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Running head: *Hippocamelus* in Ecuador

Archaeological and zoological collections do not provide evidence for taruka (*Cervidae*: *Hippocamelus antisensis*) in Ecuador

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Knowing whether a species has been extirpated, or if it ever inhabited a specific geographic area has direct importance for planning conservation activities. Here we examine whether one of the largest neotropical mammals, the taruka (*Hippocamelus antisensis*), inhabited Ecuador. Our approach consisted of three components: 1) we surveyed archaeological collections and literature for any biological remains and cultural artifacts that may represent tarukas, 2) we traced museum specimens reported in publications; and, 3) we generated ecological niche models (ENM) to determine whether Ecuador offers suitable environment for the distribution of the taruka. Our results suggest that the taruka has not inhabited Ecuador. We did not find any reliable supporting evidence in the form of specimens nor convincing literature reports. Furthermore, ENM revealed that Ecuador does not support the climatic habitat preferences for the taruka. We suggest that published records of taruka in Ecuador may have been the product of an unfortunate cascade of misinformation due to improper identifications of specimens. The methodologies used here may prove useful to research the presence of species that are either thought to be extinct, or suspected to be recently introduced into a new geographic area.

Key words: Andes, Cervidae, distribution, South America.

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Delimiting geographic distributions is key for understanding the biology and interactions of a species within its environment, and for facilitating meaningful implementation of conservation assessments and initiatives (Schipper et al. 2008). Native cervids are in peril throughout the Neotropics because of hunting pressure and habitat loss. Unfortunately, large gaps in our understanding of their distribution hinder conservation efforts. Among the most enigmatic species of Neotropical cervids is the taruka (Cervidae: *Hippocamelus antisensis*). The low population numbers and high declines of *H. antisensis* since the mid 20th century (Smith-Fleck et al. 2011) are indicators of its vulnerability to extinction (Barrio and Ferreyra 2008). Currently the distribution of *H. antisensis* includes the Andes of northwestern Argentina through Bolivia to west-central Peru, and northeastern Chile (Barrio 2013). There are also several published historical records of this species in the Ecuadorian Andes until 1940 (Table S1). However, the absolute lack of any records for *H. antisensis* during the last few decades is why this species was considered an extinct species in Ecuador (Albuja 1991; Tirira 2001). Doubts have arisen recently regarding the validity of those published records documenting the presence of *H. antisensis* in Ecuador (Barrio 2010; 2013; Tirira 2011). Nevertheless, a thorough analysis of the available evidence and an assessment of the potential suitable habitat available for *H. antisensis* have never been done.

Ecological niche models (ENM; also known as species distribution models, SDM) combine occurrence records of a species with the environmental and spatial characteristics of the landscape where they occur to create predicted distributions (Franklin 2009). This method has been used to assess distributions of organisms in biogeographic, conservation, ecological, and evolutionary contexts (e.g., Raxworthy et al. 2003; Carnaval et al. 2009; Soto-Centeno et al.

2013). These predicted distributions created via ENM represent the suitable conditions where a species could sustain viable populations across geographic space. Thus, ENM can be important to assess broad-scale patterns of biodiversity and to better understand tropical landscapes by identifying the areas of suitable habitat where a species can occur.

In this study, we analyzed whether *H. antisensis* inhabited Ecuador by using a three-pronged approach: 1) we surveyed archaeological collections and literature for biological remains and cultural artifacts that may represent *H. antisensis*; 2) we traced the museum specimens reported in publications; and, 3) we generated ecological niche models (ENM) to test whether Ecuador offers suitable climatic habitat to sustain viable populations of *H. antisensis*.

MATERIALS AND METHODS

Archaeological collections.—We searched for archaeological evidence that may indicate the pre-Columbian presence of *Hippocamelus antisensis* in Ecuador. We examined the literature for deer remains recovered in archaeological sites for evidence that may indicate the presence of *H. antisensis* specimens (e.g., Miller and Gill 1990; Stahl and Athens 2001; Stahl 2004; 2005). Also, we consulted the work of Gutiérrez-Usillos (2002), and the collections of the Museo del Banco Central del Ecuador (MBCE) for zoomorphic representations of *H. antisensis* in pre-Columbian pottery and jewelry art. Due to the inherent subjectivity of identifying a taxonomic entity from art pieces, we relied upon diagnostic external characteristics of *Hippocamelus* anatomy that may have been emphasized by artists (e.g., bifurcation of antlers, forehead markings, and short legs).

Zoological collections.—We analyzed the published literature to trace records of museum specimens of *H. antisensis* collected in Ecuador (Table S1). Additionally, we visited collections that may have curated those specimens: Field Museum (FMNH), in Chicago, USA; Museo Nacional de Ciencias Naturales (MNCN) in Madrid, Spain; and Museo Argentino de Ciencias Naturales (MACN), in Buenos Aires, Argentina. We followed Groves and Grubb (2011) when necessary to identify the material with discrete skull characteristics that enable differentiation amongst artiodactyls, including both species of *Hippocamelus*. The best cranial character to distinguish between both species of *Hippocamelus* is the number of foramina in the sulci of the orbital bone (Carlton and McKean 1977; Groves and Grubb 2011).

Species and environmental data.—Locality records of *H. antisensis* with latitude/longitude coordinates were obtained from the System of Biodiversity Information (www.sib.gov.ar) and MaNIS (<http://manisnet.org>) (Stein and Wieczorek 2004). Additional observational records were gathered from the Argentinean Administration of National Parks and from occurrences reported by Nuñez (2008). The latter were collected during an extensive survey of *H. antisensis* in the Bolivian highlands (Nuñez 2008). We plotted all locality records (N=148) in ArcGIS v10.2 (ESRI, Redlands, CA) to assess the quality of the spatial data and correct georeferencing errors. Then we developed two alternative distribution models by subsampling the original dataset to one record per 1 km² and one record per 10 km². This procedure allowed us to avoid problems with distribution overfitting in our dataset by reducing locally dense sampling at two different

scales (Elith et al. 2010). The final datasets in each model represented the known distribution of *H. antisensis* spanning the heterogeneous environmental conditions inhabited by this species.

We modeled the distribution of *H. antisensis* using current climatic conditions available from the 19-variable global climate dataset of WorldClim and altitude at 30-sec (ca. 1 km²) spatial resolution (Hijmans et al. 2005). Climate and altitude variables were masked to a regional extent that included the Andes from Colombia to Argentina and Chile using ArcGIS v10.2. A total of 3,500 background points were generated from the study region, which included the central Andes, the northern one half of the southern Andes, coastal ranges and the eastern slopes in Argentina, Bolivia, Ecuador, and Peru. Background points that were within 1 km of an occurrence point were removed from the dataset (Barbet-Massin et al. 2012). We identified correlated climate variables using a Pearson's correlation in R v3.0 and removed variables that were significantly correlated (correlation coefficient >0.8; Soto-Centeno et al. 2013).

Distribution modeling approach.—ENMs were developed using a presence-only method in MaxEnt v3.3.3 (Phillips et al. 2006). Some authors question the use of default parameters in MaxEnt because they are not generally applicable to all biological systems (Anderson and Gonzalez 2011; Warren and Seifert 2011). Therefore, we explored multiple combinations of MaxEnt features (i.e., linear, quadratic, product, threshold, and hinge) using a regularization multiplier (β) of one to obtain an optimal set of parameters for the *H. antisensis* data. To ensure replicability, we randomly partitioned our locality data into 25% testing and 75% training datasets and used this partition to test all models developed with different combinations of MaxEnt features. We used a 10-fold cross-validation approach in our final models and assessed

their predictive performance using the area under the receiver operating characteristic curve (AUC), where values >0.8 are characteristic of strong model performance (Swets 1988). We also used the true skill statistic (TSS) as a second measure of model performance and as a way to identify a threshold that maximized TSS to develop final predictions of *H. antisensis* (Allouche et al. 2006; Devitt et al. 2013). TSS accounts for omission and commission errors and values range from -1 to 1, where a value 1 indicates perfect model agreement and 0 is indicative of a model with performance no better than random (Allouche et al. 2006). Our goal was to test whether Ecuador offers suitable climatic habitat for *H. antisensis* by using multiple variables. To determine whether a simple model is more appropriate to predict the distribution of this species, we fitted our MaxEnt models using the default β of one and also fitted a smoother model with a β of 2.5 (Elith et al. 2010). Increasing the value of β reduces model complexity (Elith et al. 2010, Warren and Seifert 2011) and allowed us to explore the breadth of the *H. antisensis* climatic niche. Finally, we used the jackknife test in MaxEnt and a principal components analysis to assess the importance of each climate variable for predicting the distribution of *H. antisensis*.

RESULTS

Archaeological collections.—None of the published zooarchaeological studies conducted in Ecuador show skeletal remains identified as *Hippocamelus antisensis*. Similarly, none of the figures in Gutiérrez-Usillos (2002) represent this species. Only one of the pieces of pottery and jewelry in the MBCE collections resembles *H. antisensis* based on the bifurcation of its antlers and the presence of a Y relief in the forehead (Fig. 1). This piece is a clay fragment likely to have

belonged to a large vessel of late pre-Columbian Manteño context at Agua Blanca, Manabí province (E. Quinatoa pers. comm.).

Zoological collections.—The *H. antisensis* reported by Elliot (1907) was acquired by the FMNH through exchange with the British Museum. This specimen was thought to have been lost (Voss 2003: p. 20). However, we checked the first handwritten catalogs of the collection and traced it to specimen FMNH 1476—it was the only *Hippocamelus* in the collections previous to the publication of Elliot’s work in 1907 and there is documentation that this specimen belonged first to the British Museum. The locality data in the labels read: “South America”. The original identification on the label reads as *H. antisensis*; however, it was later emended to *H. bisulcus*. We agree with the later identification of this specimen as *H. bisulcus* due to the presence of one deep foramen, or two foramina, in the smooth supraorbital sulci, and narrow posterior ends of the nasal bones. In contrast, *H. antisensis* shows three foramina in the very distinctive supraorbital sulci and wide nasal bones at their posterior end (Fig. 2). The specimens assigned to *H. antisensis* in the MNCN in Spain, and MACN in Argentina could not be located.

Ecological Niche Models.—The final datasets of *H. antisensis* included 130 records and 83 records for the 1 km and 10 km models, respectively (Fig. 3). The modeling dataset included seven uncorrelated climatic variables (i.e., Temperature: mean diurnal range, bio 2; seasonality, bio 4; maximum of the warmest month, bio 5. Precipitation: annual, bio 12; seasonality, bio 15; warmest quarter, bio 18; coldest quarter, bio 19). In our model comparison, ENMs developed

using product (P), threshold (T), and hinge (H) features performed better than models using different combinations of features. Our PTH features model and Auto features model resulted in identical AUC values and distributions (i.e., both AUC = 0.971, SD \pm 0.007). Therefore, we present the results of models developed with PTH features only.

Our cross-validated ENMs for the 1 km and 10 km datasets performed well over the range of *H. antisensis*. All model variations had a true positive fraction (i.e., TPF, proportion of correctly predicted localities) of 98% (Table 1). The maximum AUC and TSS values were 0.969 (SD \pm 0.007) and 0.942, respectively (Table 1). The maximum TSS value of all models corresponded to the threshold of maximum training sensitivity plus specificity (MTSS) in MaxEnt for both the 1 km and 10 km datasets. Under MTSS, we used threshold MaxEnt logistic probability values to select a minimum prediction as presence (i.e., only values greater than the selected threshold indicate presence; Table 1). Ecuador did not fall within the predicted range of *H. antisensis* in any of the model variations (Fig. 4). Our models show the distribution of *H. antisensis* extends along the Peruvian Andes north to Cajamarca Department and south in northwestern Cordoba Province, Argentina. Although logistic probability values for those areas were generally low for most models and low-to-moderate only in the most relaxed model, this result is consistent with previous records (Fig. 4D). Visual inspection of all models revealed that model projections that used a β of 2.5 for the 1 km and 10 km datasets were better able to detect suitable areas between locality records where potential zones of population connectivity might occur (Fig. S1). Jackknife test of variable importance in MaxEnt showed that maximum temperature of the warmest month (bio5) when used alone contributed more to model performance. Bio5 also decreased the test gain the most when omitted from the model, which

suggests that this variable contains the most information that is not included in any of the other variables (data not shown). The PCA results revealed that the first and second principal components explained 63% and 18% of the variation, respectively. Bio5 alone was the variable with the most contribution to the second principal component, which confirmed the jackknife results and the fact that this variable contains the most information not included in any other variable. The PCA variables that had the most contribution to the first principal component were precipitation seasonality (bio15) and precipitation of the coldest quarter (bio19; data not shown).

DISCUSSION

Archaeological collections.—The published information of zooarchaeological studies in Ecuador does not report the presence of *Hippocamelus antisensis* (e.g., Miller and Gill 1990; Stahl and Athens 2001; Stahl 2004; Stahl 2005). Archaeological excavations in highland Ecuador consistently recover bone fragments of small, medium and large morphotypes of deer, which may be interpreted as *Pudu*, *Mazama* and *Odocoileus*, respectively. However, definitive identifications are mostly based on antler morphology, thus most of the material may remain unidentified, and chances are that *H. antisensis* specimens could be overlooked. Unfortunately, postcranial autapomorphies that would be useful for identifying zooarchaeological material of South American deer are poorly known. Although antlers and bones identified as *H. antisensis* in Ecuador are absent in excavations, these are regularly found in Peru, Bolivia and Argentina (e.g., Wheeler Pires-Ferreira 1976; Wing 1978; Izeta and Scattolin 2006; Moore et al. 2010).

While surveying the clay and metal zoomorphic pieces of deer, it was possible to distinguish *Odocoileus* and *Mazama*, but none clearly represent *H. antisensis*. Only the piece depicted here (Fig. 1) could be an ambiguous representation, but given that this piece comes from the lowlands of western Ecuador, it is more likely to represent a young *Odocoileus* starting to grow antlers. Another less parsimonious explanation is that this piece actually represents *Hippocamelus*, brought from the Andean highlands. There is evidence of extensive trade between Manteño people and other cultures, including northern Peru and western Mexico (Jijón y Caamaño 1941; Edwards 1965; Anawalt 1992). If this piece actually did represent *H. antisensis*, it would not necessarily indicate the presence of the species in Ecuador as it may have been brought from the Peruvian Andes. Also, the chances of bringing *Hippocamelus* to Agua Blanca appear very slim, as conditions here are ideal for other game animals including *Odocoileus*, *Mazama*, *Cuniculus paca* and *Dasyprocta punctata* (Tirira 2007).

Zooarchaeological collections provide important insights on past fauna of an area. Remarkable examples in South America include the description of *Cuscomys oblativus* (Eaton 1916) from remains found in human tombs at Machu Picchu. No new specimens of *C. oblativus* are known and it was thought to be extinct, but because of the ample forest preserved in the area it may actually indicate that the ancestral inhabitants were skilled trappers of rare small mammals (Eaton 1916; Emmons 1999). Identification of pre-Columbian specimens of domesticated Muscovy duck (*Cairina moschata*), guinea pig (*Cavia porcellus*), and camelids (*Lama glama* and *Vicugna pacos*) in the western lowlands of Ecuador, may indicate active

commerce with other settlements along the Pacific coast of the Americas (Stahl and Norton 1987; Stahl 1988; Stahl et al. 2006).

Zoological collections.—The matching of specimens FMNH 1476, a *Hippocamelus bisulcus* with no locality data other than South America, with *H. antisensis* from Ecuador reported by Elliot (1907) indicates two troublesome aspects. First, the animal was originally misidentified as *H. antisensis*, and second, the locality data were over-interpreted. At that time the misidentification of rare artiodactyl material could have been common given the absence of literature resources and comparative specimens. However, the morphological differentiation of *H. antisensis* from *H. bisulcus* using skull characters is straightforward because of the marked differences in the number of foramen at the supraorbital sulci (Groves and Grubb 2011; Fig. 2). It is likely that the locality assignment to Ecuador resulted because previous accounts mentioned the presence of *H. antisensis* in Ecuador (Table S1), and one in particular associates the specific name *antisensis* with Antisana volcano in Ecuador (Jiménez de la Espada 1872).

We failed, as previous recent attempts did (Voss 2003; Table S1), to locate the *H. antisensis* specimens at the MNCN in Madrid, Spain. However, an analysis of the literature sheds light on the dilemma. The specimens missing at the MNCN were collected by Marcos Jiménez de la Espada, reported in his results of the “Expedición al Pacífico” (Jiménez de la Espada 1872), and later analyzed by Ángel Cabrera in two subsequent publications (Cabrera 1912, 1917). In all these publications the specimens were identified as *H. antisensis*. However, no clear characters that may distinguish those animals from other cervids of the high Andes (e.g.,

Odocoileus or *Mazama*) were provided. Moreover, the only characteristics of the skins of an adult female and a young male were described as “paler and greyer than *H. bisulcus*, without the brown patch on the rump” (Cabrera 1912). Those characteristics match well with the descriptions of *Odocoileus* sp. according Nowak (1991).

In the Ecuadorian páramos, *Odocoileus* is not uncommon (Tirira 2007). Along these lines, it is highly remarkable that Jiménez de la Espada did not report any *Odocoileus* in his trip, but reported *H. antisensis* as very common in the Ecuadorian Andes (Jiménez de la Espada 1872, Cabrera 1912). Later, the outstanding encyclopedic and beautifully illustrated *Mamíferos Sud-Americanos* (Cabrera and Yepes 1940) mentioned with detail the presence of *H. antisensis* along the páramos of the Ecuadorian Andes, greatly overextending the reports of Jiménez de la Espada (1872; Table S1). While it is likely that information in *Mamíferos Sud-Americanos* was based in part on previous accounts of *H. antisensis* (Jiménez de la Espada, 1872; Cabrera 1912, 1917), it is also known that the work by Cabrera and Yepes (1940: 9) does contain information that may not be supported by published literature (Pinto et al. 2007: 246). This has caused confusion in our understanding of *Hippocamelus* species distributions.

There is no doubt that zoological collections are important to understand distributions of little-studied taxa (e.g., Graham et al. 2004, Helgen et al. 2009, 2013, Pinto et al. 2013), and when combined with archaeological evidence, these findings are stronger. A remarkable example constitutes the finding of an early twentieth century specimen of the echidna *Zaglossus bruijnii* in Australia. This record was backed up by aboriginal rock art representing a long-beaked echidna, and potentially by living memory accounts of aborigines (Helgen et al. 2012). The

evidence to whether *H. antisensis* have been present in Ecuador points out to continuous misidentifications of *Odocoileus virginianus* specimens. Thus, the absence of unambiguous archaeological evidence is not surprising. The absence of both zoological and archaeological evidence is also corroborated by our results of ecological niche models.

Ecological Niche Models.—The PCA on the variables used to summarize regional climate show that seasonality and coldest quarter precipitation (i.e., bio15 and bio19) are important factors contributing to the distribution of *H. antisensis*. This and the jackknife analysis also revealed that the most important variable when used in isolation was the maximum temperature of the warmest month (bio5). Species geographic distributions are governed by complex interactions among many abiotic and biotic variables. Thus, it is difficult to distill all factors that rule the distribution of a species into a handful of abiotic variables. Nonetheless, our models successfully captured the known habitat preferences and natural history of *H. antisensis*. For example, seasonal reproduction in *H. antisensis* peaks in the middle of the rainy season and parturition occurs when food availability is at its highest (Merkt 1985). This reinforces the importance of precipitation to develop accurate predictions of the distribution of this species. Furthermore, *H. antisensis* occurs on elevations above 3,500 m in the highlands of Peru and Bolivia and its distribution shows a decrease in elevation as it extends south into Argentina and Chile (Barrio 2013; and citations therein). This pattern suggests that *H. antisensis* prefers cool temperatures found along the high Andes. The higher temperature in Ecuador, compared to other Andean

regions to the south, may be an important factor precluding *H. antisensis* to colonize areas further north of its current distribution.

Overall, our modeling results confirm that the presence of *H. antisensis* in Ecuador is unlikely. These results also agree with Barrio's (2010) statement that the environmental conditions to sustain populations of *Hippocamelus* are currently absent in Ecuador. Ecological divergence and adaptation to particular habitats can restrict the geographic distribution of species (Sobel et al. 2010; Soto-Centeno et al. 2013). The environmental preferences of *H. antisensis* match closely with the conditions of the puna vegetation of the Central Andes, which is an arid environment characterized with open vegetation at altitudes above ca. 3,000 m. Our models included some low probability overprediction as a disjunct distribution in the Central Andes from Cajamarca Department to Lima, Peru (Fig. 4). The low probability of occurrence of *H. antisensis* in this region likely results from a significant climatic change, which is evidenced by the replacement of the puna by páramo vegetation in this area. The páramo is a wet habitat characterized by denser and richer vegetation than the puna (Simpson 1983). This climatic and habitat transition may represent a significant biogeographic barrier for some taxa. For example, the Andean tapir (*Tapirus pinchaque*) inhabits the páramos but it is absent south of the Huancabamba depression in northern Peru (Padilla et al. 2010). We suggest that these environmental differences have a clear biogeographic implication and serve as a barrier that precludes the northward movement of *H. antisensis*.

Hippocamelus antisensis could not have existed in Ecuador at least since the beginning of the last glacial maximum (ca. 33–29 ka) when large ice sheets started to cover the central and

northern Altiplano in Peru (Vuilleumier 1971; Smith et al. 2005; Clark et al. 2009). We hypothesize that this glaciation potentially eliminated favorable habitat for *H. antisensis* and restricted it only to the Altiplano in Bolivia and northern Argentina where large glacial lakes were present and could have contributed to further isolation of taruka populations (Vuilleumier 1971). If this hypothesis holds, then the current distribution of *H. antisensis* would suggest a northward postglacial expansion. However, contrary to the hypothesis presented by Barrio (2010), we argue that the Huancabamba depression is not such a strong barrier to impeding the movement of a large mammal, as for example, the white-tailed deer (*Odocoileus virginianus*), spectacled bear (*Tremarctos ornatus*), or puma (*Puma concolor*) have easily crossed this low elevation pass in northern Peru (Pacheco et al. 2009). Our methods do not allow us to make general conclusions regarding a possible northward postglacial expansion and the importance of the Huancabamba depression as a barrier to *H. antisensis*. Additional population genetic studies in combination with time-scaled ecological niche models are necessary to elucidate the historical demography of this endangered cervid. In this context, the use of coalescent-based phylogeographic analyses in a comparative approach with other South American cervids may provide a fruitful area for future research.

The absence of concrete evidence of *Hippocamelus antisensis* in Ecuador may indicate that historically and recently this species has not been a component of the Ecuadorian mammalian fauna. Mention of its occurrence in the country may have been the product of an unfortunate cascade of misinformation due to improper identifications of voucher specimens and

observations of *Odocoileus virginianus*. With the approach used in this study, of analyzing archaeological and zoological collections, as well as generating niche models, we were able to rule out the doubts regarding the existence of *H. antisensis* in Ecuador. This approach may prove useful in other cases where there are doubts concerning the occurrence of a species, or when a recent introduction of a species has occurred in an area.

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Figure legends:

Figure 1. Archaeological piece resembling a deer from late prehistoric Manteño context, Agua Blanca, Manabí province, Ecuador. Because of the bifurcated antlers and visible “Y” on the forehead resembling a dark mark, this piece could be a representation of *Hippocamelus antisensis*, or a young adult *Odocoileus*. The locality where this piece comes from suggests this is more likely the latter.

Figure 2. Details of *Hippocamelus* skulls showing the foramina in the sulci of the orbital. Skull of FMNH 1476 huemul (center), compared with a taruka, *Hippocamelus antisensis* (FMNH 88260) from Arequipa, Peru (left), and *H. bisulcus* (FMNH 23553) from Aisén, Chile (right).

Figure 3. Distribution of unique localities used to develop ecological niche models for *Hippocamelus antisensis* in South America. Locality subsampling resulted in 130 points for 1 km (A) and 83 points for 10 km (B) datasets.

Figure 4. Ecological niche models of *Hippocamelus antisensis* in South America based on 1 km (A–B) and 10 km (C–D) subsampled datasets. Two levels of regularization (β) were used for each dataset: $\beta = 1$ (A and C) and $\beta = 2.5$ (B and D). See Table 1 for low probability thresholds used for each MaxEnt logistic prediction.

Table 1. Performance statistics of ecological niche models developed for *Hippocamelus antisensis* in South America. Threshold values for maximum training sensitivity plus specificity were determined using the maximum TSS for MaxEnt logistic predictions. Each distribution was generated using two regularization multipliers (β). Performance statistics: area under the receiver operating characteristic curve (AUC); true skill statistic (TSS); true positive fraction (TPF).

| Dataset / β | AUC (SD) | TSS | Threshold value | TPF |
|-------------------|----------------------|-------|-----------------|------|
| 1 km / 1 | 0.967 (\pm 0.009) | 0.926 | 0.137 | 0.98 |
| 1 km / 2.5 | 0.966 (\pm 0.009) | 0.928 | 0.21 | 0.98 |
| 10 km / 1 | 0.969 (\pm 0.007) | 0.943 | 0.284 | 0.98 |
| 10 km / 2.5 | 0.969 (\pm 0.008) | 0.939 | 0.393 | 0.98 |

Figure 1.



Figure 2.

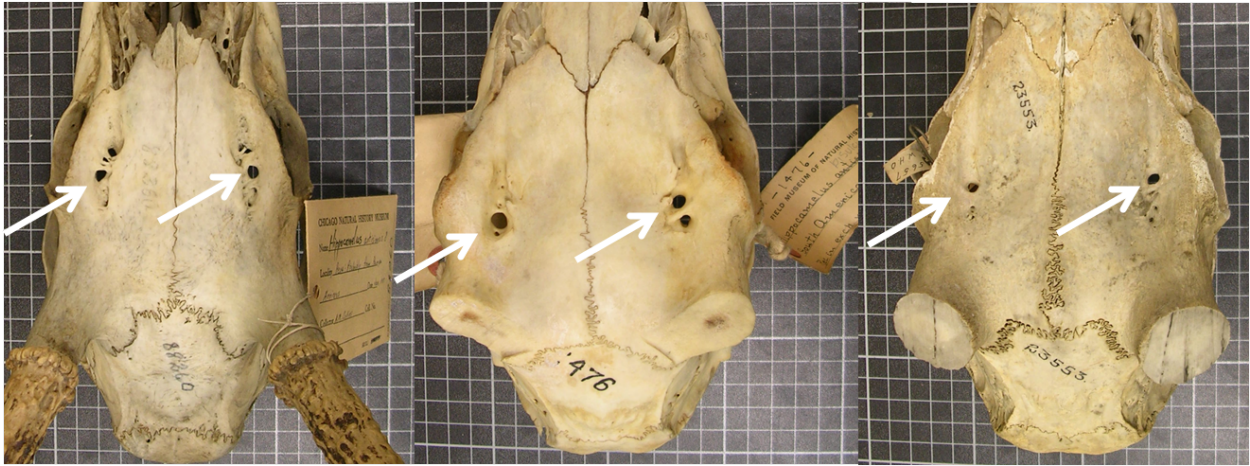


Figure 3.

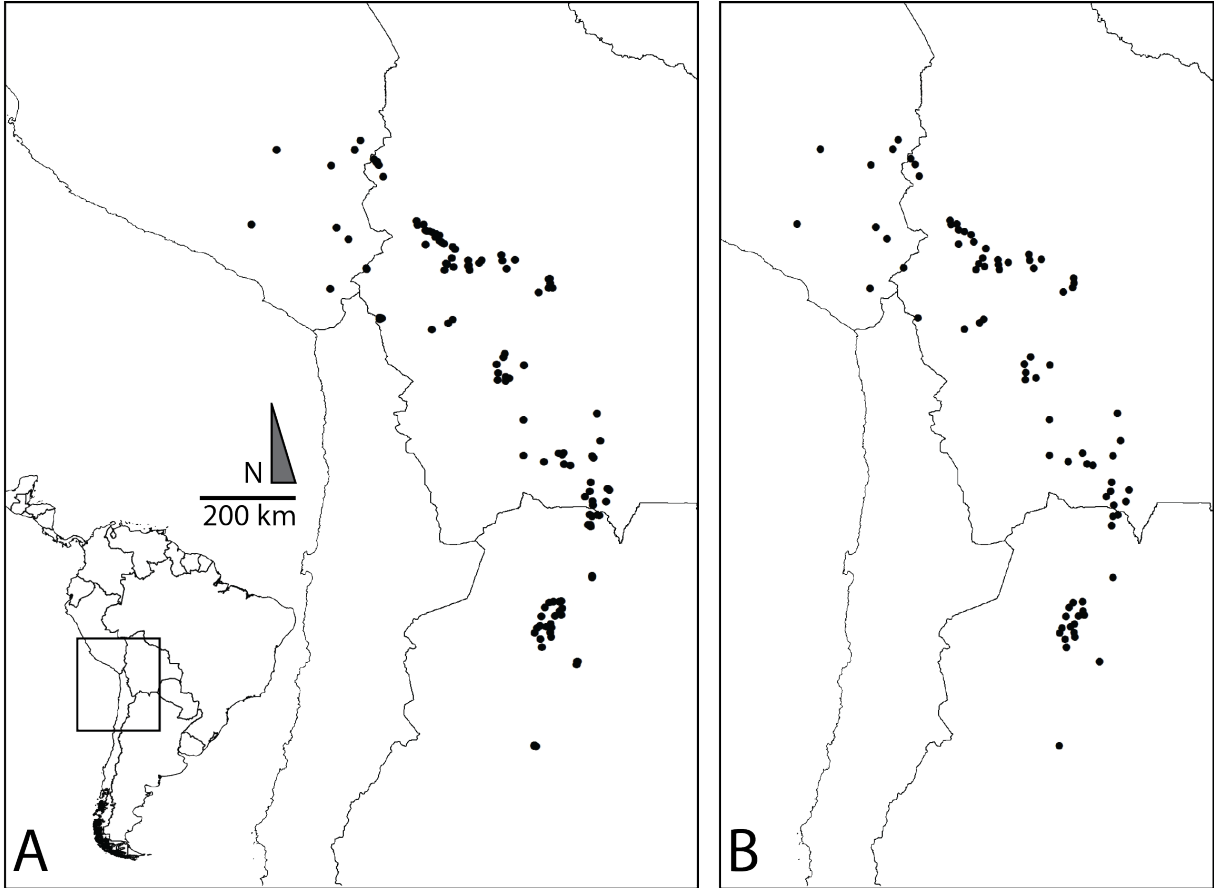


Figure 4.

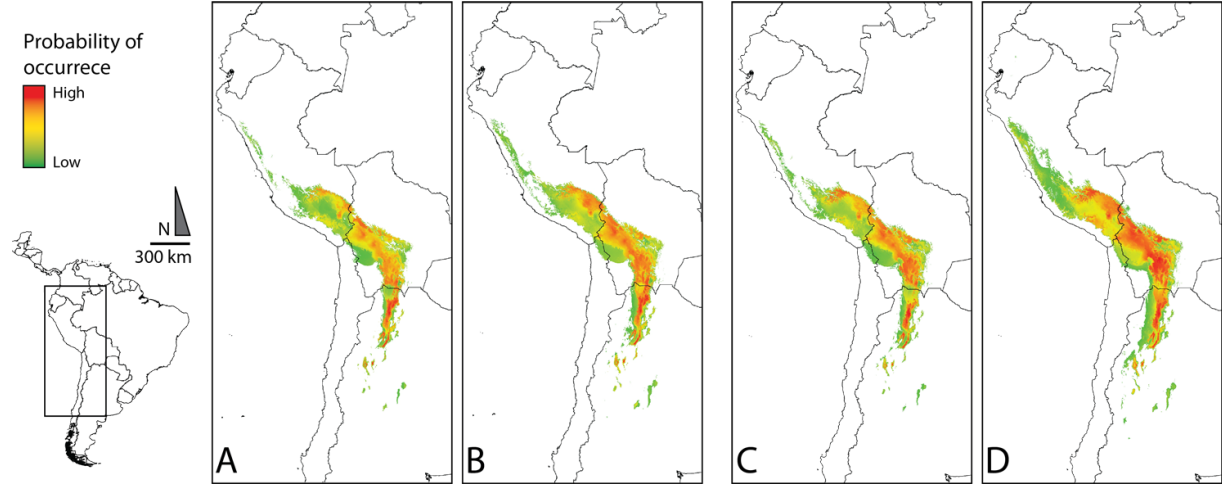


Table S1. Annotated chronological list of *Hippocamelus* reports for Ecuador.

| Taxon name | Reference | Comment |
|--|-------------------------------------|--|
| <i>Hippocamelus Antisiansis</i> | Pucheran, 1851:562 | First mention of its presence in Ecuador. Pucheran mentions that in this part of South America [Ecuador] inhabits another deer species, “le Cerf d’Antis (<i>Cervus Antisiansis</i> , d’Orb.)” and comments that this species “is located in the neighboring areas of the Chimborazo [volcano], and in [the surroundings of] the |
| <i>Cer. antisiansis</i> | Giménez de la Espada [sic], 1872:60 | Second mention for Ecuador. The species epithet <i>antisiansis</i> is associated with the Antisana volcano: “Recibenla allí irremisiblemente los Tarugas (<i>Cer. antisiansis</i>), monteados y acosados en aquella dirección, merced á las favorables condiciones venatorias del sitio, y de ahí su nombre” [There |
| <i>Cervus</i> | Wolf, 197: 155 | Report of fossil remains of a deer species Punín, Chimborazo |
| <i>Cervus</i> sp. | Branco, 1883:130–131 | Report of fossil remains of a deer species from Punín, Chimborazo province, and Alangasí, Pichincha province. Branco deposited this remains at the Museum für Naturkunde de Berlin |
| <i>Cervus chilensis</i> [<i>antisiansis</i>] | Wolf, 1892 [1993:289] | Mentions that those are the most common deer in the highlands of Ecuador, specially in the páramos, while <i>Cervus virginianus</i> is |
| <i>Mazama antisiansis</i> | Lydekker, 1898:295–296 . | Comments on the abundance and distribution in Ecuador: Inhabits Andes of Ecuador, where is abundant on Chimborazo, Pechincha [sic] and Cotopaxi [volcanoes area]. Although Lydekker does not mention the source of his information, it seems to come from the |
| <i>Furcifer antisiansis</i> | Trouessart, 1898– | Comments on the presence of the species in the Ecuadorian |
| <i>Hippocamelus antisiansis</i> | Elliot, 1907:52 | Reports an adult male from Ecuador deposited in the FMNH; Elliot mentions this specimen was obtained from the British |
| <i>H. antisiansis</i> | Cabrera, 1912:131 | Reports two specimens (male and female) collected by Jiménez de la Espada in Antisana volcano and deposited in the MNCN. |

| | | |
|------------------------------------|----------------------------------|---|
| <i>Hippocamelus antisensis</i> | Lydekker, 1915:196–197 | Comments on the abundance and distribution in Ecuador. Although Lydekker does not mention the source of his information, it seems to come from the comments in Pucheran Report and description of the specimens collected by Jiménez de la Espada near the Antisana volcano. Also indicates the existence of a third specimen, not deposited in the MNCN, from the |
| <i>Hippocamelus antisensis</i> | Cabrera, 1917:56–57 | Comments about the presence of a species of this genus in Ecuador, which inhabits the tropical, subtropical and temperate |
| <i>Xenelaphus Wagner</i> , 1844 | Spillmann, 1931:28 | Assume that the material collected in Punín and Alangasí and commented by Wolf (1875) and Branco (1883) belongs to the |
| <i>H. riobambensis</i> (Wolf) | Kraglievich and Berro, 1932:427 | Comments on its distribution: “La taruca habita los Andes del Ecuador, y desde aquí, a través del Perú y de Bolivia, hasta las altas montañas de Catamarca. En el Ecuador, donde vulgarmente se le da el nombre español de gamo, se encuentra en la zona de los páramos, así como en los nevados que se extienden en las vertientes del Antisana, del Rumiñahui, del Chimborazo y del Cotopaxi, por lo general, por encima de los 4 000 metros de altura.” “the Taruka inhabits the Andes of Ecuador, and from here through Peru and Bolivia, towards the high mountains of |
| <i>Hippocamelus antisensis</i> | Cabrera and Yepes, 1940:87–88 | Mentions that William B. Richardson, a collector of the American Museum of Natural History, did not find any specimen during his Analysis of an antler fragment that may correspond to the genus <i>Hippocamelus</i> . This piece was found in Punín, Ecuador and corresponds to the third interglacial period. The author mentions that the identification is not reliable, and also mentions that the species seem to be rare. He also mentions that if <i>Hippocamelus</i> inhabited the Ecuadorian Andes, it was never a common species, and it may have become extinct. Hoffstetter also considers that the opinion of Kraglievich and Berro (1932), about considering <i>C.</i> |
| <i>Hippocamelus antisensis</i> | G. M. Allen, 1942:413 | Restricted the type locality to the Bolivian Andes, near La Paz, |
| ? <i>Hippocamelus</i> sp. | Hoffstetter, 1952:361 | |
| <i>Hippocamelus</i> | Cabrera, 1961:333 | |

| | | |
|--------------------------------|----------------------------|--|
| ? <i>Hippocamelus</i> sp. | Hoffst tetter, 1996:210 | Comments on the same antler fragment reported in Hoffst tetter (1952) |
| <i>Hippocamelus antisensis</i> | Albuja, 1991:201 | Species reported as extinct in Ecuador, indicating that there are no concrete records in the country. |
| <i>Hippocamelus antisensis</i> | Gotch, 1995:637 | Sonsiders that the name comes from Antisana, peak in the [Ecuadorian] Andes mountains, where this deer lives, and <i>-ensis</i> , a Latin suffix meaning belonging to, “belonging to Antisana”. |
| <i>Hippocamelus antisensis</i> | Tirira, 1999:136 | Reports a skull deposited in the MACN from Concepci n in the Ecuadorian Amazon. The catalog of the collector R. Olalla, mentions that the skull was bought together with several skins. |
| <i>Hippocamelus antisensis</i> | Tirira, 2001:34 | Indicates in the first edition of the <i>Red Book of mammals of Ecuador</i> that the species is extinct in the country |
| <i>Hippocamelus antisensis</i> | Voss, 2003:20 | First author attempting to search the museum records of <i>Hippocamelus</i> , and provides an explanation for the loss of the specimens at the MNCN: “Unfortunately, both specimens were lost during the Spanish Civil War or its aftermath, when the |
| <i>Hippocamelus antisensis</i> | Tirira, 2004:38 | Comments that Antisana is a Quichua word that comes from the prefix <i>anti</i> , that meaning the place from the sun is dawn; also, it can be interpreted as the Eastern or to the East, this is consistent with D’Orbigny in Geoffroy Saint-Hilaire & de Blainville (1834): “the east versant of the cordilleras”; the prefix <i>anti</i> also |
| <i>Hippocamelus antisensis</i> | Tirira, 2007:413 | correspond to the etymology of Andes, the great South American |
| <i>Hippocamelus antisensis</i> | Barrio and Ferreyra, 2008 | Given the lack of solid evidence for its presence in Ecuador, the author considers that “the existence of this species is one of the |
| <i>Hippocamelus antisensis</i> | Barrio, 2010:79 | Comment that the species never could have reached Ecuador, indicating the northern limit is its distribution would be the |
| <i>Hippocamelus antisensis</i> | | Mentions that the habitat of the Ecuadorian Andes would not be suitable for the presence of the taruka, and argues that the animals would not be able to cross the Huancabamba depression in |

| | | |
|--------------------------------|-------------------|--|
| <i>Hippocamelus antisensis</i> | Tirira, 2010: 129 | Mentions that there is no solid evidence of its presence in Ecuador, and it is not justifiable to consider this species as native and extinct in Ecuador, and recommends removing this species |
| <i>Hippocamelus antisensis</i> | Tirira, 2011:344 | Categorizes the species as Data Deficient in the second edition of the <i>Red Book of mammals of Ecuador</i> . |

Table S2. Unique locality data of *Hippocamelus antisensis* in South America sampled at 1 km and 10 km density and used to construct ecological niche models. Localities marked with an asterisk (*) represent those used in the 10 km-subsampled models.

| Country | Locality Description | Latitude | Longitude |
|---------------------------------------|---|----------|-----------|
| Peru | 4 km N Tarata, Peru* | -17.4383 | -70.0328 |
| | 70 km E Puno, Peru* | -16.1339 | -69.9047 |
| | above La Raya Pass, Peru* | -14.4833 | -71.0833 |
| | Cuyocuyoabove, Peru* | -14.4833 | -69.55 |
| | Hacienda Checayani, Peru* | -14.8167 | -70.0167 |
| | Hacienda Sorapa, 33km S Ilave, Peru* | -16.3815 | -69.6667 |
| | La Pacheta, W of Sandia, Peru* | -14.2833 | -69.4333 |
| | Pampa de Arrieros, Peru* | -16.0667 | -71.5833 |
| Bolivia | 38 km W, 76 km N, Sajama Village Sajama National Park, Bolivia* | -18.0667 | -69.0167 |
| | Aguirre PN Carrasco, Bolivia | -17.2333 | -65.7167 |
| | Alisos El Carmen alrededores, Bolivia* | -21.9655 | -64.5897 |
| | Almona alrededores, Bolivia* | -21.1273 | -65.8154 |
| | Alrededores Anquioma, Chinja Huichuraya, Bolivia* | -16.97 | -67.6 |
| | Alrededores de Maca Maca, Malavi, Bolivia* | -17.04 | -67.78 |
| | Alrededores San Francisco Tarija, Bolivia | -21.96 | -64.85 |
| | Alto Peñas, Cerca laguna, Bolivia* | -16.0837 | -68.311 |
| | Alto Peñas, Laguna Leche Khota, Bolivia* | -15.9896 | -68.3321 |
| | Andes of Bolivia, near La Paz, Bolivia* | -16.5 | -68.15 |
| | Atocha, Bolivia* | -20.9904 | -66.2112 |
| | Azanaques, Bolivia* | -18.8988 | -66.618 |
| | Calientes, Bolivia* | -17.0115 | -66.5516 |
| | Canquichico, Bolivia* | -16.8889 | -67.0927 |
| | Cerro de la taruka, alrededores Papachacra, Bolivia | -21.6934 | -64.5635 |
| | Cerro Juno, Bolivia* | -17.4167 | -65.7167 |
| | Cerro Potosi Cotapata, Bolivia | -16.269 | -67.9425 |
| Cerro San Benito, Bolivia* | -17.5167 | -65.9167 | |
| Cerro Sipicercade, El Monte, Bolivia* | -20.9949 | -64.8664 | |

| | | |
|--|----------|----------|
| Cerro Tumula, near Yura, Bolivia* | -20.2333 | -66.2167 |
| Choquetanga, Bolivia* | -16.8277 | -67.3064 |
| Condado, Bolivia | -16.898 | -67.7461 |
| Condo, Bolivia* | -19.0439 | -66.7453 |
| Copapugio, Bolivia* | -16.998 | -69.3139 |
| Cordillera Mochara, Bolivia* | -21.17 | -65.42 |
| Crucero grande, alrededores de Collpa Uno, Bolivia | -20.9725 | -65.4499 |
| Culimayo Pampa, Bolivia* | -20.9447 | -65.5147 |
| Cusmina, Bolivia | -18.82 | -66.59 |
| El Carmen, Bolivia* | -22.048 | -64.8478 |
| El Mesón, Bolivia* | -21.5655 | -64.8905 |
| Falsuri, Bolivia* | -16.84 | -66.6341 |
| Frutillani, Bolivia | -16.8355 | -67.04 |
| Head of río Aceramarca valley, Bolivia* | -16.3 | -67.8833 |
| Huno, Bolivia* | -17.3238 | -65.6939 |
| Jakañan Chipa, Bolivia | -20.9562 | -65.4416 |
| Japo Khasa, Bolivia* | -20.0963 | -64.7711 |
| Junthuma Khuchu PN Sajama Hito 16, Bolivia | -18.0834 | -69.05 |
| Kelkatani, Bolivia | -20.942 | -65.5247 |
| La Torre, Bolivia* | -21.2024 | -65.2931 |
| Ladera Sur, Bolivia | -21.6931 | -64.5629 |
| Laguna Chiarkkota PN Sajama, Bolivia | -18.0455 | -69.0534 |
| Laguna, alrededores de Papachacra, Bolivia* | -21.72 | -64.5208 |
| Lambate Yunga Cruz, Bolivia | -16.55 | -67.6167 |
| Llallagua alrededores, Bolivia* | -18.3102 | -68.0279 |
| Llaullini, alrededores de Zongo, Bolivia* | -16.1982 | -68.1504 |
| Mina Arminda, alrededores Quime, Bolivia* | -16.932 | -67.2964 |
| Mina Reconquistada, Bolivia | -16.4184 | -67.8739 |
| Mina San Francisco, alrededores Taquesi, Bolivia | -16.4782 | -67.7821 |
| Molino El Potrero, Bolivia* | -16.5899 | -67.5706 |
| Nevado Akhamani, Apolobamba, Bolivia* | -15.0502 | -68.9834 |
| Onduras, Bolivia | -21.0125 | -64.8514 |
| Pagoni, Punta Incacasani, Bolivia* | -16.8199 | -66.3876 |

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| Picotani, Bolivia* | -19.3856 | -66.7247 |
| Piedras Blancas, Bolivia | -21.0359 | -64.8312 |
| Pongo, Bolivia | -16.3351 | -67.9556 |
| Portillo, Bolivia* | -20.6801 | -64.7012 |
| Puina, Apolobamba, Bolivia* | -14.6834 | -69.1669 |
| Pulluni, Apolobamba, Bolivia* | -14.8 | -69.0667 |
| Quello C'ocha, Apolobamba, Bolivia | -14.7336 | -69.1 |
| Represa Pacuni, alrededores Quime, Bolivia | -16.9511 | -67.3105 |
| Reserva Biológica Cordillera de Sama, Bolivia* | -21.7488 | -64.9136 |
| Reserva Biológica Cordillera de Sama, Bolivia* | -21.8673 | -65.0067 |
| Río LP, Valle de Araca, Bolivia* | -16.7897 | -67.6337 |
| San Jacinto PN Carrasco, Bolivia* | -17.2167 | -65.7 |
| San Miguel, Bolivia* | -16.7126 | -66.6548 |
| Sancayani Alto, Bolivia | -17.4243 | -65.6474 |
| Santiago de Paria, Bolivia* | -19.3398 | -66.5036 |
| Sawisa, Bolivia | -19.3135 | -66.5683 |
| Takesi, Bolivia* | -16.4508 | -67.8279 |
| Tarucachi, Bolivia* | -18.1718 | -67.6961 |
| Taruja Maya, Bolivia | -17.0176 | -69.3068 |
| Tijllacahua, Bolivia* | -18.0989 | -67.6177 |
| Umopalca, Cotapata, Bolivia | -16.2167 | -68.0667 |
| Urmiri, Bolivia* | -19.2274 | -66.7197 |
| Valle de Araca, Bolivia | -16.7824 | -67.6305 |
| Valle de Makara, Apolobamba, Bolivia | -14.75 | -69.1169 |
| Ventilla, camino Oruro Potosí, Bolivia* | -19.0713 | -66.2067 |
| Wayñakhota, Bolivia* | -17.0371 | -67.2845 |
| Wila Kollu Azanaques, Bolivia | -19.4 | -66.5667 |
| Wila Kollu Luribay, Bolivia* | -16.92 | -67.72 |
| Yama Moco, Bolivia | -20.9355 | -65.422 |
| Zongo Coscapa alrededores, Bolivia* | -16.0667 | -68.1833 |
| Zongo Tiquimani, Bolivia | -16.2167 | -68.1167 |
| Zongo, Bolivia* | -16.2311 | -68.0244 |

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| Argentina | A la altura de La Cueva bajando hacia el Ro Pavas, Argentina | -27.1696 | -65.9925 |
| | Abra del Mojón, Argentina | -22.4669 | -64.9002 |
| | Abra del Mojón, Cerro Llorón, Argentina | -22.4778 | -64.895 |
| | Abra del Mojón, Cerro Llorón, Argentina | -22.4856 | -64.8916 |
| | Abra del Mojón, Cerro Llorón, Argentina | -22.504 | -64.8942 |
| | Abra del Mojón, Cerro Llorón, Argentina* | -22.4814 | -64.8938 |
| | Alto Calilegua Yaretal, Argentina | -23.5702 | -64.8642 |
| | Alto Calilegua, Abra Fundición, Argentina | -23.556 | -64.8627 |
| | Alto Calilegua, Filo N Cerro Amarillo, Argentina | -23.5533 | -64.861 |
| | Alto Calilegua, pueblito Cerro Calilegua, Argentina | -23.5636 | -64.8615 |
| | Area entre Cerro Hermoso y Cerro Amarillo, Argentina | -23.5714 | -64.8601 |
| | ca Cruz del Cerro Los Toldos, Argentina | -22.269 | -64.7198 |
| | Camino Abra del Mojón, Salviayoc, Argentina | -22.4871 | -64.9101 |
| | Camino al Cerro Crestón, Argentina* | -25.3746 | -65.152 |
| | Camino Cerro Blanco-Barittú, Esquina de Lajar, Argentina | -22.4692 | -64.9397 |
| | Camino Los Toldos, Santa Victoria Oeste, Cerro San José, Argentina* | -22.285 | -64.8638 |
| | Cerro Hermoso, Argentina | -23.5839 | -64.8565 |
| | Cerro Hermoso, Argentina* | -23.5904 | -64.8599 |
| | Co Malcante, Argentina* | -25.0742 | -65.8566 |
| | Desde el Cerro Amarillo el segundo cañadón hacia el Oeste, PN Calilegua, Argentina | -23.5751 | -64.8593 |
| | El Nogalar, Argentina* | -22.2565 | -64.758 |
| | Entre el Cerro Crestón y el Morro del Venado, Argentina | -25.4424 | -65.1655 |
| | Filo hacia Fundición, Argentina | -23.5467 | -64.8641 |
| | La Cascada laguna seca, Argentina | -27.1826 | -65.9691 |
| | La Cascada, Argentina | -27.1769 | -65.972 |
| | La Cascada, sobre la ladera del Vallecito Ao, Argentina | -27.1765 | -65.9722 |
| | La Ciudadcita, Argentina | -27.1734 | -66.0101 |
| | La Cueva arriba, Las Yaretas, Argentina* | -27.1619 | -66.0063 |
| | Ladera oeste del Cerro Amarillo, Argentina | -23.5562 | -64.8616 |
| | Lagunita, Filo Cerro Blanco, Argentina* | -24.1016 | -65.5112 |

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| Los Quencos, Argentina | -27.1731 | -65.9734 |
| Los Quencos, arriba de La Cascada, Argentina | -27.1724 | -65.973 |
| Mountains W of Yala, Argentina* | -24.1167 | -65.7079 |
| Piedra Batea, abajo de Los Quencos, Argentina | -27.1733 | -65.9723 |
| RN Nogalar, Argentina | -22.2539 | -64.7634 |
| RN Nogalar, Argentina | -22.2595 | -64.7632 |
| Sa del Cerro Crestón, Argentina | -25.3776 | -65.1632 |
| Sasal E de Santa Victoria, Argentina | -22.2474 | -64.9153 |
| Taruca 1, Argentina* | -24.8979 | -65.8857 |
| Taruca 2, Argentina* | -24.77 | -65.9975 |
| Taruca 3, Argentina* | -24.8518 | -65.6771 |
| Taruca 5, Argentina* | -24.7605 | -65.6901 |
| Taruca 7, Argentina | -24.6574 | -65.667 |
| Taruca 8, Argentina* | -24.6392 | -65.7698 |
| Taruca 9, Argentina | -24.6166 | -65.8887 |
| Taruca 10, Argentina* | -24.6598 | -65.9483 |
| Taruca 11, Argentina* | -24.576 | -65.6798 |
| Taruca 14, Argentina* | -24.3883 | -65.4735 |
| Taruca 15, Argentina* | -24.4087 | -65.601 |
| Taruca 16, Argentina* | -24.4124 | -65.8607 |
| Taruca 22, Argentina* | -24.2997 | -65.4992 |
| Taruca 23, Argentina | -24.2493 | -65.452 |
| Taruca 24, Argentina* | -24.2276 | -65.7993 |
| Taruca 28, Argentina | -24.1061 | -65.6245 |
| Taruca 29, Argentina | -24.0889 | -65.4716 |
| Zona de La Cascada y de Los Quencos, Argentina | -27.1767 | -65.9726 |

Figure S1. Close up view showing localities and model fit for four ecological niche models developed for *Hippocamelus antisensis* in South America. Overall, a $\beta = 2.5$ resulted in an improved ability to detect suitable areas between locality records where potential zones of population connectivity might occur.

