially fragmented, and the fragmented habitat areas extend through Jalisco and include small portions of Zacatecas, Aguas Calientes, Guanajuato and Michoacan (2). In the coast of Jalisco begins an area

![Fig. 1. Occurrence localities used to build the distribution model.](image_url)
that continues through Colima and a small portion of Michoacan (3). In the centre of the country, the potential distribution largely matches the Balsas River depression and includes parts of Jalisco, Michoacan, Guerrero, Mexico, Morelos, Puebla and northwest Oaxaca (4). In southern Mexico, the potential distribution extends along the coast of Guerrero (5) and the west coast of Oaxaca (6). From the central coast of Oaxaca the potential distribution continues through central Chiapas and ends in Guatemala (7). In southeastern Puebla and northern Oaxaca, there is a small area of potential distribution where the species has not yet been reported (8). The potential south most distribution areas for H. horridum (9) fall within the Motagua valley (Fig. 3). The range of H. horridum found within the natural protected areas in Mexico and Guatemala (Fig. 2) is 5576 km². This area is distributed in 15 PNAs in Mexico and 16 in Guatemala, which together protects 1.5% of the potential distribution of H. horridum.

The most important variables in determining habitat suitability of H. horridum were: bare soil coverage; percentage of annual precipitation occurring in the dry season; perennial vegetation cover; percentage of annual precipitation occurring in the rainy season; and, minimum precipitation of the rainy season. Together these variables accounted for 78% of the explained variation in the model (Table 3). The habitat use index shows that H. horridum makes selective use of some classes of habitat features. However, differences are only significant for the variables: percentage of annual precipitation occurring in the dry season (G = 81.418); percentage of annual precipitation occurring in the rainy season (G = 97.026); and, minimum precipitation in the rainy season (G = 53.944; p < 0.05, df=9 for all). In the variable rainfall in the dry season, there is a preference for class 3 (4.4–6.1%) and 8 (12.9–14.6%). The same variable shows a strong avoidance by the class 2 (2.7–4.4%) and a slight evasion class 4 (6.1–7.8%). The variable rainfall in the rainy season provides a preference for class 3 (62.2–69.3%) and minimum precipitation in the rainy H. horridum select the class 5 (189–237 mm). In the two variables were obtained that the other classes are used in proportion to their disposition. Standardised niche breadth obtained (Hurlbert’s niche breadth index) was 0.001 indicating that H. horridum is highly specialist.

**Discussion**

Validation tests indicate that the ensemble model has greater predictive ability than the individual models (Table 2). Based on these results we assume, the proposed distribution of H. horridum should more accurately reflect the actual distribution of the species. In comparing the potential distribution of H. horridum determined in this study (Fig. 2) with the distribution presented by Beck (2005), we can see that there are four important differences: (1) the potential range of H. horridum in the north (Sonora) is larger; (2) the potential range along the coastline is about 25% lower; (3) the potential range in the centre of the country is larger, and mainly restricted to the Balsas Basin; (4) the estimated distribution presented here suggests that there is an area of species occurrence (Fig. 3) that has yet to be confirmed. Previous observations proposed that the northern limit of the distribution of H. horridum is in southern Sonora, near the border with Sinaloa. Our study suggests that potential habitat in this area is wider than previously thought. Recent sightings (Lemos-Espinal 2007; Muñiz-Martínez & Rojas-Pérez 2009) confirm our model, and prove that the occurrence of H. horridum in northern Mexico is broader than previously thought. In Nayarit and Jalisco, the potential habitat area also appears to
be larger than suggested by previous observations. However, in this region the potential habitat is quite fragmented (Trejo & Dirzo 2000) and extends toward the centre of the country to zones of Zacatecas, where the presence of *H. horridum* was only recently reported (Avila-Villegas 2007). In Michoacan, Guerrero, Mexico, Morelos, Puebla and Oaxaca, there are larger and more continuous areas adjacent to the Balsas Basin. As for the continuity of the distribution along the coast, the potential habitat appears to be very scarce on the coast of Oaxaca and any populations there may be quite isolated.

The potential distribution of *H. horridum* in Guatemala appears to be similar to the distribution described by Beck (2005). Both historical observations (Campbell & Vannini 1988) and our model predictions agree that the species distribution in Guatemala is likely limited to the Motagua valley. This population is the only completely geographically isolated population of *H. horridum*. Eastern Puebla and northern Oaxaca (Fig. 3) is the only area where the potential distribution proposed by this study has not yet been confirmed by the occurrence of *H. horridum*. These areas are isolated by the presence of two major mountain ranges (Conabio 2007).

The potential barriers to the dispersal of *H. horridum* include altitude and vegetation type. The altitudinal limit of this species has not been well defined, but some accounts report presence in higher altitude habitats (1861 m in pine-oak woodland; Monroy-Vilchis et al. 2005). It is unlikely that high elevation environments can maintain viable populations of *H. horridum*, however, individuals are likely able to disperse through high elevations in order to colonise new lowland areas.

Only 5576 km² (1.5%) of potential habitat for *H. horridum* is within PNA's (Fig. 1). This shows the low representation of this species under government protection; this situation has been reported in general for the biodiversity of Mexico (Rodriguez-Soto et al. 2011; Sánchez-Cordero & Figueroa 2007), and for the herpetofauna (Urbina-Cardona & Flores-Villela 2010). The model developed in this study identifies important areas for conservation of *H. horridum*, but more detailed studies are needed in order to incorporate relevant aspects of the species ecology into the selection of appropriate sites for protection. The potential habitat of *H. horridum* in Mexico appears to largely coincide with the distribution of tropical deciduous forest in Mexico (Trejo 2005).

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Table 3

<table>
<thead>
<tr>
<th>Variable</th>
<th>Contribution to the model (%)</th>
<th>Interval of <em>Heloderma horridum</em> occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bare soil cover</td>
<td>19.8</td>
<td>0–10%</td>
</tr>
<tr>
<td>Annual dry season precipitation</td>
<td>19.6</td>
<td>0–10%</td>
</tr>
<tr>
<td>Perennial vegetation cover</td>
<td>17.4</td>
<td>0%</td>
</tr>
<tr>
<td>Annual rainy season precipitation</td>
<td>13.1</td>
<td>70–100%</td>
</tr>
<tr>
<td>Minimum rainy season precipitation</td>
<td>8.3</td>
<td>90–300 mm</td>
</tr>
</tbody>
</table>
In Guatemala, vegetation in the areas *H. horridum* occurrence is similar to tropical deciduous forest in Mexico, being forested environments having a marked seasonality (Murphy & Lugo 1995). These settings match the tropical sub-humid ecological zone proposed by Challenger (1998) for Mexico, which includes thorn scrub, lowland tropical forests, and low elevation pine-oak woodlands.

Tropical deciduous forests are one of the most threatened environments worldwide (Janzen 1988), and among the largest remaining fragments of this vegetation type in America are located in central and western Mexico (Ceballos 1995). Tropical deciduous forests in Mexico are extremely biologically important and they contain around 67% of endemic vertebrates in the country (Conservancy 2007), but occupy only about 15% of the land area (Trejo 2005). Because the distribution of *H. horridum* largely coincides with tropical dry forests, this species could be used to propose protection areas for this ecosystem but it is necessary to undertake a more detailed study to determine which characteristics of the tropical dry forest (i.e. species richness, vegetation quality) could be favoured. So, it is proposed that the areas for the protection of this species are located in the main areas identified as potential distribution (Fig. 3).

Beck and Lowe (1991) and Ariano-Sánchez (2003) describe the general features of habitats used by *H. horridum*, however, no study has yet looked at the habitat selection of this species. We identified five environmental variables as the primary determinants of the presence of *H. horridum*. The results indicate that areas where bare soil is from 0 to 10% are suitable for the species. The second significant variable was rainfall in the dry season. The results show that *H. horridum* occurs in areas with low rainfall at this time between 0 and 10% of the total. This provides quantitative data and strengthens the hypothesis that seasonality is important for this species (Beck 2005; Lovich & Beamond 2007), particularly seasonally dry conditions, and might provide important cues for reproductive events, such as ovulation, spermiogenesis (Goldberg & Beck 2001), and timing of hatching (Gieger et al. 2005). The third variable in importance was the absence in perennial vegetation cover, confirming the preference of the species in the tropical deciduous forest. Although it can be found in pine and oak, this coverage is seldom used (Beck 2005; Monroy-Vilchis et al. 2005). The fourth and fifth most important variables were related to rainfall in the rainy season and the results show that at sites where occurrence of the species was recorded precipitation during this period is very high (75–90% of total). These variables are indicators of environmental seasonality and suggest that this feature is essential for *H. horridum*.

Indices of habitat use identified important ranges of the environmental variables used by the species. Statistically significant results were only present in the three variables related to environmental seasonality (percentage of annual precipitation occurring in the dry season, percentage of annual precipitation occurring in the rainy season, and minimum precipitation of the rainy season). For precipitation in the dry season, the results show that the species prefers classes 3 (4.4–6.1%) and 8 (12.9–14.6%), corresponding with sites of low and high rainfall respectively. For the same variable, it appears that there is avoidance for the class 2 (2.7–4.4%) and other classes were used in proportion to their availability.

In the variables of percentage of annual precipitation occurring in the rainy season, and minimum precipitation of the rainy season, the results suggest that this species prefers areas with a very narrow range of variation. These results coincide with that obtained by the niche breadth index, which indicates that *H. horridum* is highly specialist (0001). Despite the uneven dispersion of recent verified sightings over the beaded lizards’ extensive range, we believe our ensemble model provides a defensible coarse-scaled delineation of this species’ current distribution. We believe our model lays a foundation for focusing further surveys and then the development of finer-scale models that will define suitable habitat and identify boundaries for new conservation areas to ensure the protection of beaded lizards.

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