

Speed of extirpation of the huemul in the history of human occupation in Patagonia

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ABSTRACT

Context. The Patagonian huemul, an endangered Odocoileine deer, has an estimated 350–500 individuals remaining in Argentina. Today's population size, representing a numerical reduction of >99% of original estimates, is fragmented into small groups along ~2000 km of Andean mountains. The species' numbers were heavily reduced by past overexploitation and they disappeared in areas of high anthropogenic activity, predominantly the fertile valley bottoms.

Aims. This research delineates the current potential distribution of Patagonian huemul by using climatic indicators, topographic and vegetational proxies, and anthropogenic pressure, to determine the relevance of the climatic envelope on current distribution. **Methods.** Occurrence records (latitude and longitude) were compiled ($n = 159$) by consulting the literature. Twenty environmental variables were used (WorldClim database) and two other representative environmental variables (normalised difference vegetation index (NDVI) and enhanced vegetation index (EVI)) were added to test their predictive power. We added the human footprint index (HFP) as a variable to control for model bias. Using the maximum entropy algorithm (MaxEnt), we modelled the species' potential distribution. We designated the historical distribution as area M. Additionally, we calculated three areas of distribution: current, historical and potential. Finally, we calculated distributional retraction of the species and area lost per year. **Key results.** The model showed good predictive power ($AUC_{Test} = 0.764 \pm 0.091$). However, low values were obtained for AUC_{train} and AUC_{prom} for the different predictor scenarios. Although the model shows the interaction among several climatic, environmental, and topographic variables, the human footprint index (39.9%) was the variable that most influenced the current potential distribution of this species. **Conclusion.** Our model shows that most of Patagonia's surface is climatically suitable for huemul. This suggests that the causes of distributional retraction are not related to limitations imposed by the climate envelope, but rather concur with recent research showing impact owing to the species' behavioural response to anthropogenic activity. **Implications.** Current populations are small, fragmented, and confined to poor-quality sites. Although the species is currently found mainly within protected areas, management actions must be initiated that promote innovative strategies in unprotected areas, as well as high-value habitats, particularly as protected areas contain limited fertile lower-valley habitats.

Keywords: climate envelope, conservation, distribution model, endangered species, historical distribution, Patagonian huemul, potential distribution, retraction.

Introduction

The geographic range of species, size and area of distribution, which includes the size and area of the population distribution, is a complex expression of their ecology and evolutionary history (Brown 1995). This range is shaped by multiple factors (e.g. biotic, abiotic, and human interactions) that act dynamically with different strengths and at different scales (Pulliam 2000). In turn, the interaction with these factors influences the shape and size of species ranges (Rapoport 1982; Soberon and Peterson 2005). Of the aforementioned factors, climate is the one that exerts the greatest influence on distribution

limits, whose patterns are detectable at regional or continental scales (Pearson and Dawson 2003).

The Patagonian huemul (*Hippocamelus bisulcus*), an endangered Odocoiled deer, has an estimated 350–500 individuals remaining in Argentina. Today's population size, representing a numerical reduction of >99% from estimates before European arrival (Díaz and Smith-Flueck 2000), is fragmented into small groups along an approximate ~2000 km of Andean mountains (Vila et al. 2006). With their numbers heavily reduced by past overexploitation, they disappeared wherever anthropogenic activity was highly concentrated, predominantly the fertile valley bottoms (Huemul Task Force (HTF) 2012; Flueck et al. 2022). Today, they are the only known cervid worldwide to remain year-round in summer range, having lost the ability to migrate (Flueck et al. 2022).

The huemul has been negatively affected mainly by past overexploitation, but also loss and fragmentation of habitat, malnutrition, diseases, dogs, and possibly by the introduction of alien wild and domestic ungulate species (Bessera 2006). Unrestricted killing in the past was one of the main factors that resulted in widespread population declines and the endangered status of this species (Flueck et al. 2022). Being extremely tolerant of human presence (Flueck and Smith-Flueck 2011a; Smith-Flueck et al., In press), their unique docile behaviour towards humans resulted in their local extirpation, especially in those areas used by indigenous people and early colonists (Flueck et al. 2022). An additional critical factor was when cattle ranching was introduced to Patagonia at the end of the 19th century and the beginning of the 20th century.

Conservation planning and forecasting rely on detailed knowledge of the ecological and geographical distribution of species. Ecological Niche Model provides detailed predictions about the potential distribution of species by relating presence records to relevant environmental factors (Phillips et al. 2006; Elith et al. 2006). If implemented accurately, species distribution models are a powerful and repeatable means of mapping the potential distribution of species (Wintle et al. 2005). Models based on bioclimatic variables at macro scales have proven successful in predicting known distributions, and refined algorithms perform well with presence-only data and a limited number of localities (Elith and Leathwick 2009). A major goal of species distribution models is to predict which areas within a region meet the characteristics of a species' ecological niche, which is part of the species' potential distribution (Anderson and Martínez-Meyer 2004).

This research aims to outline the potential distribution of Patagonian huemul by using climatic indicators, topographic and vegetational proxies, and anthropogenic pressure, and to define the species' climate envelope (niche), to then determine relevance of various variables on current distribution. Our model incorporates credible historical presence data, as well as current presence data, to further increase the model performance, and thus the reliability of the prediction

(Lütolf et al. 2006). There is great potential to understanding current patterns through the historical dimension, i.e. the past is the key to the present (Lütolf et al. 2006). Furthermore, historical presence data provide an opportunity to evaluate the speed by which the species was extirpated throughout the Patagonian landscape.

Materials and methods

Our study area encompasses Patagonia in Argentina. Latitudes fall between 32°S and 55°S and elevations from sea level to 3000 metres above sea level (masl). With an area of ~750 000 km², a great diversity of flora and fauna covers this area, units that range from tundra environments in the far south, to shrubby steppes and grasslands in the east, centre, and north, and cold forests dominating the western Andean slopes (Leon et al. 1998). The climate of this region is temperate–cold (Paruelo et al. 1998), with a steep precipitational gradient, and a moderate temperature gradient.

The deer species (*Hippocamelus bisulcus*) was included in our analysis. First, to model potential distribution, we compiled past and current occurrence records (latitude and longitude) of this species ($n = 159$) by consulting the literature, which were retrieved from different published and unpublished sources (e.g. museum specimens, biodiversity information system of the National Parks Administration of Argentina, Lifemapper, Global Biodiversity Information Facility [GBIF], papers and unpublished theses). Twenty environmental variables were selected (1 elevation and 19 bioclimatic; arcoseg resolution of 30; WGS84; Table 1; Hijmans et al. 2005) from the WorldClim database. After an initial inspection, environmental variables combining temperature and precipitation (e.g. Bio 8, 9, 18, and 19) were excluded because they show odd spatial anomalies in the form of discontinuities between neighbouring pixels (Escobar et al. 2014; Zuliani and Monjeau 2021). Two other representative environmental variables, namely, normalised difference vegetation index (NDVI) and enhanced vegetation index (EVI), were added to test the predictive power of the environmental variables; these two indexes were obtained from processing a series of MODIS satellite images. We added the human footprint index (HFP; Sanderson et al. 2002) as a variable to control for model bias.

We modelled the species' potential distribution by using the maximum entropy algorithm (MaxEnt; Phillips et al. 2004), chosen because it generates optimal results by using only points of presence, as is our case (Elith et al. 2006). It also performs well with small sample sizes (Wisz et al. 2008), incorporates interaction effects of environmental variables, and is a deterministic algorithm, meaning that results always converge on a single optimal probability distribution (Phillips et al. 2004). We designated the historical distribution as area M (Barve et al. 2011). The data were cleaned to avoid false

Table 1. Estimates of relative contributions of the environmental variables for *Hippocamelus bisulcus*.

Variable	Percentage (%) contribution
BIO1 = annual mean temperature	–
BIO2 = mean diurnal range (mean of monthly (max temperature–min temperature))	2.8
BIO3 = isothermality (BIO2/BIO7) ($\times 100$)	–
BIO4 = temperature seasonality (standard deviation $\times 100$)	4.5
BIO5 = max temperature of warmest month	–
BIO6 = min temperature of coldest month	17.2
BIO7 = temperature annual range (BIO5–BIO6)	–
BIO8 = mean temperature of wettest quarter	Removed
BIO9 = mean temperature of driest quarter	Removed
BIO10 = mean temperature of warmest quarter	0.4
BIO11 = mean temperature of coldest quarter	1.5
BIO12 = annual precipitation	7.5
BIO13 = precipitation of wettest month	–
BIO14 = precipitation of driest month	–
BIO15 = precipitation seasonality (coefficient of variation)	–
BIO16 = precipitation of wettest quarter	19.9
BIO17 = precipitation of driest quarter	–
BIO18 = precipitation of warmest quarter	Removed
BIO19 = precipitation of coldest quarter	Removed
Elevation	4.7
Enhanced vegetation index	1.2
Normalised difference vegetation index	0.6
Human footprint	39.9
Total	100
% explained by the two most important variables	59.8
% explained by variables above 10% (<i>n</i>)	77 (3)
AICc	1599.275
Rm	5.5
AUC _{Train}	0.59
AUC _{Test}	0.764 \pm 0.191
AUC _{Prom}	0.56

The variables are expressed as a percentage; the variable with the highest score is indicated in bold. For this model, we used the regularisation parameter $\beta(0.5)$ to map and describe the key environmental variables. Environmental variables that combined temperature and precipitation (e.g. 8, 9, 18, and 19) were ‘removed’ because they showed odd spatial anomalies in the form of discontinuities between neighbouring pixels.

positives and pseudoreplicates, which can produce an erroneous model. First, records falling within lakes or the ocean were removed from our analyses. Later, to avoid biases in the selection of presence points for each model, we used a 50 \times 50 km grid and a randomly selected, single locality

within that grid, resulting in 196 points of 804 total points. Finally, we used 196 sighting points in the model, which were also confirmed through photos and geographic coordinates.

To validate each of our models, we cross-validated and calculated the area under the curve (AUC), which is an operational characteristic of the receiver (ROC) (Kuemmerle *et al.* 2011). We performed an exploratory analysis using MaxEnt 3.3.3k (Phillips *et al.* 2004). To discard all highly correlated variables, we conducted a Pearson correlation analysis (>0.8 ; Dormann *et al.* 2012). Next, within each group of uncorrelated variables, we used the Jackknife test to determine which variables showed the greatest contribution, and also have biological significance for the huemul (Nuñez-Penichet *et al.* 2016). All others were discarded to make a new set of variables, with which a second analysis was performed with MaxEnt.

MaxEnt models were generated for this species by using 25% test data, random seed, 1000 iterations, 10 replays, 10 000 background points, and the cumulative option as an output format (Merow *et al.* 2013). To obtain a single model that presents the best values and estimates, a series of steps must be followed. First, we generated preliminary models by using three regularisation multipliers (i.e. $\beta = 0.5, 1,$ and 2 ; Warren and Seifert 2011); each value generates a different result. Second, as an estimator of the predictive power of each generated model, we used the AUC (Phillips *et al.* 2004), by using training (AUC_{Train}) and test (AUC_{Test}) values. Third, for selected model fit, we used the ENMevaluate function of the R package ENMeval (Muscarella *et al.* 2014), which uses functions depending on the number of observations. When having more than 80 records for this species, we used L, LQ, LQP, H, LQH, LQHP, and LQHPT combination of functions (Merow *et al.* 2013). These functions were combined with regularisation multipliers (rm: 0.5–5, in increasing steps of 0.5), across the method of cross-validation of block partitions (González *et al.* 2021). Fourth, to avoid possible overfitting, we used AUC differences (AUCDiff; Gutiérrez *et al.* 2014). Finally, the ‘huemul’ map was generated using the median values of the model selected and provided by MaxEnt. These values represent the environmental suitability of the different habitat types for huemul. Values were oscillated 100–75 for the highest prediction, 74–50 for high, 49–25 for medium, 24–10 for low, and 9–0 for very low (Ruiz Barlett *et al.* 2019; Zuliani and Monjeau 2021). The map for this species was evaluated by qualitative visual examination, on the basis of our field experience, the current distribution of this species (e.g. Patton *et al.* 2015), and habitat types where huemul are known to occur (Leon *et al.* 1998; Pardiñas *et al.* 2003). In addition, on the map, the model shows the historical area of the species with a dotted line, which was built using different sources (Escobar Ruiz *et al.* 2020; Flueck *et al.* 2022), and with a solid line for the current distribution (Pastore and Aprile 2019).

The calculation of the following three areas of distribution was made: current distribution (Cd), historical distribution

(M) and potential distribution (Pd), which is the percentage greater than 50% produced by the MaxEnt model); these calculations were made through use of Qgis software. Finally, the distributional retraction was calculated for the species. Using the different distributions calculated (Cd), namely, historical distribution (M) and potential distribution (Pd)), we set the deadline to the year 1950 to separate historical data from current data. The time of retraction was estimated from the year 1780, considering the record of acquisition of the horse by the native peoples. Then, the difference in surface area between the historical and current distribution was calculated, dividing it by the number of years, which resulted in the calculation of lost area per year.

Results

The model showed good predictive power ($AUC_{Test} = 0.764 \pm 0.191$). However, low values were obtained for AUC_{train} and AUC_{prom} for the different predictor scenarios (Table 1). The AICc behaved disparately for the different rm values, but as these values increased ($rm = 5.5$), the models improved, increasing the yields for the species ($AICc = 1599.275$; Table 1).

Although this climate envelope model shows interactions among several climatic, environmental and topographic variables (Table 1), the human footprint index (39.9%) was the variable that most influenced the potential distribution of this species (Table 1). The environmental suitability values showed that most of Patagonia is climatically suitable for huemul. The potential distribution model showed that the species seems to be associated with the forest and steppe (Fig. 1). In turn, the huemul's current distribution is concentrated in the Patagonian Andes (Fig. 1). It also shows that, climatically, the huemul would find suitable habitat over a large area, including the low elevation areas, but the human influence is keeping it from occupying those lower areas.

The results of the distribution areas were as follows: current distribution $Cd = 123.328 \text{ km}^2$; historical distribution $M = 961.446 \text{ km}^2$; and potential distribution $Pd = 326.361 \text{ km}^2$. Estimating a time range of 250 years, we obtained that the huemul retreated at a speed of 3.352 km^2 per year, or what is equivalent to 9.18 km^2 per day.

Discussion

If we compare the area of distribution calculated by Maxent with historical data (961.446 km^2) with the currently calculated distribution (123.328 km^2) and we estimate a temporal range of 250 years (taking as a starting point 100 years before the conquest of the desert by the Argentine army in 1880 to consider the impact of the equestrian pre-colonial humans), we obtain that the huemul lost 87% of

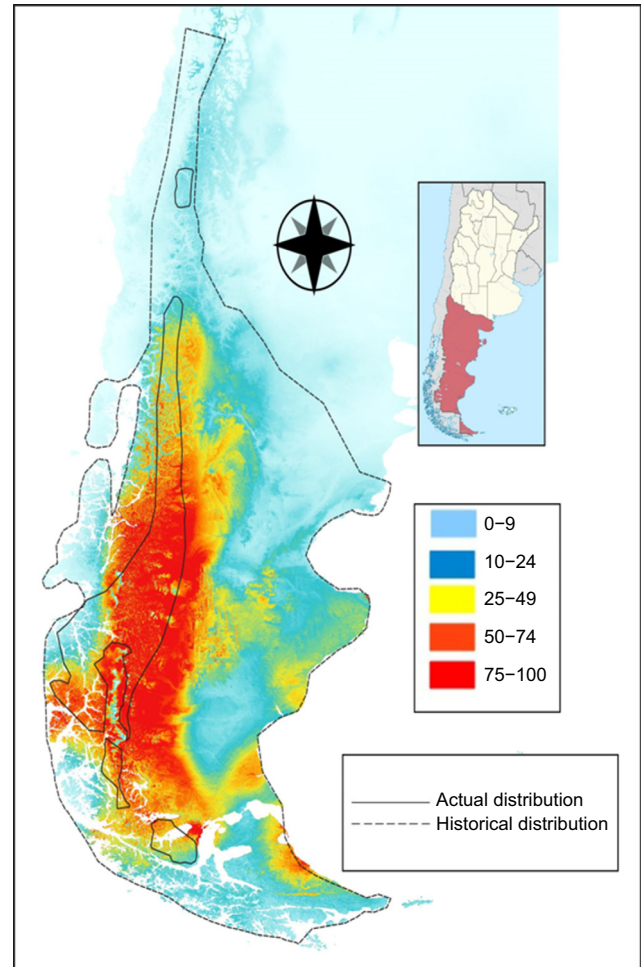


Fig. 1. Potential distribution models generated for *Hippocamelus bisulcus*. The suitability level is represented by a colour gradient in the legend of the figure from clear sky (not suitable) to red (most suitable), with the mountain range being the most suitable area and part of the steppe. The current distribution is represented by solid lines, and the historical distribution by black dotted lines. In the upper right box, we highlight in brown the map of Patagonia, our study area.

its historical distributional range in little over two centuries. Going back a century before the first historical data, when the first colonists settled in Patagonia, takes us to a time when Patagonia was home only to the Indigenous people, who also were influential in the extirpation of local huemul populations (described in Flueck et al. 2022, supplement 1, and Huemul Task Force (HTF) 2012), thus causing the distribution to retract before colonisation. The map (Fig. 1) reflects that which was already stated by some early explorers (Onelli 1905), namely that the huemul had already been pushed up into the mountains from along the waterways in the steppe, even as far as the pampa region, because of unrestricted hunting by the start of 18th century (Onelli 1905). Horses, first liberated in Buenos Aires, had reached the Straits of Magellan by 1580 (Huemul Task Force (HTF) 2012).

Equestrian precolonial humans rarely hunted huemul in the forests, because horses and their weapons, known as 'boleadoras', were useless there. However, they killed huemul out in the open foothills, lowlands or open valleys (Falkner 1774; de la Cruz 1835). The process of range contraction was facilitated by easy hunting of huemul, energetic incentives from seasonal fat cycles and huemul concentrations, the change from hunting–gathering to a mobile equestrian economy, and colonisation with livestock (Flueck and Smith-Flueck 2012; Huemul Task Force (HTF) 2012). If the reader allows us to elucidate a linear-retraction speed hypothesis, using the estimated historical and current ranges from our model, we obtain that the huemul retreated at an average speed of 3350.7 km² per year, or what is equivalent to 9.18 km² per day. It is probable that the retraction speed is not linear but rather had a great initial acceleration when cattle ranching was introduced in Patagonia at the end of the 19th century and beginning of the 20th century, and then a slower speed until stabilising in the forested areas of the Andes mountains, where today it takes refuge from the advance of the human footprint (the most influential factor in explaining the distribution in the Maxent).

Knowledge of historical ranges is important regarding endangered species (Flueck and Smith-Flueck 2012). Anthropogenically caused range contraction of ungulates with broad former historic distributions affected losses mainly at low elevation ranges (Laliberte and Ripple 2004). When analysing many cases of range contractions, Channell and Lomolino (2000) found that most species persist only in marginal peripheries of their historical ranges, and persisted the longest at the edge of their ranges, on isolated and undisturbed islands, including high-elevations refuges.

Our model shows that most of Patagonia is climatically suitable for huemul, including the current distribution of this species (Quevedo *et al.* 2017; Rosas *et al.* 2017). These results suggest that the causes of the distributional retraction are not linked to limitations imposed by the climatic envelope, but to other factors derived from the combination of characteristics of the species' biology and the increased anthropogenic pressure on land use. Although current distribution was within the zone climatically suitable in the model, being a refugee species year-round in summer mountain habitat leaves the animal exposed to winter conditions, that, when severe enough, further exasperates the lack of sufficient essential nutrients in these upper elevations (e.g. Se, Cu, and Mn), and for the weaker animals, ultimately ends in death by starvation (Flueck *et al.* 2022).

Traditional claims of being a mountain specialist of the Andes were refuted by empirical evidence showing huemul morphology to coincide with other cervids rather than the commonly implied homology to rock-climbing ungulates (Flueck and Smith-Flueck 2011b). This species is not morphologically adapted to year-round habitation in the mountains nor to closed habitats (i.e. forested areas, Curran 2015; Flueck *et al.* 2022). Our model supports this by showing that areas

of southern, central and eastern Patagonia fall within the potential distribution, which is explained by the historical distribution of the species (Riquelme *et al.* 2018). Historical records show that the huemul once inhabited the steppe and ecotone areas between forests and open land (Díaz and Smith-Flueck 2000; Flueck and Smith-Flueck 2012; Flueck *et al.* 2022). The areas shown with highest potential distribution in the Patagonian steppe are those areas where explorers crossed, and thus are biased by more sightings.

Our model includes historical data, which allowed us to describe the Argentine Patagonian steppe as suitable habitat for the huemul. Descriptions of suitable habitats, produced from potential species distribution models that are based solely on current presence data, will fail to show past habitat use as suitable if animals no longer live in those environments. It is not uncommon today to find species in areas outside their original distribution. One example, the highly endangered bird, the takahe (*Porphyrio mantelli*) of New Zealand (NZ), was once found throughout NZ, being most abundant along forest margins and streams in lowland regions. Their numbers declined dramatically since human colonisation about 800–1000 years ago. Currently, the takahe lacks wild populations in the lowlands, while predominately existing in an isolated alpine habitat (Mills *et al.* 1984; Bunin and Jamieson 1995). As with the huemul, using the data solely on current distribution of this species to model habitat suitability would severely impair conservation efforts and paint an unrealistic picture of this species' requirements.

Important to point out is that our model describes well the species' potential distribution, but one must practice caution when interpreting and making comparisons about which areas are more or less suitable. The number of presence data collected from the steppe region were low, being based on the few explorers who passed through small transitable areas of that vast open grassland plains. From that small database, the model can point out the species' potential distribution, but comparisons of habitat cannot be made without introducing biases related to the underlying biological requirements of the species. This model describes where huemul is more likely to be found today, but it is not because the red areas are necessarily more suitable in terms of the best biological conditions to meet the animal's needs, but rather more suitable in terms of avoiding people and their activities (i.e. human footprint).

In agreement, the most influential variable in our model was the human footprint, which suggests that it is the variable that most influences the potential distribution of this species, due to a high level of environmental disturbance, including, but not restricted to, livestock production, agriculture, timber extraction, firewood production, and hunting of other species. Direct or indirect anthropogenic pressure has caused distributional retraction towards the most inaccessible sites. Species such as the huemul, which is confined to mountain and forest environments, have even more restricted distributions. This leads to small, fragmented huemul populations (Vila *et al.* 2006) confined to poor-quality sites

(Heitzmann 2008; Flueck et al. 2022). Several of these huemul subpopulations are known to be severely affected by diseases resulting from micronutrient deficiencies, which explains their short lifespans and lack of both population growth and spatial expansion (Flueck et al. 2022). Multiple studies worldwide have demonstrated that protected areas are necessary, but insufficient, for the conservation of many species, especially to meet the territorial demands of large vertebrates (Rapoport 1982; Chauvenet and Barnes 2016).

Although management actions are mainly within protected areas, these areas are not enough to reduce the risk of extinction. Management should promote innovative strategies in areas of high-value habitats, including those areas outside protected areas, which alone are not enough to reduce the risk of extinction. At the same time, connectivity between zones should be sought and fragmentation of natural environments avoided. This would not only reduce the risk of extinction but also the maintenance of ecological processes (Sepúlveda et al. 1997). At the same time, it is necessary to conduct management and protection actions for the species, and to promote innovative management strategies in areas with high-value habitats (Smith-Flueck et al. 2011).

The protection of suitable habitat for species survival or reintroduction in rapidly changing landscapes is a high priority among conservationists (Lütolf et al. 2006). To this regard, potential species distribution models must be applied critically and cautiously (Loiselle et al. 2003). Historical species data and subfossil records should be incorporated to refine model performance for species with highly retracted distributional ranges.

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Data availability. Given this species is endangered and likely to be hunted, it does not seem correct to publicly share the data on the current or recent locations of individuals. To this regard, any researcher interested in obtaining these data should write to the corresponding author, who will provide the data privately.

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