Species distribution and conservation assessment of the black-headed night monkey (*Aotus nigriceps*): a species of Least Concern that faces widespread anthropogenic threats

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Received: 16 October 2020 / Accepted: 1 June 2021 / Published online: 12 June 2021
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Abstract
Deforestation rates in the Brazilian Amazon have been steadily increasing since 2007. Recent government policy, the projected growth of agriculture, and the expansion of the cattle industry are expected to further pressure primates within the Amazon basin. In this study, we examined the anthropogenic impact on the widely distributed black-headed night monkey, *Aotus nigriceps*, whose distribution and population status have yet to be assessed. We (1) modeled potential species distribution in *A. nigriceps*, (2) estimated the impact of habitat loss on population trends, and (3) highlight landscape-based conservation actions that maximize the potential for their long-term sustainability. We found the black-headed night monkey to be restricted by several biotic and environmental factors including forest cover, isothermality, precipitation, temperature, and elevation. Over the last two decades, over 132,908 km² of tree cover (18%) has been lost within their currently recognized range based on satellite imagery. Based on a balance training omission, predicted area, and threshold values (BPTP), suitable habitat was only 67% (1,069,948 km²) of their hypothesized range, a loss of 16.5% from 2000, with just nearly a third of suitable habitat currently within protected areas. Over the last two decades, an estimated minimum 1.6 million individuals have been lost due to loss of suitable habitat. Projected deforestation rates equate to an additional loss of 94,458 km² of suitable habitat over the next decade. Although classified as a species of Least Concern, we suggest that *A. nigriceps* may likely be more at risk than previously described. The future impact of the continued expansion of monoculture crops, cattle ranching, and wildfires is still unknown. However, we outline several steps to ensure the long-term viability of this nocturnal primate and other sympatric species throughout the Amazon Basin.

Keywords Amazon · *Aotus nigriceps* · Peru · Deforestation · Maxent · Primate · Red list · Rainforest

Introduction
Deforestation rates in the Amazon rainforest are at their highest levels since 2007 due to the expansion of monoculture agriculture (e.g., palm oil and soy), cattle ranching, wildfires, and urban expansion (Davidson et al. 2012; PRODES 2020); with models predicting up to 40% of all Amazonian forests will be lost by 2050 (Gomes et al. 2019). These at-risk areas overlap with many neotropical primate species whose populations may suffer large declines. This includes the black-headed night monkey, *Aotus nigriceps* (Dollman 1909), one of eleven currently recognized species of night monkey found in Central and South America (Hershkovitz 1983; Defler and Bueno 2007; Plautz et al. 2009; Babb et al. 2011; Ruiz-Garcia et al. 2011). *Aotus nigriceps* is a wide-ranging nocturnal monkey species found across much of the central and upper Amazon, including the moist forests of the Southwest Amazon, Jurua-Purus, Purus-Maderia, and Maderia-Tapajos. They are also typically found in degraded forest, agro-forested landscapes, and areas in proximity to humans (Wright 1994; Helenbrook et al. 2020). While night monkeys are adaptable and found to persist in degraded landscapes, they still require connective forest cover, access to seasonally available fruiting trees,
sleeping sites, and are restricted by environmental conditions (Aquino and Encarnación 1994; Helenbrook et al. 2020). Although thought to be a common species, it is currently listed as Appendix II of CITES [Convention on International Trade in Endangered Species of Wild Fauna and Flora], and the impact of anthropogenic disturbances on the long-term viability of A. nigriceps remains unknown.

Aotus nigriceps is found in southern Peru, northern Bolivia, and central-western Brazil according to the IUCN and based on literature and biogeographic limitations such as major river systems (Shanee et al. 2018). However, discrepancies remain regarding the extent of their eastern distribution in the state of Rondonia, and additional taxonomic analysis is needed from the area (e.g., Pieczarka et al. 1993; Plautz et al. 2009; Menezes et al. 2010; Babb et al. 2011; Ruiz-Garcia et al. 2011). The species is not considered under threat due to their presumed extensive range, their large and sustained population size (Shanee et al. 2018), and high-density estimates ranging from 19 to 50 individuals/km² (Helenbrook et al. 2020). However, no known population size estimates or trends have been described despite large portions of the range of A. nigriceps overlapping with areas experiencing some of the highest deforestation rates in the world (Estrada et al. 2018). Besides habitat loss, their long-term viability is also projected to be further impacted by altered phenology and increased average maximum temperatures from climate change, which may result in phenotypic change due to adaptive evolution of primate physiology, or indirectly through changes in resource availability (Raghunathan et al. 2015; Ho and Zhang 2018; Carvalho et al. 2019; Cohn et al. 2019).

Assessing the population status of Aotus nigriceps, and any species, in general, requires accurately describing their distribution, baseline population size, and predicting future population growth or loss. This information can be used to build predictive models that can indicate priority regions for conservation action. Species distribution modeling is a well-known approach, which predicts a species distribution across a landscape based on the environmental conditions necessary for species presence (e.g., Bett et al. 2012; Kamilar and Tecot 2016; Rabelo et al. 2020). The Maxent program is especially suited for this task and is considered the most accurate maximum entropy machine learning model, achieving high predictive accuracy without true absence data, incomplete data, and relatively small sample sizes (Phillips and Dudik 2008; Merow et al. 2013; van Proosdij et al. 2016). Maxent has recently been used in primate studies to determine the current and future distribution of snub-nosed monkeys (Wong et al. 2013; Luo et al. 2015; Nüchel et al. 2018), habitat suitability of Sichuan golden monkeys (e.g., Liu et al. 2017), potential distribution of Caatinga howler monkeys (Filho and Palmeirim 2019), and conservation efforts for the brown-headed spider monkey (Peck et al. 2011). However, it is typically not used for species of Least Concern, but only after a species is considered Threatened.

For this study, we used species distribution modeling with Maxent to estimate A. nigriceps distribution and projected density across their predicted distribution. The objectives of this study are to (1) develop baseline distribution models on the presence of A. nigriceps utilizing ecological, biogeographical, and environmental data; (2) project population losses due to habitat loss and degradation; and (3) identify priority conservation actions needed to sustain black-headed night monkey populations.

**Methods**

**Species occurrence**

We constructed an occurrence data set (N=75) of Aotus nigriceps observations throughout their range (Fig. 1; Supplementary Table 1), by using several available sources, including published manuscripts, field records provided by the Wildlife Conservation Society (Wallace et al. 2013), and citizen science data points (iNaturalist 2020) (Fig. 1b). To ensure accuracy, we only included data from peer-reviewed sources or those entries in iNaturalist that had photo documentation. We plotted all coordinates to ensure they fell within the currently described distribution and aligned with forested habitat obtained from satellite imagery. For their range, we created a polygon layer which represented their maximum extent of occurrence as described by several peer-reviewed sources (e.g., Plautz et al. 2009; Menezes et al. 2010; Babb et al. 2011). Their range extent is the most currently accepted IUCN Red List description based on literature and biogeographic limitations such as major river systems (Shanee et al. 2018).

**Environmental data**

We used bioclimatic variables as environmental predictors based on their presumed ecological or physiological relationship to black-headed night monkey suitability as previously used in other neotropical primate studies (e.g., Holzmann et al. 2014; Rabelo et al. 2020). Climatic variables were downloaded from WorldClim version 2.1 (https://worldclim.org/data/bioclim.html) and included the annual temperature and precipitation (average, minimum, and maximum), annual temperature range, and isothermality (defined as mean diurnal range [mean of monthly (max temperature – min temp)] divided by temperature annual range) (Fick and Hijmans 2017). For elevation, we used the Shuttle Radar Topographic Mission elevation dataset (SRTM 2020: https://www2.jpl.nasa.gov/srtm/). To avoid overfitting, pairwise Pearson correlation coefficients were
analyzed, and highly correlated variables with a greater than 0.85 were removed from the analyses. Minimum temperature was highly correlated with the annual temperature range (−0.94) and annual mean temperature (0.94), so it was not included in the analyses.

To determine forest cover, we obtained percent forest cover data from 2000, forest gain from 2000 to 2012, and forest loss between 2000 and 2018 from Earth Engine Partners (Hansen et al. 2013: http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.7.html). To calculate the most current cover percentage for the year 2018, the cumulative gain and loss between 2000 and 2018 were added and subtracted from the 2000 cover layer within their range, respectively. The 2018 forest cover layer was used to predict their most current distribution, while the 2000 forest cover was used to model their predicted distribution in 2000. We calculated protected areas within A. nigriceps range and predicted distribution using polygons obtained from Protected Planet (UNEP-WCMC and IUCN 2020: https://www.protectedplanet.net/en/thematic-areas/wdpa). All layers utilized in the study were in 30 s (1 km) spatial resolution.

Fig. 1 (a) Currently described Aotus nigriceps range based on biogeographical limitations and literature. Percent of forest cover within their range in (b) 2018, (c) 2000, and within (d) protected areas based on satellite imagery obtained from Earth Engine Partners. Points represent presence data used in Maxent models.
### Table 1 Relative contribution estimates of environmental variables to the MaxEnt model predicting *Aotus nigriceps* occupancy

| Variable              | Percent contribution | Permutation importance |
|-----------------------|----------------------|------------------------|
| Forest cover          | 19.2                 | 9.3                    |
| Elevation             | 2.5                  | 0.1                    |
| Isothermality         | 24.1                 | 22.8                   |
| Maximum precipitation | 15.0                 | 4.2                    |
| Maximum temperature   | 14.8                 | 23.4                   |
| Mean temperature      | 1.5                  | 8.5                    |
| Minimum precipitation | 15.8                 | 24.8                   |
| Temperature range     | 7.1                  | 6.9                    |

For percent contribution, the increase in regularized gain for each iteration of the training algorithm is added to the contribution of the corresponding variable or subtracted if the change to the absolute value of lambda is negative. For permutation importance, the values of the environmental variable on training presence and background data are randomly permuted. The model is re-evaluated on the permuted data, and the resulting drop in training AUC is normalized to percentages. Values shown are averages over 15 replicate runs.

### Distribution models

All statistical models and analyses were conducted using the R program (R Core Team 2020). We used Maxent version 3.4.1 (Phillips et al. 2017; Phillips and Dudík 2008) in the ‘dismo’ package (Hijmans et al. 2017) to develop a species distribution model for *A. nigriceps* by relating known geographic occurrences to available environmental variables to estimate suitable habitat (Phillips and Dudík, 2008; Franklin 2013). To minimize spatial autocorrelation, which can lead to an overestimation of certain environments and inaccurate models (Kramer-Schadt, 2013; Van Proosdij et al. 2016), the occurrence data were spatially thinned with a 1 km radius rule with 1,000 iterations using the ‘spThin’ package, which imposes a minimum permissible nearest-neighbor distance and finds the set that retains the most samples through repeated random samples (Aiello-Lammens et al. 2015). The default Maxent settings of cloglog were used as it is the easiest to conceptualize by giving an estimate between 0 and 1 of the probability of presence.

Model calibration and evaluation were conducted with the ‘ENMeval’ package to optimize the trade-off between goodness-of-fit, model complexity, and overfitting (Muscarella et al. 2014). We compared MaxEnt models using different combinations of regularization multiplier (RM) values and feature combinations (FCs): linear (L), quadratic (Q), hinge (H), and product (P). Although the threshold feature is also available, it was not used as it results in overfitting, and omitting this feature has been found to improve model performance, resulting in more realistic predictions (Phillips et al. 2017). We set the RM range between 0.5 to 6.0 with 0.5 increments as well as a combination of eight FCs, i.e., linear (L), linear and quadratic (LQ), hinge (H), linear and hinge (LH), linear and product (LP), linear, quadratic and hinge (LQH), linear, quadratic and product (LQP), and linear, quadratic, product and hinge (LQPH), resulting in 96 models with all possible combinations of features and regularization multipliers. The models were fitted using the thinned occurrence data of 50 occurrence points with 10,000 random background points and partitioned using the ‘block’ method, which partitions data according to latitude and longitude, dividing the occurrence data into four bins of equal numbers. This method reduces spatial autocorrelation between points that are included in testing and training, which can overinflate model performance, especially from biased sampling (Muscarella et al. 2014; Radosavljevic and Anderson 2014). The resulting models were evaluated using the corrected Akaike information criterion (AICc), with the optimal model chosen corresponding to the one with the lowest AICc value (Burnham and Anderson 2002). Of the 96 models evaluated, the model with the lowest AICc was RM = 0.5 and FC = LQ.

The optimal model was used to fit a final model based using the cross-validation method, with a maximum of 5,000 iterations, 10,000 randomly selected background points, a prevalence of 0.75, and 15 replicates. To measure variable importance and determine which variables contributed most to the model, we performed a jackknife analysis with and without each variable in isolation. Predictor variables with permutation importance of zero were then removed and the new model reran until all variable contributions were greater than zero. This resulted in a model with eight predictor variables: cover, elevation, isotherm, minimum and mean temperature, mean and maximum precipitation, and temperature range. To assess model discriminatory power and compare the performance of species distribution models, we measured the area under the receiver operating characteristic curve (AUC) using the testing set (Fieldling and Bell 1997; Babar et al. 2012; Phillips and Dudík 2008; Stohlgren et al. 2011).

To calculate the total area of suitable habitat in 2018 and 2000, probability of presence values were transformed into presence/absence by using a selection threshold. For this study, we identified suitable areas based on the balance training omission, predicted area, and threshold value (BTPT) threshold to calculate the total area of suitable habitat in 2018 and 2000. This threshold provides a balance between overfitting and overestimation (Jobe and Zank 2008; Svančara et al. 2019). However, the selection of a suitable threshold to identify areas of species presence differs depending on the specific question and the species of interest (Liu et al. 2005; Hernández-Baz et al. 2016), with a conservative and more restrictive threshold suitable for rare species or conservation purposes, while wider and more liberal thresholds are adequate when the interest is general patterns or the species is more widely distributed (Liu et al. 2005; Pearson et al. 2019).
Therefore, we also considered the maximum specificity and sensitivity threshold (MSS) which is the value at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) is the highest. This more conservative threshold has been found to produce the most accurate results (Liu et al. 2005, Jimenez-Valverde and Lobo 2007). These two thresholds provided a lower and upper estimate of suitability for comparison.

**Population size estimates and threat assessment**

To estimate the loss of habitat over time we (1) calculated tree cover loss within their documented range from Global Forest Watch data layers (Hansen et al. 2013), and (2) calculated the area of their occurrence between 2000 and 2018 using the Maxent-modeled species distribution. We then used the lower population density estimates summarized from literature in Helenbrook et al. (2020) to extrapolate across projected habitat using area of occurrence calculations from our greater and less restrictive thresholds. Future deforestation projections and diminished habitat loss were projected for the next decade (2020–2030) based on past deforestation rates for the past decade (Bullock et al. 2020; Junior et al. 2021; Trancoso 2021). Extrapolated 2000–2018 habitat loss of 18% of forest cover (132,908 km²) between 2000 and 2018 satellite imagery data (Fig. 1b, c). Protected areas represented 28.2% of forest cover within their recognized range in 2000 and exhibited forest cover loss of 4.9% over the past decade (Fig. 1d). Their predicted distribution based on the balanced BTPT threshold indicated suitable habitat in 67.2% (1,069,948 km²) of their known range (Fig. 2b), a loss of 16.5% from the predicted 80.5% in 2000 (Fig. 2a). The more conservative MSS threshold indicated they were present in 16.0% of their range in 2018 (238,757 km²) (Fig. 2d), a loss of 26.7% compared to their 2000 predicted range of 20.5% (Fig. 2c). Of their predicted distributions, a third (32.7%) is within protected areas using the BTPT threshold and a quarter (29.7%) for the narrower MSS threshold.

Using the lowest published density estimates (Helenbrook et al. 2020), the current population size varies between 4,536,383 and 20,329,012 individuals under the MSS and BTPT threshold, respectively. A contraction of suitable habitat under either of the model thresholds would have resulted in a substantial loss of animals between 2000 and 2018, with an estimated loss of 1,654,254 and 4,022,262 individuals with the MSS and BTPT habitat suitability estimates, respectively. Deforestation rates have accelerated for the past six years with 2020 exceeding all year-over-year deforestation rates for the past decade (Bullock et al. 2020; Junior et al. 2021; Trancoso 2021). Extrapolated 2000–2018 habitat suitability losses from both MSS and BTPT models equate to an additional loss of between 33,073 and 94,458 km² of A. nigriceps habitat over the next decade—a contraction of between 8.83 and 13.85% of suitable habitat, respectively. Using extrapolated minimum density estimates coupled with estimated habitat loss over the next 10 years equates to a further hypothetical loss between 628,387 (MSS) and 1,794,702 (BTPT) individuals.

**Results**

**Species distribution modeling**

Maxent models showed high support for predicting observed distribution (AUCtest = 0.89). Probability of presence increased with greater forest cover with a peak between 40 and 80% (range 0–100%) and highest between 500 to 1,000 m elevation with low probabilities in the lowest and highest elevations (range 1–3,062 m) (Supplementary S1a, b). Probability also increased with greater minimum (34,973–752.46 mm; Supplementary S1c) and maximum (range 819–4,797 mm) precipitation (Supplementary S1c, d). Presence decreased with increasing maximum temperature (range 20–35 °C; Supplementary S1e), but was greatest within the midrange values of mean temperature (range 10.6–27.9 °C; Supplementary S1f). Probability of presence also decreased with isothermality (range 6.4–8.8%; Supplementary S1g) and was within the midrange values temperature range (range 10.1–20.8 °C; Supplementary S1h). Similar relationships were found when keeping all values at their mean values (Supplementary S2). Minimum precipitation, maximum temperature, and isothermality had the highest permutation importance (Table 1). Forest cover, elevation, and maximum temperature were the most effective variables for predicting the distribution of the occurrence data set aside for training and testing (Supplemental 3a, b). Forest cover, elevation, and mean temperature were the most effective variables using AUC on test data (Supplemental 3c). The largest contributing environmental variables when omitted in all jackknife tests were isothermality minimum precipitation and cover, suggesting that they contribute the most information not found in the other variables (Supplemental 3).

The estimated current extent of A. nigriceps is 1,591,711 km² based on the most currently available literature (Hershkovitz 1983; Defler and Bueno 2007; Plautz et al. 2009; Babb et al. 2011; Ruiz-Garcia et al. 2011: Fig. 1a). We calculated a loss of 18% of forest cover (132,908 km²) between 2000 and 2018 satellite imagery data (Fig. 1b, c). Protected areas represented 28.2% of forest cover within their recognized range in 2000 and exhibited forest cover loss of 4.9% over the past decade (Fig. 1d). Their predicted distribution based on the balanced BTPT threshold indicated suitable habitat in 67.2% (1,069,948 km²) of their known range (Fig. 2b), a loss of 16.5% from the predicted 80.5% in 2000 (Fig. 2a). The more conservative MSS threshold indicated they were present in 16.0% of their range in 2018 (238,757 km²) (Fig. 2d), a loss of 26.7% compared to their 2000 predicted range of 20.5% (Fig. 2c). Of their predicted distributions, a third (32.7%) is within protected areas using the BTPT threshold and a quarter (29.7%) for the narrower MSS threshold.

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**Discussion**

This is the first study to assess the species distribution, population status, and conservation management implications for the black-headed night monkey. Although considered Least Concern due to their adaptability towards a variety of habitat...
types, *A. nigriceps* distribution appears restricted by biotic and environmental factors. We found they were more likely to be present in habitats represented by moderate elevation, cover and temperature range, lower isothermality and maximum temperature, and greater minimum and maximum precipitation. Although *A. nigriceps* has not been considered a species of conservation concern due to its extensive range across several Amazon Basin ecoregions, we provide evidence that *A. nigriceps* has experienced sharp declines in forest cover in portions of their range over the last couple of decades. These populations declines will continue in the future based on projected habitat loss and degradation rates due to accelerated deforestation in Brazil as a result of heavy pressure from cattle ranching, monoculture agriculture, and new road construction that has been occurring since 2015 (Gomes et al. 2019; Bullock et al. 2020; IMAZON 2020; Mataveli et al. 2021). Of concern is that some of the highest deforestation rates in the Amazon occur in the Brazilian States of Pará, Rondonia, and Mato Grosso where this study species occurs.

We estimate population size and loss of individuals during the previous nearly two-decade period of 2000–2018 to be between 1 and 4 million individuals. Although this species is currently considered common, they will likely continue to decline due to widespread anthropogenic pressures, especially since only a quarter to a third of their suitable habitat is within protected areas. We are aware that these population estimates are likely to vary based on habitat heterogeneity, but believe these estimates provide a necessary, more tangible perspective on the plight of this species. Nevertheless, additional population density estimates should be conducted throughout their range to better assess whether variability exists based on habitat quality and type. Furthermore, these estimates do not consider potential range shifts or diminished suitable habitat due to climate change as described in recent primate Amazonian studies (Sales et al. 2020).

Systematic conservation planning based solely on the black-headed night monkey appears premature at this time due to the broad distribution of the species, limited knowledge of underlying taxonomic diversity, molecular phylogeographic variability throughout its range, and no evidence of a negative species response to climate change or Amazonian fires. However, the expansion of several existing conservation strategies would likely benefit *A. nigriceps* and contribute to overall biodiversity conservation. Extensive protected areas and indigenous territories exist in Peru, Bolivia, and Brazil, where the level of protection varies

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**Fig. 2** The predicted distribution of *Aotus nigriceps* using the balance training omission, predicted area, and threshold value (BTPT) for (a) 2000 and (b) 2018; and using the maximum specificity and sensitivity threshold (MSS) for (c) 2000 and (d) 2018. Black areas represent areas exceeding the threshold.
widely (Amazonia Socioambiental 2019; Paiva et al. 2020). Forest loss and degradation still occur within protected and indigenous lands, though the degree to which these areas are impacted depends on the type of protected area and management (e.g., indigenous, federal, or state: Herrera et al. 2019).

Regardless of governance, primates benefit from protected areas (e.g., Paim et al. 2019). Continued support for participatory and jurisdictional REDD+ programs also appears effective, though this approach requires realistic expectations among local communities regarding benefits and participation, secured land tenure, and a mix of intervention strategies including incentives, disincentives, and introduction of alternative livelihoods (e.g., Davis and Goldman 2019; Simonet et al. 2019; Dupuits and Cronkleton 2020). Agroforestry research related to night monkey species is limited, though a study in the northern Andes suggests that coffee plantations can benefit night monkeys while also providing farmers with income (Guzmán et al. 2016). We have previously documented that A. nigriceps is quite common in secondary forest and that they make use of orchards (Helenbrook et al. 2020). The main issue would appear to be whether a connected canopy is maintained in order for night monkeys to traverse a complex matrix with forest fragmentation and diverse land uses.

Here, we presented an assessment of the current state of forest degradation and loss in the Amazon, coupled with an analysis of the associated anthropogenic impact on a common primate species. Our goal is not to suggest that the black-headed night monkey is under immediate threat but to show that even widely distributed primates face extensive risks. More specialized sympatric primate species likely face a far greater threat from habitat loss and degradation. However, by using the black-headed night monkey species as an indicator of landscape and forest health, solutions that mitigate their decline would also favor those that are much more vulnerable—either because they are more sensitive to habitat disturbances, have far smaller numbers, or have yet to even be discovered. Additionally, there is also the issue of A. nigriceps phylogenetic uncertainty. Aotus evolutionary history is quite complicated, potentially due to introgression (Valencia et al. 2018). Furthermore, there have been no known attempts to understand the molecular systematics and phylogeography of Aotus within the Amazon basin. Many other sympatric primates that share a similar range as Aotus show far more taxonomic diversity across their range purportedly driven by riverine barriers (e.g., Marsh 2014; Carneiro et al. 2018; Lima et al. 2017). This species is distributed across the Amazon but could potentially include evolutionarily significant units that each have their own unique stressors and face reduced viability compared to the whole.

This study provides critical information on areas likely to support black-headed monkeys, which can be applied to future conservation monitoring and planning. Aotus nigriceps has experienced extensive habitat loss over the past two decades, and there is likely to be continued habitat loss and degradation, threatening this relatively common species. A regional landscape-level conservation plan that maintains forest connectivity and minimizes habitat loss would benefit not only the black-headed night monkey, but also the many other sympatric species who are under increasing threat in the region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-021-00922-w.

Acknowledgements Thank you to Hillary Fenrich, Sheridan Plummer, and Ben Sharaf who assisted in original model development. Thank you to Rob Wallace for sharing Wildlife Conservation Society occurrence data from Bolivia. We are indebted to the anonymous reviewers who provided constructive feedback.

Author contributions Study design, data collection, analysis, and writing: WDH; Modeling, analyses, and assistance with writing: JWV.

Declarations Conflict of interest None.

Ethical standards This research complies with the Code of Conduct outlined by the journal.

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