# Predictive Habitat Model Reveals Specificity in a Broadly Distributed Forest Raptor, The Harpy Eagle

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# PREDICTIVE HABITAT MODEL REVEALS SPECIFICITY IN A BROADLY DISTRIBUTED FOREST RAPTOR, THE HARPY EAGLE

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Abstract.—The identification of breeding habitat is essential for the implementation of conservation efforts for threatened species. Using seven natural and anthropogenic variables, and based on 27 nesting attempts over 17 yr, we created a species distribution model for Harpy Eagle (*Harpia harpyja*) breeding habitat across 5636 km$^2$ in the Pacific Region of Darien Province, Panama. Highly suitable habitat had high forest cover, low elevation, and a relatively low distance to rivers. We identified specific breeding habitat associations for Harpy Eagles and found that 34% of the area analyzed contained highly suitable breeding habitat. At the regional level, highly suitable habitat was found predominantly in the northern portion of the study area in the four watersheds occurring there, and along the Pacific Coast. The Juradó watershed in the south contained relatively little habitat, owing to a high amount of mountainous terrain. Among three protected areas in the region, Darien National Park contained an equal amount of habitat as the relatively smaller and neighboring Chepigana Forest Reserve and Serranía de Bagre Biological Corridor, a fact that highlights the importance of northern forests for the conservation of Harpy Eagles in Darien. Generally speaking, areas with the greatest amount of human influence were associated with greater forest loss and less suitable habitat. We therefore propose that community-based strategies for sustainable resource management are needed to mitigate forest disturbance levels in areas where the Harpy Eagle coexists with humans. Considering the high importance of the breeding habitat for the Harpy Eagle in the Serranía de Bagre Biological Corridor and Chepigana Forest Reserve, we recommend a revision of the legislation that governs the extractive use of the natural resources in these two protected areas.

Key Words: *Harpy Eagle*; Harpia harpyja; *conservation*; *habitat suitability*; *predictive model*; *protected area*; *species distribution model.*

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## UN MODELO PREDICTIVO DE HÁBITAT REVELA ESPECIFICIDAD EN *HARPIA HARPYJA*, UNA RAPAZ FORESTAL AMPLIAMENTE DISTRIBUIDA

Resumen.—La identificación del hábitat reproductivo es esencial para la implementación de esfuerzos de conservación en especies amenazadas. Usando siete variables naturales y antropogénicas y basados en 27 intentos de anidación a lo largo de 17 años, creamos un modelo de distribución de especies para el hábitat de cría de *Harpia harpyja* a través de 5636 km$^2$ en la Región del Pacífico de la Provincia de Darién, Panamá. El hábitat más adecuado tuvo una alta cobertura de bosque, una baja altitud y una proximidad relativamente cercana a ríos. Identificamos asociaciones de hábitat reproductivo específicas para *H. harpyja* y encontramos que el 34% del área analizada incluyó hábitat reproductivo muy adecuado. A escala regional, el hábitat más

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adecuado fue encontrado predominantemente en las cuatro cuencas presentes en la porción norte del área de estudio y también a lo largo de la costa del Pacífico. La cuenca del Juradó, en el sur, presentó relativamente poco hábitat adecuado, debido a una alta cantidad de terreno montañoso. De las tres áreas protegidas en la región, el Parque Nacional Darién incluyó una cantidad similar de hábitat comparada con las vecinas y relativamente menores Reserva Forestal Chepigana y Corredor Biológico Serranía de Bagre. Esto resalta la importancia de los bosques del norte para la conservación de *H. harpyja* en Darién. En términos generales, las áreas con mayor cantidad de influencia humana estuvieron asociadas con mayor pérdida de bosque y menos hábitat adecuado. Por ende, proponemos la necesidad de estrategias comunitarias para la gestión sostenible de los recursos y mitigar los niveles de disturbios forestales en áreas donde *H. harpyja* coexiste con humanos. Considerando la gran importancia del hábitat reproductivo para *H. harpyja* en el Corredor Biológico Serranía de Bagre y la Reserva Forestal Chepigana, recomendamos una revisión de la legislación que gobierna el uso extractivo de los recursos naturales en estas dos áreas protegidas.

[Traducción de los autores editada]

INTRODUCTION

The Harpy Eagle (*Harpia harpyja*) has a broad distribution from southern Mexico to northern Argentina yet has been extirpated across much of its former range, particularly Mexico and much of Central America (Ferguson-Lees and Christie 2001, Vargas González et al. 2006). Due to recognized declines, its global conservation status is Near Threatened (International Union for Conservation of Nature 2017), while its national conservation status in many countries is Endangered (e.g., Panama: Ministry of the Environment of Panama [MiAMBIENTE] 2016; Belize: Meerman and Clabaugh 2010).

Behaviors that render Harpy Eagles largely inconspicuous (e.g., individuals rarely soar, still-hunt from perches inside the canopy, and are often silent; Stiles and Skutch 1989) and low breeding densities (Piana 2007, Muñiz-López 2008, Vargas González and Vargas 2011) make them difficult to locate, thus presenting challenges for observing breeding biology and behavior. Pairs build nests in canopy-emergent trees (Schulenberg 2020), where they raise a single young that requires 2.5 to 3 yr to reach independence (Vargas González and Vargas 2011). Breeding occurs at low elevations (e.g., 300–500 masl) in primary and mature secondary forests (Vargas González and Vargas 2011, Schulenberg 2020), a habitat that provides suitable nesting sites and abundant large, arboreal prey needed for reproduction (Brown 2001, Geise et al. 2004, Please et al. 2016). Harpy Eagles are often considered to be sensitive to anthropogenic disturbances including habitat alteration (Thiollay 2007, Aguiar-Silva et al. 2012) and human persecution (e.g., shooting due to fear or curiosity; Trinca et al. 2008, Curti and Valdez 2009, Muñiz-López 2017), both of which are factors that potentially limit breeding near human popula-

tion centers (Vargas González 2008). At the micro-habitat scale, Harpy Eagles show specific preferences in habitat selection at nesting sites (Giudice et al. 2007, Piana 2007, Vargas González et al. 2014) that probably derive from the distribution and availability of prey and high perches, and offer ease of mobility between forest strata to move and hunt, features that contribute to breeding success and survival of the offspring during the dependency period (Vargas González 2008).

Although we possess basic knowledge about Harpy Eagle breeding biology, habitat selection at landscape levels remains unquantified. Given the increasing pressures on Harpy Eagle habitat and conflicts with humans, the development of a breeding habitat distribution model could help in conservation planning and prioritization of conservation actions.

Species distribution models relate environmental variables to species occurrences to gain an understanding of ecological drivers or to help predict habitat suitability across landscapes (Elith and Leathwick 2009, Kramer-Schadt et al. 2013). Numerous studies have documented the practical usefulness of predictive models for habitat suitability (Sara 2014, Cardador et al. 2015, Hamilton et al. 2015, Maleki et al. 2016, Munro et al. 2016, Gallardo and Vilella 2017) for the conservation and management of species. Some authors have indicated that the use of these models for threatened species is essential because they aid in prioritizing areas for conservation and facilitate the development of management recommendations (Moisen et al. 2006, Seoane et al. 2006).

Our aim was to develop a predictive model for Harpy Eagle breeding habitat as a tool to aid in the species' conservation. We included in the analysis natural and anthropogenic variables taken from 27
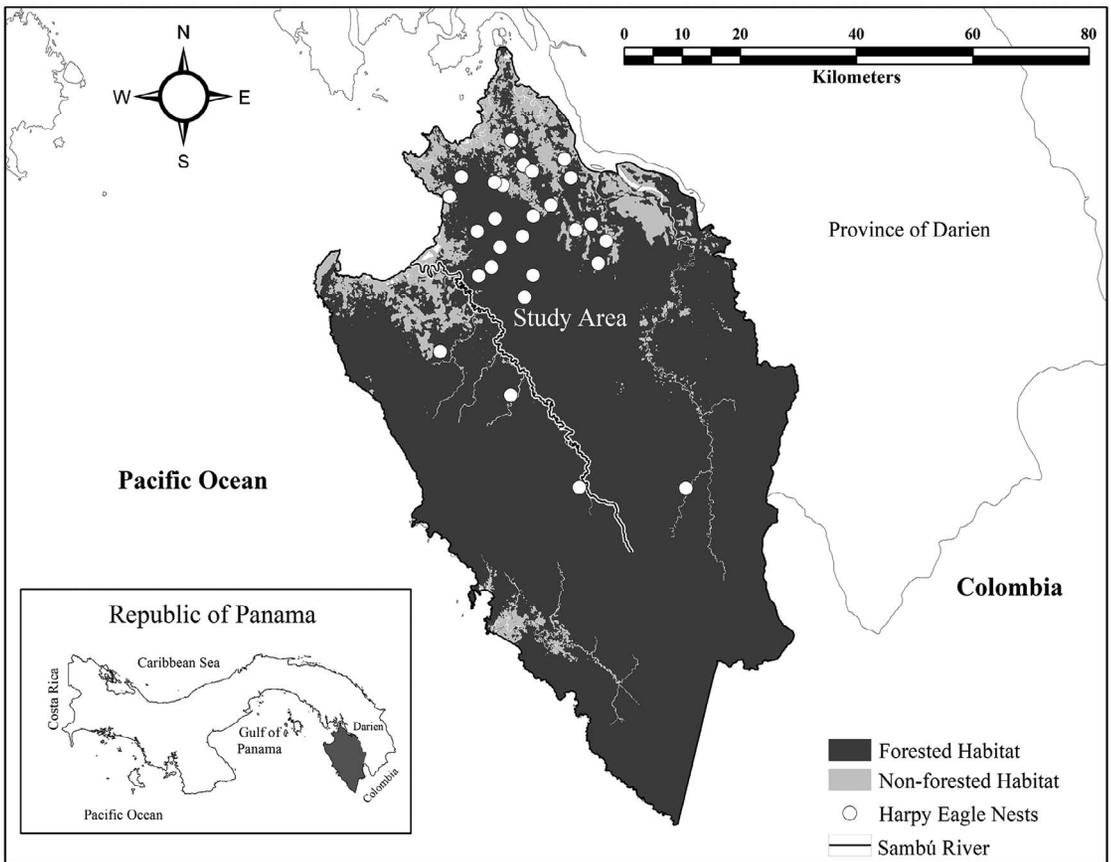
Figure 1.    Map delineating the study area, forested habitat, and nest sites used in the habitat distribution model for Harpy Eagle habitat suitability in Darien Province, Panama.

nesting sites in the western Pacific region of Darien Province, Republic of Panama, and used MaxEnt to identify and quantify suitable breeding habitat. We then compared proportions of suitable habitat among watersheds and landscapes with varying levels of administrative oversight and protection.

STUDY AREA AND METHODS

**Study Area.** Our study area is located in Darien Province, Panama, between 7°33.0′ and 8°18.0′N latitude and 77°24.6′ and 78°12′W longitude, totaling 5636 km$^2$ (Fig. 1). The area experiences marked dry (January–April) and wet (May–December) seasons, with an annual average rainfall of 1372 mm and average temperature of 28°C (Instituto Nacional de Estadística and Censo de Panamá 2016).

Darien is considered part of the Chocó biogeographic region, which extends from southern Panama to northern Ecuador and is globally recognized as one of the world's most biologically diverse (Gentry 1986, Dinerstein et al. 1995). Three of the five climatological regions of Panama (classified according to Köppen 1936) are found in Darien, which creates niches for biodiversity, and consequently makes Darien an ecological region of international conservation importance (Myers et al. 2000, Olson and Dinerstein 2002). A large part of Panama's biodiversity is found in Darien ecosystems, with 54% of Panama's vertebrate species and 47% of endemic species occurring there (Tosi 1971, United Nations Development Program – Ministry of Economics and Finance of Panama 2003). Four protected areas occur in Darien: Darien National Park, Chepigana Forest Reserve, Serranía de Bagre Biological Corridor, and Punta Patiño Wetland.

Table 1.   Mean, standard deviation, and range of the seven variables used in the predictive habitat suitability analysis for Harpy Eagle nest locations, background points, and the entire study extent.

| | NEST LOCATIONS | | BACKGROUND POINTS | | STUDY EXTENT | |
|---|---|---|---|---|---|---|
| VARIABLE | MEAN ± SD | RANGE | MEAN ± SD | RANGE | MEAN ± SD | RANGE |
| Elevation (masl) | 138 ± 62 | 31–312 | 145 ± 111 | 4–813 | 309 ± 344 | 3–5922 |
| Forest cover 250 m (%) | 93.0 ± 21.8 | 0.0–100.0 | 83.1 ± 33.1 | 0.0–100.0 | 88.1 ± 29.3 | 0.0–100.0 |
| Forest cover 1 km (%) | 93.7 ± 17.6 | 8.5–100.0 | 85.1 ± 25.5 | 0.0–100.0 | 89.1 ± 24.5 | 0.0–100.0 |
| Forest cover 4 km (%) | 88.4 ± 13.9 | 42.9–100.0 | 84.6 ± 20.8 | 0.0–100.0 | 88.3 ± 22.5 | 0.0–100.0 |
| Distance to large communities (km) | 16.9 ± 7.3 | 0.4–44.4 | 17.5 ± 8.8 | 0.4–44.4 | 24.5 ± 13.2 | 0.1–58.0 |
| Distance to rivers (km) | 1.3 ± 0.70 | 0.0–3.8 | 1.0 ± 0.7 | 0.0–3.8 | 1.1 ± 0.8 | 0.0–7.4 |
| Slope (°) | 10.2 ± 5.4 | 3.4–25.1 | 9.3 ± 6.0 | 0.0–33.6 | 12.8 ±8.7 | 0.0–47.1 |

**Nesting Sites.** We follow Franke (2017) in defining nesting sites as the specific location on the landscape where nests (the actual structure where eggs are laid) are located. We georeferenced (10-m accuracy) 41 Harpy Eagle nesting sites monitored as part of our long-term (2000–2017) research, primarily in the northern section of the study area (Fig. 1). Due to access issues, local permit acquisition, and safety issues, the northern area of the study region was sampled more heavily than the southern. This information was collected as part of a long-term program for Harpy Eagle conservation and research conducted by The Peregrine Fund in Panama and supported by local people, who offered anecdotal information that we systematically verified to confirm Harpy Eagle nesting sites. We verified whether sites were occupied or unoccupied through direct observation, and used as evidence of breeding the observation of an incubating adult or a nestling, fledgling, or dependent juvenile < 1 yr old (identified by plumage coloration). We followed the recommendation of previous authors and excluded alternate nesting sites from analyses to reduce the chance of pseudoreplication (Álvarez-Cordero 1996, Vargas González and Vargas 2011). In Panama, the use of alternate nests is uncommon and usually results from a mitigating factor (e.g., habitat alteration near the original nest), and we expect that excluding alternate nests from analysis is biologically and statistically justifiable.

**Nesting-site Variables.** Harpy Eagle home ranges in Panama average 16–24 km$^2$ (Vargas González and Vargas 2011). Based on prior research, we considered five natural and anthropogenic nesting site-level variables within 250 m (the resolution of our coarsest spatial data) of the nest and assumed to be important in selection of nesting habitat by Harpy Eagles (Vargas González 2008, Vargas González and Vargas 2011, Vargas González et al. 2014): slope, elevation, distance to rivers, distance to large communities (>500 inhabitants), and percent forest cover within 250m. We also included two additional forest cover variables that represent selection of primary breeding habitat at larger landscape scales (within 1 km and within 4 km of the nest), for a total of seven variables (Table 1). All variables of interest and their derived products were projected in EPSG: 32617, WGS 84, with a resolution of 250 m.

We used Program R (R Core Team 2016) to process the spatial data. To extract elevation and calculate slope, we used a digital terrain model (DEM) from the Shuttle Radar Topography Mission project (Shuttle Radar Topography Mission 2000, US Geological Survey 2006). Large communities were delineated according to the criteria of the Panama Statistics and Census Institute. Rivers were digitized (maximum scale 1:20,000) from parameters obtained at the Ministry of Public Works and the Cartographic Institute of Panama. The land cover layer was obtained through Panama's Ministry of the Environment (MiAMBIENTE 2003). We then aggregated primary and mature secondary forested land cover into one forested type excluding all non-forest land cover types (water, agriculture, flooded vegetation, urban, and mangrove). Lastly, to calculate percent of forested habitat within 1 km and 4 km of nests, we used a moving window method (raster package in R; Hijmans 2016). This method retains the 250-m resolution; however, each cell or "window" represents 1 km or 4 km surrounding each focal cell. Eagles might actually be selecting breeding sites at even larger scales than 4 km, however, we were limited to a distance of 4 km from the nest because our land cover data did not extend into Colombia, which borders our study region along the southeast (Fig. 1).
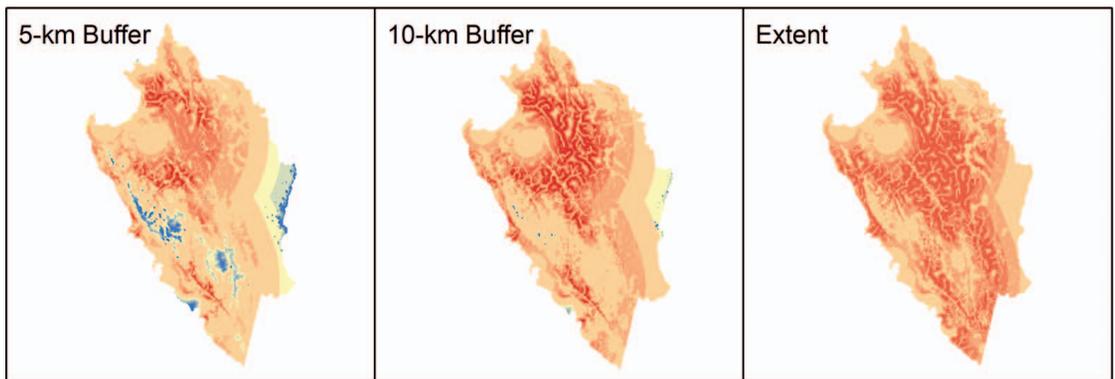
Figure 2.    Multivariate environmental similarity surface (MESS) depicting the similarity between three training samples (5-km buffer, 10-km buffer, and the study extent) for Harpy Eagles in Darien Province, Panama. Red indicates high similarity (positive values) between samples and extent, while blue (negative) shows the areas with the highest differences (i.e., areas where extrapolation is likely to occur).

**Modeling Habitat Suitability.** We modeled relative probability of occurrence, hereafter referred to as habitat suitability, using known nesting sites and available sites (i.e., background data) as a function of seven nest- and landscape-level covariates. We used MaxEnt 3.4.1 (Phillips et al. 2006, Phillips and Dudík 2008) in the R *dismo* environment (Hijmans et al. 2017). MaxEnt is a general-purpose machine learning method with a predictive performance consistently competitive with the highest performing presence-only methods (Elith et al. 2006, 2011), especially for small sample sizes (Hernandez et al. 2006).

A key assumption of presence-only models is that sampling is either random or representative throughout the landscape (Yackulic et al. 2013). However, presence-only data typically result from studies where presence records are spatially biased toward better surveyed areas (Kramer-Schadt et al. 2013). Since spatial bias generally results in environmental bias, the difference between occurrence records and background sampling may lead to inaccurate models (Phillips et al. 2009, Kramer-Schadt et al. 2013, Merow et al. 2013, Yackulic et al. 2013). Ideally, sampling bias would be incorporated into the model using a "bias file" representing the relative sampling effort (Kramer-Schadt et al. 2013) or "target-group" sampling, using presence locations of taxonomically similar species to estimate effort, under the assumption that those surveys would have recorded the focal species had it occurred (Phillips and Dudík 2008, Merow et al. 2013). However, because nests were most often

found opportunistically by local villagers who reside in the northern region of Darien, no survey effort or additional species occurrences were collected. All nests found by villagers were then validated by researchers to confirm species identification and eagle breeding status. To account for the strong bias in survey effort in the northern region, we chose background points to match the sampling bias. We randomly selected 10,000 background points from a buffer of 5 km surrounding the nesting sites. Means of the seven variables used in our analyses were relatively similar among nests, background points, and the entire study area (Table 1). Knowing we were extrapolating to unsampled areas, we created multivariate environmental similarity surfaces (MESS; Elith et al. 2010, 2011) to visually depict a measure of similarity between the training sample and the study extent, therefore, indicating where extrapolation will occur (Fig. 2). As expected, dissimilarity decreased as the extent of availability points got larger. However, dissimilarity was low even for the 5-km buffer, with only 17% of the cells indicating a negative dissimilarity value and only 3% showing high (dark blue) negative values, meaning increased extrapolation in those areas (Fig. 2).

Additionally, we spatially thinned the 41 nests by a distance of 1.24 km, the mean distance reported for alternative nests (Vargas González and Vargas 2011). This was done to reduce individual bias due to pooling nests across years and some pairs (33%) having multiple nests (Vargas González and Vargas 2011). Spatially thinning reduced the sample size to 27 nesting sites and only two nesting sites were from

the same pair; however the nests were found in different years (Fig. 1).

To generate models with maximum predictive ability, we considered models that exhausted potential covariate combinations with restrictions on model complexity. We only considered additive combinations of linear and quadratic covariate relationships because of the small sample size. All seven covariates were included, regardless of multi-collinearity. However, only the three forest cover variables were significantly correlated using Pearson's correlation coefficient ($>0.7$: Dormann et al. 2013) with each other (Table S1). Machine learning algorithms can receive correlated predictors and many studies have shown little difference in results when correlated variables are excluded (Elith et al. 2011, Kramer-Schadt et al. 2013). However, care should be taken when interpreting response curves of correlated predictor variables (Boria 2014). To reduce overfitting, MaxEnt allows a user-defined parameter to adjust the strength of the regularization penalty that penalizes the model proportional to the magnitude of coefficients, in turn shrinking many coefficients to zero, essentially removing them from the model (Phillips et al. 2006, Merow et al. 2013). Models were tuned across a range of complexity by varying the regularization multiplier from 0.5 to 4.0 in stepwise increments of 0.5. This resulted in a candidate set of eight models. We used the package ENMeval (version 0.3.0; Muscarella et al. 2014) to tune the models.

ENMeval also allows various methods to partition occurrence locations into testing and training groups for $k$-fold cross-validation. We chose the "block" method, which partitions the data according to latitude and longitude lines, and divides the data into four folds of equal numbers. Models are then run iteratively using $k - 1$ bins for training and the remaining one for testing (Muscarella et al. 2014). We chose this method because it accounts for spatial autocorrelation between testing and training data resulting from biased sampling and has shown greater transferability across time and space than other methods (Wenger and Olden 2012, Muscarella et al. 2014).

**Model Evaluation.** The final model was selected using two evaluation metrics: omission rates and area under the curve (AUC). Omission rates calculated using the 10% calibration omission threshold (OR) reflect overfitting to the calibration data when over 10% test omission (Shcheglovitova and Anderson 2013, Boria 2014). AUC of the receiver evaluates the model's ability to discriminate conditions at with-held occurrence locations from those at the background samples (Muscarella et al. 2014, Radosavljevic and Anderson 2014). An AUC = 0.5 indicates discrimination that is no better than random and AUC = 1 indicates prefect discrimination (Fielding and Bell 1997, Pearce and Ferrier 2000). Models with AUC $> 0.7$ have good discriminatory power (Hosmer and Lemeshow 1989, Kramer-Schadt et al. 2013). However, Yackulic et al. (2013) states AUC for presence-only modeling is a relative value for comparing performance between different models created from the same data and should not be subject to a singular threshold. Therefore, we chose the model with the lowest omission rate and highest AUC. Additionally, we tested the predictive ability of our final model using an out-of-sample method. We binned our predicted habitat suitability values into six bins using a quantile method (Morris et al. 2016). This method divides the continuous values of 0–1 into six bins of equal number of data points (i.e., cells). We chose six bins for two reasons; first, ten bins are excessive with only 14 out-of-sample nests, and second, we wanted to combine an equal number of bins to create a low-med-high suitability gradient for our conservation areas analysis. We then calculated a Spearman-rank correlation coefficient between frequency of the excluded data points within each bin and the bin rank (1 = low to 6 = high). A strong positive correlation indicates the model has good predictive accuracy (Boyce et al. 2002).

**Prioritization of Areas for Conservation.** We obtained protected area boundaries for the Republic of Panama from MiAMBIENTE and overlaid these and the study regions' watersheds to locate and quantify areas with suitable habitat. We examined habitat suitability at the watershed scale because MiAMBIENTE is currently using watersheds as a method to systematize conservation actions. For both protected areas and watersheds analysis, we reduced the six habitat suitability bins to three, resulting in a low–medium–high suitability gradient.

Results

The 27 Harpy Eagle nests used in the analysis were found in areas of high forest cover at the level of nesting site and surrounding landscape (Table 1). Nesting sites had a mean elevation of 138 masl, mean slope of 10°, and on average were found 1.3 km from a river and within 16.9 km of a large community (Table 1). We selected the model with the highest
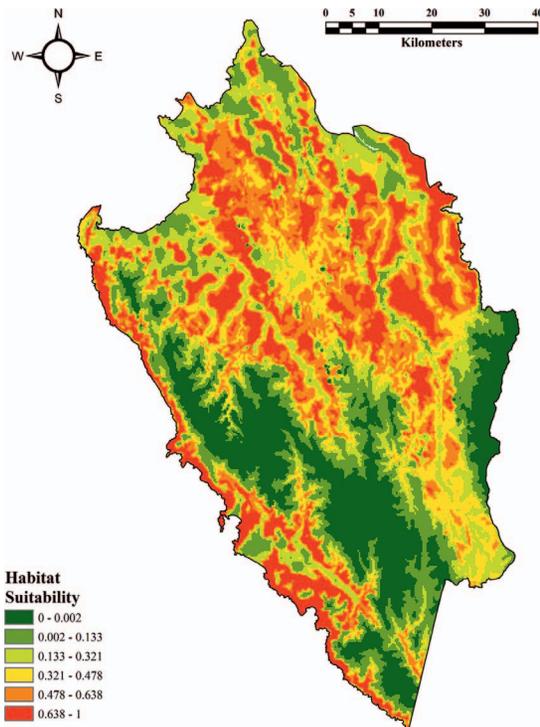
Figure 3.    Predicted binned cloglog habitat suitability (0 = low to 1 = high) for Harpy Eagle nesting sites in the Darien Province, Panama, study area.

Table 2.    Percent contribution of each predictor variable to the final model of habitat suitability for Harpy Eagles in Panama.

| Variable | Percent Contribution |
| --- | --- |
| Forest cover 1 km | 33.7 |
| Elevation | 32.7 |
| Distance to rivers | 24.5 |
| Slope | 5.2 |
| Forest cover 4 km | 3.8 |
| Distance to large communities | 0.1 |
| Forest cover 250 m | 0.0 |

cover within 1 km of the nesting site, elevation, and distance to rivers (Table 2). Habitat suitability values were nearly identical at forest cover (1 km) from 0–40%, whereas the increase was nearly exponential from 40–100% (Fig. 4). Contrary to forest cover 1 km, habitat suitability decreased abruptly in areas where elevation was greater than 300 masl (Fig. 4). Distance to rivers showed a positive relationship with habitat suitability. However, habitat suitability was never <0.5 (Fig. 4). Slope, forest cover at 4 km, and distance to large communities added little to the model (Table 2). Habitat suitability increased with increasing slope; the highest suitability was between

AUC and lowest OR from the candidate model set of eight models that varied in regularization coefficients. The regularization coefficient of the top model was MaxEnt's default of 1. The model fit the training data and discriminated nesting sites from background locations relatively well with AUC values of 0.76 and 0.74, respectively. The model had an OR of 0.18, indicating very slight overfitting (i.e., >0.10). For comparison, models fit with regularization coefficients of 0.5–2.5 had the same OR values, and coefficients of 3–4 had values >0.22. We transformed the raw model output using a complementary log-log (cloglog) transform (Phillips et al. 2017; Fig. 3).

Our out-of-sample predictive performance test indicated the final model showed high predictive performance. The Spearman-rank correlation between bin rank (1–6) and frequency of out-of-sample nests was strongly positive ($r = 0.95$, $P = 0.005$).

The final model contained all predictor variables except forest cover within 250 m of the nesting site (Table 2). The most influential variables were forest
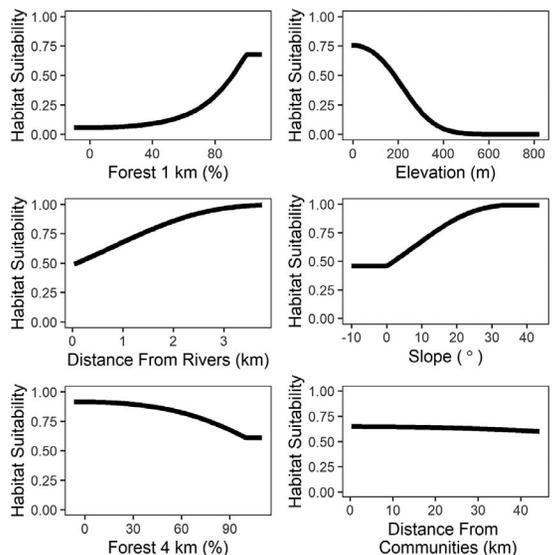


Figure 4.    Partial dependency plots showing the marginal effect of the predictor variables and the predicted habitat suitability for Harpy Eagles, Darien Province, Panama. Percent forest at the nest site (forest cover 250 m) is not shown here because it did not contribute to the model.
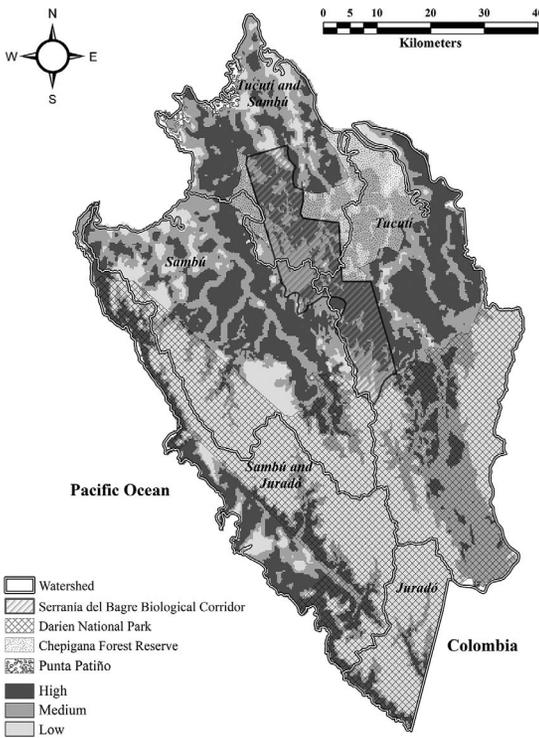
Figure 5. High – medium – low habitat suitability gradient for Harpy Eagles overlaid with watershed boundaries (labeled), and four protected areas in Darien Province, Panama. Cells were classified using a quantile method. Watersheds are identified by the names of their respective rivers (Tucutí, Sambú, and Juradó), or by rivers that mark their boundaries (Tucutí and Sambú, Sambú and Juradó), a naming protocol used by Panama's Ministry of the Environment (MiAMBIENTE).

approximately 10–50° (Fig. 4), which corresponded to the range of slopes in the study extent (Table 1). Forest cover at 4 km and distance to large communities both had a slightly negative relationship with habitat suitability, and although the relationship was negative, habitat suitability never fell below 0.5, as also found for distance to rivers (Fig. 4).

By collapsing six bins into three, we created a habitat suitability gradient from low to high (Fig. 5). Of the 5636 km$^2$ of land area analyzed, 1888 km$^2$ (34%) showed highly suitable breeding habitat, 1868 km$^2$ (33%) ranked medium suitability, and 1880 km$^2$ (33%) ranked low habitat suitability for the Harpy Eagle according to the model (Table 3). Of the 14 out-of-sample nest sites, 12 were located in highly suitable habitat, two in medium, and none in low suitability.

Of the five watersheds we examined separately, the Tucutí watershed was the largest with 1838 km$^2$ (33% of total land area), followed by the Sambú, the watershed between the Sambú and Jurado rivers, the watershed between Tucutí and Sambú rivers, and the Juradó watershed with areas of 1496 km$^2$ (26%), 1070 km$^2$ (19%), 891 km$^2$ (16%), and 341 km$^2$ (6%), respectively (Table 3, Fig. 5). The basin with the greatest area of highly suitable habitat was Tucutí (665 km$^2$, 35% of total) followed by Sambú (462 km$^2$, 25% of total), the watershed between the Tucutí and Sambú rivers (399 km$^2$, 21%), the watershed between Sambú and Juradó rivers (329 km$^2$, 17%), and Juradó (33 km$^2$, 2% of total; Table 3, footnote 1). When considering both high and medium suitable habitat together, the pattern

Table 3. Estimates of the extent of breeding habitat for the Harpy Eagle in five watersheds of Darien, Panama. Breeding habitats are classified as high suitability, medium suitability, or low suitability, based on our modeling, and estimates of area and proportion of suitable habitat for each watershed are shown. Watersheds are identified by the names of their respective rivers (Sambú, Tucutí, and Juradó), or by rivers that mark their boundaries (Tucutí and Sambú, Sambú and Juradó), a naming protocol used by Panama's Ministry of the Environment (MiAMBIENTE).

| | WATERSHED | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | SAMBÚ | | TUCUTÍ | | JURADÓ | | SAMBÚ & JURADÓ | | TUCUTÍ & SAMBÚ | | TOTAL |
| HABITAT SUITABILITY | AREA (km$^2$) | % | AREA (km$^2$) | % | AREA (km$^2$) | % | AREA (km$^2$) | % | AREA (km$^2$) | % | AREA (km$^2$) |
| High[1] | 462 | 31 | 665 | 36 | 33 | 10 | 329 | 31 | 399 | 45 | 1888 |
| Medium | 514 | 34 | 695 | 38 | 52 | 15 | 226 | 21 | 381 | 43 | 1868 |
| Low | 520 | 35 | 478 | 26 | 256 | 75 | 515 | 48 | 111 | 12 | 1880 |
| **Total Area** | **1496** | | **1838** | | **341** | | **1070** | | **891** | | **5636** |

[1] Of the 1888 km$^2$ of highly suitable land in the study, land in Sambú watershed made up 25%; land in Tucutí, 35%; land in Juradó, 2%; land in Sambú and Juradó, 17%; and Tucutí and Sambú, 21%.

Table 4. Estimates of the extent of breeding habitat for the Harpy Eagle in three protected areas of Darien Province, Panama. Breeding habitats are classified as high suitability, medium suitability, or low suitability, based on our modeling. Estimates of area and proportion of suitable habitat for each protected area are shown.

| | PROTECTED AREA | | | | | | |
|---|---|---|---|---|---|---|---|
| | CHEPIGANA FOREST RESERVE | | DARIEN NATIONAL PARK | | SERRANÍA BAGRE BIOLOGICAL CORRIDOR | | TOTAL |
| HABITAT SUITABILITY | AREA ($km^2$) | % | AREA ($km^2$) | % | AREA ($km^2$) | % | AREA ($km^2$) |
| High[1] | 209 | 57 | 392 | 15 | 232 | 54 | 833 |
| Medium | 136 | 37 | 704 | 27 | 175 | 41 | 1015 |
| Low | 20 | 6 | 1516 | 58 | 24 | 5 | 1560 |
| **Total Area** | **365** | | **2612** | | **431** | | **3408** |

[1] Of the 1888 $km^2$ of highly suitable land identified in our study area, land in Chepigana Forest Reserve made up 11%; land in Darien National Park, 21%; Serranía Bagre Biological Corridor, 12%.

remained the same: Tucutí watershed with the most suitable habitat (36% of total), followed by Sambú (26%), Tucutí and Sambú (21%), Sambú and Juradó (15%), and Juradó (2%). Of four protected areas located in the study area, 833 $km^2$ (15% of total) had highly suitable habitat (Fig. 5). The protected area with the greatest proportion of highly suitable habitat was Darien National Park with 21% (392 $km^2$), followed by the Serranía de Bagre Biological Corridor with 12% (232 $km^2$), and finally, the Chepigana Forest Reserve with 11% (209 $km^2$; Table 4, footnote 1). The same pattern holds true when considering both high and medium suitable habitat together; Darien National Park contains the most (29% of total), then the Serranía de Bagre Biological Corridor (11%), and lastly the Chepigana Forest Reserve (9%). The fourth, Punta Patiño Wetland, located within the northern region of the La Palma watershed, contained <1% suitable habitat and is not further addressed here.

DISCUSSION

The observed specificity of suitable habitat for nesting sites suggests that the Harpy Eagle has a reduced ecological amplitude. In particular, we observed a positive association with forest cover in the landscape (1 km), a greater likelihood of occurrence below 300 masl, and distances of <1 km to rivers. Habitat specificity observed in this study, combined with the eagles' nearly clumped distribution at landscape and regional levels, their low abundance, and the progressive destruction of forests in the study region, argues for recognition of the Harpy Eagle as a conservation-dependent species (Global Raptor Information Network 2017), and

designation of their breeding habitat as vulnerable and requiring sustainable management.

We developed the first predictive habitat distribution model for Harpy Eagle breeding habitat. We found the model had good predictive ability, and therefore can be used to guide conservation actions benefitting Harpy Eagles. Variables included in our habitat distribution model suggest that Harpy Eagle nesting sites occurred in areas with high forest cover. Forest cover within 1 km of nesting sites made the greatest contribution to the models, whereas forest cover within 4 km had a minor influence, and forest cover within 250 m had no influence. We speculate that high forest cover within 1 km of nesting sites may provide complex forest structure and sufficient prey densities needed by juvenile eagles to improve flight and hunting skills during their nearly 2-yr post-fledging dependency period. Limited data on juvenile dispersal indicate that most movements in the first 2 yr after fledging occur within approximately 1 km of the nest (Muniz-Lopez 2012). The dependency on forests for nesting is consistent with results from prior research in Panama (Vargas González and Vargas 2011), Peru (Giudice et al. 2007), and Ecuador (Muñiz-Lopez 2008).

Elevation and slope are two important physiographic factors that influence suitability of Harpy Eagle nesting sites. Although elevations in the study area ranged from 0 to 5922 masl, nesting sites were found at low elevations, predominantly approximately 100 masl, and elevation was the second-most important variable in the model. The biological reasons Harpy Eagles nest at lower elevation are less clear. Preferred prey, especially sloths (*Bradypus variegatus* and *Choloepus hoffmanni*) and kinkajous (*Potus flavus*), occur from low to middle elevations

(Muñiz-Lopéz 2008, Vargas González and Vargas 2011), and diversity and abundance of Harpy Eagle prey may be greater at lower elevations (Pires et al. 2000). Additionally, forest structure at lower elevations may be more suitable for breeding and hunting. A common trend in Neotropical forest structure is a decrease in forest height with elevation, with most canopy volume found in mid-levels of lowland forests (Asner et al. 2014, Girardin et al. 2014). Lower elevations have tall trees suitable for nesting; in addition, lower elevations provide a forest profile of emergent canopy above the dense mid-story, a structure suitable to the perch-and-ambush hunting method favored by Harpy Eagles. Despite published records of Harpy Eagles observed at high elevations (Álvarez del Toro 1980), our observation of nesting at low elevations is consistent with findings from Peru (Giudice 2007), Guyana (Rettig 1978), and Ecuador (Muñiz-Lopez 2008). Slope was only minimally influential in informing the model, and we observed Harpy Eagle nests on slopes averaging 10°. Perhaps the association between elevation and slope influences microclimatic factors (e.g., temperature, light intensity, and humidity) favorable to incubation, hatching, or nestling-rearing.

We found that Harpy Eagle nests were more likely to be closer to rivers (mean distance 1.25 km) compared to available locations. Harpy Eagles use open spaces around rivers to observe, chase, and catch prey (Vargas González 2008). Forest openings associated with rivers also promote the growth of plant species (e.g., *Cecropia* spp.) with leaves and fruits favored by primary (kinkajous and sloths) and secondary (primates) prey species (Franco-Rosselli and Berg 1997, Kays 1999, Ramirez et al. 2011). Interestingly, the model indicated a positive relationship, meaning suitable habitat increases with increasing distance to rivers, which may have been an artifact of the small range of distance values due to the extensive river system in the study area.

Given our approach, and the conservative distance from nests that available points were selected, distance to large communities (mean 17 km) was not an important predictor in our model (Table 2). Prior research in Panama and Venezuela (Álvarez-Cordero 1996) and in Peru (Piana 2007) documented some tolerance to anthropogenic pressure in their breeding habitat, but the level and type of disturbance that breeding Harpy Eagles can tolerate remain unquantified. We suspect that probability of incidental shooting increases directly with the number of humans living near nesting sites (Trinca et al. 2008), and that increasing distance from nesting sites to population centers provides a buffer against persecution. Further, habitat disturbance increases with size of settlements, and diminishes with distance from settlements, such that intact forests needed for nesting are likely to occur at greater distances from large settlements than small ones. As human populations grow and spread in Darien, the availability of intact forests free from persecution will increasingly become a limiting factor for Harpy Eagle reproduction.

Eighty-six percent ($n=12$) of the nesting sites used in the out-of-sample validation process were found in highly suitable habitat, while the remaining two validation nests were found in medium suitable habitat and none in low suitability. Based on area requirements and density estimates (Vargas González and Vargas 2011), the highly suitable breeding habitat in the study region can harbor a population of between 76 and 113 breeding Harpy Eagle pairs. We recognize that additional improvements to the model could be derived by including other data that condition the selection of nesting sites, such as the abundance and diversity of prey and human hunting pressure, data that are unavailable at the present time. We envision practical uses for the model, such as testing hypotheses regarding productivity at sites with high and low habitat suitability.

Despite the ability of our model to discriminate high quality nesting habitat, we still observed one Harpy Eagle pair (of the 27 used to create the model) nesting in low suitability habitat and three in medium suitability habitat. We suspect that the existence of such nesting sites at the time of analysis may have been due to fidelity to ancestral nesting sites (Viter 2013) despite recent anthropogenic changes to surrounding habitat. Since 2000, Panama has experienced significant deforestation (Food and Agriculture Organization of the United Nations 2011). To explore forest loss within the landscape around the nests used in the model building, we calculated the percent forest loss within 1 km of nests using the Hansen et al. (2013) global forest loss layer. We chose the 1-km scale because it proved the most important scale in the model (Table 2), with the highest habitat suitability between 40% and 80% forest cover. We found that nest sites experienced highly variable forest cover loss, with a median loss of 3.4% (range = 0.1–45.5%) between 2000 and 2018; our monitoring in 2017 indicated 88% of the monitored nests were unused (i.e., alternative nests

were not known, and we assume that breeding attempts did not occur at 88% of territories in 2017). Whether the abundance of unused sites was due to forest loss or another human pressure is unknown. As stated above, data on human persecution would be invaluable in determining nesting-site selection. We also note that converting the continuous model output to a gradient of low to high may not be biologically meaningful for the Harpy Eagle.

In terms of protected areas, Darien National Park contained 392 km$^2$ of highly suitable habitat, approximately equal to the combined areas of Chepigana Forest Reserve (209 km$^2$) and Serranía de Bagre Biological Corridor (232 km$^2$), two administrative units that share a common border (i.e., geographically and biologically they are a single forest). This observation highlights the fact that lands outside Darien National Park in the northern portion of the study area are equally important for conservation of Harpy Eagles. This is a concern for Harpy Eagle conservation in Darien, because extractive forestry and other land use practices that damage forest cover and, according to our model, will reduce habitat suitability, are permitted under authority of MiAMBIENTE (Panamá 1960, 1980, 1994, 1995a, 1995b) in both Chepigana and Serranía de Bagre. There are initiatives for forest use and exploitation in these regions, for which rapid ecological assessments have been developed (González et al. 2011, Fuenmayor 2011) that do not describe the importance of these habitats for the species; a situation that potentially puts the largest known population of Harpy Eagles in Central America at risk (Vargas González et al. 2006).

The Harpy Eagle is the National Bird of Panama (Panamá 1995, 2002) where its conservation status is classified as Endangered (MiAMBIENTE 2016). Considering the spatial distribution of suitable breeding habitat for Harpy Eagles in and outside protected areas with varying levels of forest exploitation, improvements to current initiatives in place for conservation are warranted. We recommend reevaluation of the management categories of the Chepigana Forest Reserve and the Serranía de Bagre Biological Corridor, given the importance of their ecosystems for the reproduction and stability of Harpy Eagle populations.

**Implications for Conservation.** Our predictive model clearly identified areas of importance for the conservation of Harpy Eagles. The greatest conservation implication of this model lies in its practical utility to identify the landscape where a population that is in danger and vulnerable is concentrated due to the accelerated and dynamic transformation of the habitat. Our model allows managers to prioritize targeted conservation initiatives, such as environmental education, community development programs, and sustainable community-based activities, to help curb the deterioration of natural ecosystems, and to combat Harpy Eagle persecution. Likewise, it allowed us to determine that the areas with high suitability lacked governmental legislation restricting the use of forest resources, a situation with negative implications for the eagle and the underlying biodiversity that coexists in the natural environment where it is found. Although the effect of the extirpation or population reduction of the Harpy Eagle in the ecosystems where it coexists with other species has not been evaluated, the importance of top predators to maintain the integrity and equilibrium in the ecosystem is well known (Bierregaard 1998, Beschta and Ripple 2011). Finally, this study offers a replicable methodology to be applied and tested in other regions.

SUPPLEMENTAL MATERIALS (available online). Table S1: Pearson's correlations coefficients for all predictor variables used in the model.

## Literature Cited

Aguiar-Silva, F. H., T. M. Sanaiotti, O. Jaudoin, A. C. Srbek-Araujo, G. Siqueira, and A. Banhos (2012). Harpy Eagle sightings, traces and nesting records at the Reserva Natural Vale, a Brazilian Atlantic Forest remnant in Espírito Santo, Brazil. Revista Brasileira De Ornitologia 20:148–155.

Álvarez-Cordero, E. (1996). Biology and conservation of the Harpy Eagle in Venezuela and Panama. Ph.D. dissertation, University of Florida, Gainesville, FL, USA.

Álvarez del Toro, M. (1980). Las Aves de Chiapas, Second Ed. Universidad Autónoma de Chiapas, Tuxtla Gutiérrez, Chiapas, México.

Asner, G. P., C. B. Anderson, R. E. Martin, D. E. Knapp, R. Tupayachi, F. Sinea, and Y. Malhi (2014). Landscape-scale changes in forest structure and functional traits along an Andes-to-Amazon elevation gradient. Biogeosciences 11:843–856.

Beschta, R. L., and W. J. Ripple (2011). The role of large predators in maintaining riparian plant communities and river morphology. Geomorphology 157:88–98.

Bierregaard, R. O. (1998). Conservation status of birds of prey in the South American tropics. Journal of Raptor Research 32:19–27.

Boria, R. (2014). Methodological advancements for improving performance and generating ensemble ecological niche models. M.S. thesis, City College of the City University of New York, NY, USA.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow (2002). Evaluating resource selection functions. Ecological Modelling 157:281–300.

Brown, J. H. (2001). Mammals on mountainsides: Elevational patterns of diversity. Global Ecology and Biogeography 10:101–109.

Cardador, L., M. De Cáceres, D. Giralt, G. Bota, N. Aquilué, B. Arroyo, F. Mougeot, C. Cantero-Martínez, L. Viladomiu, J. Rosell, F. Casas, et al. (2015). Tools for exploring habitat suitability for steppe birds under land use change scenarios. Agriculture, Ecosystems and Environment 200:119–125.

Curti, M., and U. Valdez (2009). Incorporating community education in the strategy for Harpy Eagle conservation in Panama. Journal of Environmental Education 40:3–16.

Dinerstein, E., D. M. Olson, D. J. Graham, A. L. Webster, S. A. Primm, M. P. Bookbinder, and G. Ledec (1995). Conservation Assessment of the Terrestrial Ecoregions of Latin America and the Caribbean. The World Bank, Washington, DC, USA.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, B. Gruber, B. Lafourcade, P. J. Leitão, T. Munkemüller, et al. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Elith, J., S. Ferrier, A. Guisan, C. H. Graham, R. P. Anderson, M. Dudi, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, et al. (2006). Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., and J. R. Leathwick (2009). Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology and Systematics 40:677–697.

Elith, J., M. Kearney, and S. Phillips (2010). The art of modelling range-shifting species. Methods in Ecology and Evolution 1:330–342.

Elith, J., S. J. Phillips, T. Hastie, M. Dudík, Y. E. Chee, and C. J. Yates (2011). A statistical explanation of MaxEnt for ecologists. Diversity and Distributions 17:43–57.

Ferguson-Lees J., and D. A. Christie (2001). Raptors of the World. Houghton Mifflin Company, Boston, MA, USA.

Fielding, A. H., and J. F. Bell (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Food and Agriculture Organization of the United Nations (2011). State of the World's Forests 2011. Food and Agriculture Organization of the United Nations, Rome, Italy.

Franco-Rosselli, P., and C. C. Berg (1997). Distributional patterns of Cecropia (Cecropiaceae): A panbiogeographic analysis. Caldasia 19:285–296.

Franke, A., C. McIntyre, and K. Steenhof (2017). Terminology. In Applied Raptor Ecology: Essentials from Gyrfalcon Research (D. L. Anderson, C. J. W. McClure, and A. Franke, Editors). The Peregrine Fund, Boise, ID, USA. pp. 33–42.

Fuenmayor, Q. D. (2011). Producción Forestal Sostenible y Conservación con Participación Comunitaria en la Reserva Forestal de Chepigana de Darién. Evaluación Ecológica Rápida, Autoridad Nacional del Ambiente (ANAM) Proyecto PD 482/02 Rev. 2. Panama City, Panama Province, Panama.

Gallardo, J. C., and F. J. Vilella (2017). Conservation status assessment of the Sharp-shinned Hawk, an endangered insular raptor in Puerto Rico. Journal of Field Ornithology 88:349–361.

Geise, L., L. G. Pereira, D. E. P. Bossi, and H. G. Bergallo (2004). Pattern of elevational distribution and richness of non-volant mammals in Itatiaia National Park and its surroundings, in southeastern Brazil. Brazilian Journal of Biology 64:599–612.

Gentry, A. H. (1986). Contrasting phytogeographic patterns of upland and lowland Panamanian plants. In The Botany and Natural History of Panama: La Botánica e Historical Natural de Panama (W. G. Darcy and M. D. Correa-A., Editors). Missouri Botanical Garden, St. Louis, MO, USA. pp. 146–160.

Girardin, C. A. J., W. Farfan-Rios, K. Garcia, K. J. Feeley, P. M. Jørgensen, A. A. Murakami, L. C. Pérez, R. Seidel, N. Paniagua, A. F. Fuentes Claros, C. Maldonado, et al. (2014). Spatial patterns of above-ground structure,

biomass and composition in a network of six Andean elevation transects. Plant Ecology and Diversity 7:161–171.

Giudice, R., R. Piana, and M. Williams (2007). Tree architecture as a determinant factor for nest-tree selection by Harpy Eagles. In Neotropical Raptors (K. L. Bildstein, M. J. Bechard, P. Porras-Peñaranda, E. Campo, and C. J. Farmer, Editors). Hawk Mountain Sanctuary, Orwigsburg, PA, USA. pp. 14–22.

Global Raptor Information Network (2017). Species account Harpy Eagle *Harpia harpyja*. http://www.globalraptors.org.

González, M., M. Guevara, and K. Aparicio (2011). Producción Forestal Sostenible y Conservación con Participación Comunitaria en la Reserva Forestal de Chepigana de Darién, Panamá. Evaluación Rural Participativa para la Reserva Forestal de Chepigana. Autoridad Nacional del Ambiente (ANAM). Proyecto PD 482/07 REV. 2(F). Panama City, Panama Province, Panama.

Hamilton, S. H., C. A. Pollino, and A. J. Jakeman (2015). Habitat suitability modelling of rare species using Bayesian networks: Model evaluation under limited data. Ecological Modelling 299:64–78.

Hansen, M. S., P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, et al. (2013). High-resolution global maps of 21st-century forest cover change. Science 342:850–854.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography 5:773–785.

Hijmans, R. J. (2016). Raster: Geographic data analysis and modeling. R Package version 2.9-5. https://CRAN.R-project.org/package=raster.

Hijmans, R. J., S. J. Phillips, J. Leathwick, and J. Elith (2017). Dismo: Species distribution modeling. R Package version 1.1-4. http://CRAN.R-project.org/package=dismo.

Hosmer, D., and S. Lemeshow (1989). Applied Logistic Regression. John Wiley and Sons, New York, NY, USA.

Instituto Nacional de Estadística and Censo de Panamá (2016). Meteorología de la república de Panamá. http://www.contraloria.gob.pa/.

International Union for Conservation of Nature (2017). *Harpia harpyja*. Red List of Threatened Species. http://www.iucnredlist.org.

Kays, R. (1999). Food preferences of kinkajous (*Potos flavus*): A frugivorous carnivore. Journal of Mammalogy 80:589–599.

Kramer-Schadt, S., J. Lindenborn, V. Reinfelder, M. Stillfried, B. Schr, I. Heckmann, A. K. Scharf, D. M. Augeri, S. M. Cheyne, A. J. Hearn, J. Ross, et al. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions 19:1366–1379.

Köppen. W. 1936. Das geographische system der klimate, *fide* Handbuch der Klimatologie. 1 (W. Kóppen and M. Geiger, Editors). Borntraeger, Berlin, Germany.

Maleki, S., A. R. Soffianian, S. S. Koupaei, S. Saatchi, S. Pourmanafi, and F. Sheikholeslam (2016). Habitat mapping as a tool for water birds conservation planning in an arid zone wetland: The case study Hamun wetland. Ecological Engineering 95:594–603.

Meerman, J. C., and J. Clabaugh (2010). Biodiversity and environmental resource data system of Belize. Belmopan, Belize. www.biodiversity.bz/find/species/profile/profile.phtml?species_id51963.

Merow, C., M. J. Smith, and J. A. Silander (2013). A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. Ecography 36:1058–1069.

Ministerio de Ambiente de Panamá (MiAMBIENTE) (2003). Informe Final de Resultados de la Cobertura Boscosa y Uso del Suelo de la República de Panamá: 1992–2000. Panama City, Panama Province, Panama.

Ministerio de Ambiente de Panamá (MiAMBIENTE) (2016). Reglamentación de especies de fauna y flora amenazada y en peligro de extinción, y se dictan otras disposiciones. Resolución No. AG.0051-2008. http://www.miambiente.gob.pa.

Moisen, G. G., J. Edwards, and P. E. Osborne (2006). Further advances in predicting species distributions. Ecological Modeling 199:129–131.

Morris, L. R., K. M. Proffitt, and J. K. Blackburn (2016). Mapping resource selection functions in wildlife studies: concerns and recommendations. Applied Geography 76:173–183.

Muñiz-López, R. (2008). Revisión de la situación del águila harpía *Harpia harpyja* en Ecuador. Cotinga 29:42–47.

Muñiz-López, R., R. Liminana, G. D. Cortes, and V. Urios (2012). Movements of Harpy Eagles *Harpia harpyja* during their first two years after hatching. Bird Study 59:509–514.

Muñiz-López, R. (2017). Harpy Eagle (*Harpia harpyja*) mortality in Ecuador. Studies on Neotropical Fauna and Environment 52:81–85.

Munro, K. I., I. G. Warkentin, and Ch. M. Doucet (2016). Testing a habitat suitability index model for Boreal Owls in western Newfoundland, Canada. Journal of Raptor Research 50:325–337.

Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, and R. P. Anderson (2014). Enmeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods in Ecology and Evolution 5:1198–1205.

Myers N., R. Mittermeier, C. Mittermeier, F. da Fonseca, and J. Kent (2000). Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Olson, D. and E. Dinerstein (2002). The Global 200: Priority ecoregions for global conservation. Annals of the Missouri Botanical Garden 89:199–224.

Panamá (1960). Decreto No. 94 (De 28 de septiembre de 1960) por el cual se delimitan las reservas forestales en la República de Panamá. Gaceta oficial, martes 25 octubre de 1960.

Panamá (1980). Decreto ejecutivo No. 21, por el cual se declara Parque Nacional, a un área determinada en la provincia de Darién. Gaceta oficial, miércoles 27 de agosto de 1980.

Panamá (1994). Ley No. 6 (De 17 mayo de 1994) por la cual se modifican los Decretos No. 94 de 28 de septiembre de 1960 y la ley No. 52 de 2 de diciembre de 1977 y se faculta al Instituto de Recursos Naturales Renovables (INRENARE) para que se efectúe nueva demarcación de las Reservas Forestales de Tonosí, Chepigana y La Tronoea. Gaceta oficial, jueves 19 mayo de 1994.

Panamá (1995a). Ley No. 24 del 7 de Junio de 1995 sobre Vida Silvestre. República de Panamá.

Panamá (1995b). Resolución J.D. No. 01-95 (De 26 de julio de 1995) por medio de la cual se crea el Corredor Biológico de La Serranía de Bagre en la provincia de Darién. Gaceta oficial, viernes 11 de agosto de 1995.

Panamá (2002). Ley No. 18 del 10 de Abril de 2002 que declara al águila arpía como Ave Nacional de Panamá, y dicta otras disposiciones. República de Panamá.

Pearce, J., and S. Ferrier (2000). Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133:225–245.

Phillips, S. J., R. P. Anderson, M. Dudík, R. E. Schapire, and M. E. Blair (2017). Opening the black box: An open-source release of Maxent. Ecography 40:887–893.

Phillips, S. J., R. P. Anderson, and R. E. Schapire (2006). Maximum entropy modeling of species geographic distributions. Ecological Modelling 190:231–259.

Phillips, S. J., and M. Dudík (2008). Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. Ecography 31:161–175.

Phillips, S. J., M. Dudík, J. Elith, C. H. Graham, A. Lehmann, J. Leathwick, and S. Ferrier (2009). Sample selection bias and presence-only distribution models: Implications for background and pseudo-absence data. Ecological Applications 19:181–197.

Piana, R. P. (2007). Anidamiento y dieta de *Harpia harpyja* Linnaeus en la comunidad nativa de Infierno, Madre de Dios, Perú. Revista Peruana de Biología 14:135–138.

Pires, C. L., Y. L. R. Leite, G. A. B. da Fonseca, and M. T. da Fonseca (2000). Biogeography of South American forest mammals: Endemism and diversity in the Atlantic forest. Biotropica 32:872–881.

Please, T., N. Reyes-Amaya, L. Castro-Vásquez, S. Giraldo and O. Feliciano (2016). Distribution and current state of knowledge of Hoffmann's two-toed sloth (*Choloepus hoffmanni*) in Colombia, with comments of the variations of its external morphological traits. Therya 7:407–421.

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Radosavljevic, A., and R. P. Anderson (2014). Making better Maxent models of species distributions: Complexity, overfitting and evaluation. Journal of Biogeography 41:629–643.

Ramirez, O., C. Vaughan, G. Herrera, and R. Guries (2011). Temporal and spatial resource use by female three-toed sloths and their young in an agricultural landscape in Costa Rica. Revista Biología Tropical 59:1743–1755.

Rettig, N. (1978). Breeding behavior of the Harpy Eagle (*Harpia harpyja*). The Auk 95:629–643.

Sara, M. (2014). Spatial analysis of Lanner Falcon habitat preferences: Implication for agroecosystems management at landscape scale and raptor conservation. Biological Conservation 178:173–184.

Schulenberg, T. S. (2020). Harpy Eagle (*Harpia harpyja*), version 1.0. In Birds of the World (T. S. Schulenberg, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.hareag1.01.

Seoane, J., J.-H. Justribo, F. Garcia, J. Retamar, C. Rabadan, and J. C. Atienza (2006). Habitat-suitability modeling to assess the effects of land-use changes on Dupont's lark *Chersophilus duponti*: A case study in the Layna Important Bird Area. Biological Conservation 128:241–252.

Shcheglovitova, M., and R. P. Anderson (2013). Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. Ecological Modelling 269:9–17.

Shuttle Radar Topography Mission (2000). Shuttle Radar Topography Mission. NASA Jet Propulsion Laboratory, California Institute of Technology. http://www2.jpl.nasa.gov/srtm/index.html.

Stiles, F. G., and A. F. Skutch (1989). A Guide to the Birds of Costa Rica. Comstock Publishing Associates, Ithaca, NY, USA.

Thiollay, J. M. (2007). Raptor communities in French Guiana: Distribution, habitat selection, and conservation. Journal of Raptor Research 41:90–105.

Tosi, J. A. (1971). Inventariación y Demostraciones Forestales, Panamá: Zonas de Vida. Organización de las Naciones Unidas para el Desarrollo, Roma, Italy.

Trinca, C. T., S. F. Ferrari, and A. C. Lees (2008). Curiosity killed the bird: Arbitrary hunting of Harpy Eagles *Harpia harpyja* on an agricultural frontier in southern Brazilian Amazonia. Cotinga 30:12–15.

United Nations Development Program – Ministry of Economics and Finance of Panama (2003). Diversidad Biológica de Darién: Situación Actual e Indicadores para su Integración al Desarrollo de la Región. Programa de las Naciones Unidas para el Desarrollo y Ministerio de Economía y Finanzas, Panamá City, Panamá.

US Geological Survey (2006). Shuttle Radar Topography Mission. "Finished". https://www.usgs.gov/centers/eros/science/usgs-eros-archive-digital-elevation-shuttle-

radar-topography-mission-srtm-non?qt-science_center_objects=0#qt-science_center_objects.

Vargas González, J. de J. (2008). Estrategia para la conservación del hábitat reproductivo del águila arpía (*Harpia harpyja*) en la región de Darién, Panamá. M.S. thesis, Universidad Nacional Experimental de los Llanos Occidentales Ezequiel Zamora, Guanare, Venezuela.

Vargas González, J. de J., and F. H. Vargas (2011). Nesting density of Harpy Eagles in Darien with population size estimates for Panama. Journal of Raptor Research 45:199–210.

Vargas González, J. de J., F. H. Vargas, D. Carpio, and C. J. W. McClure (2014). Características de la vegetación en sitios de anidación del águila arpía (*Harpia harpyja*) en Darién, Panamá. Ornitología Neotropical 25:207–218.

Vargas González, J. de J., D. Whitacre, R. Mosquera, J. Albuquerque, R. Piana, J. M. Thiollay, C. Márquez, J. Sánchez, M. Lezama-López, S. Midence, S. Matola, et al.

(2006). Estado y distribución actual del águila arpía (*Harpia harpyja*) en Centro y Sur América. Ornitología Neotropical 17:39–55.

Viter, S. G. (2013). Nest site fidelity and occupancy in birds of prey (Falconiformes) in specially protected and unprotected areas of eastern Ukraine. Russian Journal of Ecology 44:36–42.

Wenger, S. J., and J. D. Olden (2012). Assessing transferability of ecological models: An underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3:260–267.

Yackulic, C. B., R. Chandler, E. F. Zipkin, J. A. Royle, J. D. Nichols, E. H. Campbell Grant, and S. Veran (2013). Presence-only modelling using Maxent: When can we trust the inferences? Methods in Ecology and Evolution 4:236–243.

ERRATUM

# Geophagy by a Wild Merlin

Jake Burroughs

*The Journal of Raptor Research* would like to clarify the author's affiliation. Although Jake Burroughs was a volunteer with the Seattle Merlin Project when the reported observation (*Journal of Raptor Research* 54:356) was made, questions about the Seattle Merlin Project should be addressed to the Project directors, Kim McCormick (kim.mccormick@comcast.net) and Ben Vang-Johnson (bvjohnson87@gmail.com).

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