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Review of Historical and Zooarchaeological Data to Trace Past Biogeographic Distribution of Endangered Huemul (*Hippocamelus bisulcus*) to Enhance Conservation Strategies

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Abstract: Conservation strategies for huemul (*Hippocamelus bisulcus*), listed as an endangered cervid by IUCN, have not helped to reverse its declining population trends. Recent evaluations of historical data revealed that they also inhabited lower valleys and grasslands as residents or only during winter. However, the dogma persists that huemuls do not need such habitats. To determine if more solid evidence exists to back up or refute our hypothesis that huemuls once inhabited lower valleys and grasslands, we researched the literature and discovered additional relevant historical sources on this species. These new findings substantiate that huemuls also occupied unforested areas, reaching the Atlantic coast, and resided on various islands including Tierra del Fuego, and that their co-occurrence with guanaco was frequent. Their extreme naivety towards humans resulted in their extirpation on winter ranges settled by humans, resulting in refugee huemuls year-round on remote mountain summer ranges. The ease by which indigenous people could kill them for subsistence and commercial export of hides to Europe, followed by the lowlands becoming modified by settlers and their exotic species facilitated the huemuls' extirpation. The hypothesis of a dramatic modification of the original biogeographical distribution of huemuls is supported by anatomical and ecological features along with historical accounts. Sedentariness on only rugged summer ranges makes long-term survival of this species crucially challenging and requires sound conservation strategies that incorporate geographical areas of their former distribution.

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1. Introduction

In modern times, large mammals are frequently reduced to small and fragmented populations as a result of past anthropogenic impacts. The endangered huemul (*Hippocamelus bisulcus*) presents a textbook case, having been reduced by 99%, with the approximately 1500 remaining individuals being split into over 100 subpopulations and spread along nearly 2000 km of rugged habitats in the Andes mountains [1,2]. The remaining total population size continues to decline, further subpopulations are being lost, and there is a high prevalence of disease problems currently. Thus, this flagship species of both Argentina and Chile is classified by IUCN to be under high risk of going extinct [2].

Understanding the historical distribution and use of huemuls' habitat corresponding to the 'source areas' is fundamental for conservation planners in designing strategies allowing their recovery in the face of past and current environmental changes [3]. This may be especially important for refugee species, which, after having been extirpated from the most suitable portions of their historical range, are now prevailing only in marginal and 'sink habitat' [4,5].

Given the tremendous spatial and numerical reduction of huemuls, basing conservation strategies on their modern distribution can be misleading by them being an anthropogenic artifact. For other ungulates, studying species that had been subjected to widespread range loss and failing to refer to historical information can lead to stereotyped interpretations about such species and their conservation needs [5]. Many species have become absent from large portions of their distributions owing to human-induced local or regional extinctions [6,7], and frequently with the concomitant loss of their migratory culture [8]. Remarkably, Grzimek in 1973 recognized how huemuls had been recently extirpated from most of their historically inhabited sites, and that they only persisted in a few small refuge areas ("bis auf wenige winzige Rückzugsgebiete ausgerottet") [9] (p. 233). Even earlier, it was commonly described that huemuls already had been locally reduced or eliminated [10] (p. 593), [11] (p. 14), and that their refuge areas were in remote and high parts of the Andes mountains: to be able to see a wild huemul "now" (1949), "one has to hike to high mountains and always far from any human settlement" [11] (p. 14). This might explain why huemul subpopulations within most modern protected areas do not have a positive recruitment and thus lack population expansion [12].

The largest risk for refugee species occurs when the currently occupied suboptimal habitats are identified as the conservation priority areas for the species in question [13,14]. This risk is especially important when the species has been limited to a suboptimal habitat for numerous decades, or even centuries [4,5], as we hypothesize to have occurred with the resilient huemul, and while confronting nutritional limitations [15]. Recognizing historical species ranges is thus important for allowing the recovery of an endangered species such as the huemul [4,5,13,16–21].

For non-recovering subpopulations, it is essential to differentiate whether extant groups live in a marginal, sub-optimal or natural sink area, or in an artificial ecological trap, as the latter two will drive local subpopulations to become extirpated. When habitat use patterns are artificially modified, applying the current distribution to deduce the extent of suitable habitat can lead to declaring a false endemism, which will obscure the existence of former natural 'source areas'. Moreover, if it resulted in sedentariness in seasonal summer ranges due to the loss of migratory culture, this may be one of the largest problems challenging the long-term persistence, as has happened for many huemul subpopulations [22], and as shown for some bighorn sheep populations (*Ovis canadensis*) [7].

Several authors have contributed historical data about huemuls. Díaz (1990, 1993) provided 102 historical locations based on fossils, archaeological data and historical bibliog-

raphy, along with a vivid description of the past history of this species and its interaction with pre-colonial humans [23,24]. She discussed how huemuls descended to lower ranges in winter; occurred in the steppe plains and even as far as the Atlantic coast; the use of dogs in past hunting practices; and the usage and trading of skins. She concluded that the data she provided showed that "past ideas about the huemul being only restricted to forested habitats will have to be revised" [24] (p. 349). Subsequently, these conclusions were updated based on a total of 230 references [25]. Later on, a chapter about huemuls also concurred that they were once present in the Patagonian steppe at 140–200 km from the nearest forests; that it had reached the Atlantic Ocean; and that their grass consumption reached 16% in forested mountains [26,27]. Several subsequent articles also treated historical data based on their 167 citations [15,22,28,29]. Given the importance of historical distribution ranges in allowing the recovery of this endangered species [13,28,30], we provide additional sources to substantiate and strengthen prior observations, with historical sources ranging from 1779 onward (Tables 1 and 2), to support our hypothesis that the current huemul distribution is an artifact of its past and ongoing interactions with humans [4,5,13,17,19]. We predict that historical records of huemul distribution on lowlands, in addition to behavioral and morphological adaptations to cope with a grassier diet and local predators, support its ability to thrive in lowland and open ranges. Aside from the previously used literature (see Supplementary Table S1) to describe the past distribution and ecology of huemuls [22,28,29,31], additional sources of information presented here allow us to reinforce these prior conclusions [22], indicating that many extant huemul populations have lost their migratory traditions and no longer exist in typical winter ranges used historically, which likely explains the lack of the species' recovery in numbers and spatial extent.

Table 1. (**a**) Recordings of archaeological and fossil data, (**b**) huemul encounters since 1900 in steppe and ecotones, (**c**) behavioral and biological observations relevant to huemul ecology.

(a-I) Archaeological Sites and Their Analyses	
Records of only huemuls	
1947 Vignati [32]	A vertebra was found in a cave site, from a huemul and perforated with an arrow head, in steppe area about 160 km from forest, 39°31′ S, 69°15′ W.
1963 Emperaire et al. [33]	Fossil **huemul** found some **100 km from forests** in Fell's Cave.
1972 Laming-Emperaire et al. [34]	Huemul antler found in cave on **Tierra del Fuego**.
1985 Ochsenius [35]	Hippocamelus today is restricted to boreal biomes (Andes), but continentally had retreated from east to west (p. 39).
1991 Cardenas et al. [36]	Fossil **huemul** found on **Chiloe island** (p. 113).
1993 Bridges [37]	Yamana natives on **Tierra del Fuego**: they referred to how "**deer cast or shed their anthers**" (his dictionary from 1879, p. 609).
2009 Sierpe et al. [38]	**Significant presence of huemul bone remains in a steppe** zone (grassland with some brush) occupied by terrestrial and maritime hunter-gatherers is emphasized; **huemul bones (14.1%) and guanaco bones (27%)**, but **some levels of deposits had huemul as predominant remains**, 51°32′47.70″ S, 72°34′13.16″ W; guanaco and huemul still occur in this area.
2011 Borrero and Borrazzo [39]	Fossil **huemul found some 120 km from forests, by Atlantic coast** and on **island Isabel only 12 km from Tierra del Fuego Island.**
2013 De Nigris and Tecce [40]	Fossil **huemul** found some **30 km from forests**, 47°15′54″ S, 71°48′38″ W.
2017 Pallo [41]	Fossil **huemul** in several sites **100 km from forests** (52°02′ S, 70°03′ W; **near Atlantic** 52°33′18″ S, 70°24′28″ W); also on **Tierra del Fuego.**

Table 1. *Cont.*

(a-I) Archaeological Sites and Their Analyses	
2019 Sierpe et al. [42]	**Huemul** remains were found on **Tierra del Fuego**; 53°30′40″ S, 69°16′11″ W.
2023 Garvey et al. [43]	An **archaeological site** in a valley in **steppe ecotone has dominantly huemul remains, being the highest-ranking species for hunters**.
2023 Navarrete et al. [44]	Huemul were highly important in maritime hunter-gatherer diets **(huemul remains were 78%)**; prehistoric **natives commonly used dogs for their hunting; huemul skins provide great buoyancy and explains its swimming ability and presence on many islands**; in the past, huemul were abundant in the forest-steppe **ecotone** of Ultima Esperanza and Antonio Varas Peninsula (p. 11).
Records of huemul together with guanaco	
1979 Ortiz-Troncoso [45]	Bones of **guanacos and huemuls** were present at several sites of the Tierra del Fuego Archipelago.
1991 Mena and Jackson [46]	**Steppe site** Alero Entrada Baker used by hunter-gathers for thousands of years up to a few centuries ago, **hunting huemul, rhea, and guanaco all year**; hunting intensity increased over time, likely due to the increasing human population; 47°12′ S, 71°53′ W.
1997 Munoz [47]	Fossil **guanaco and huemul** remains in Ultima Esparanza; **huemul remains in Tierra del Fuego** (his Table 6, p. 224; 53°21′ S, 68°39.7′ W).
2004 Mena et al. [48]	Sites in **steppe** and **ecotone**, with **huemul remains dominating**; and together with **guanaco**.
2007 De Nigris [49]	Bones of **guanaco and huemul** often coexist, as in Cerro Casa de Piedra, Cueva 5, steppe, 47°57′53″ S, 72°4′55″ W (p. 255).
2008 Bellelli et al. [50]	Animal remains with signs of human use; Cholila site (ecotone-steppe) had more **huemuls than guanaco**; Río Manso site (forests) had huemul and guanaco; Río Epuyén (ecotone-steppe) site had only huemul (pp. 45, 53).
2008 Labarca et al. [51]	There were caves with bones of **guanaco, huemul, and pudu together**.
2008 Rindel [52]	Several sites with fossil **huemul and guanaco** bones, in **steppe area.**
2011 Borrero et al. [53]	Bones of **guanacos and huemuls** were present at several sites of the Tierra del Fuego archipelago.
2016 Martínez Tosto et al. [54]	Hair of **guanaco and huemul** in human feces; at Cerro Casa de Piedra, Cueva 5/7, steppe; caves only used in summer, some 8600 years ago (p. 206).
2016 L'Heureuxa and Borrero [55]	Fossils **guanaco and huemul** were together.
2017 Castro Esnal et al. [56]	Two sites in ecotonal areas had **guanaco and huemul, the latter dominating in some layers**; the nearest forest is some 20 km.
2017 Kelly [57]	Fossil remains of **guanacos and huemuls** were present in a cave of hunter-gatherers at 30°21′ S.
2018 Christensen et al. [58]	Bones of **guanacos and huemuls** were present at several sites of the Tierra del Fuego archipelago, in **steppe and ecotonal areas**.

Table 1. *Cont.*

2021 Carballido Calatayud, Fernández [59]	Forest and **steppe** sites dated to the last 3500 years both had **huemul and guanaco** as **main human prey** (p. 209); through human pressures, huemul is **now restricted to forested mountain** areas of difficult access, but in the past, the forest-steppe **ecotone would have been its optimal habitat** (p. 213); most data on past hunting techniques utilized in Patagonia are from societies that had already incorporated the horse, at least since the beginning of the 17th century (p. 215); huemul was hunted using lasso and boleadoras facilitated by the use of open areas, it was possible to approach it and kill it with **hand-held weapons** or even with heavy items with no archaeological visibility, such as **sticks and stones** (p. 218).
1984 Wheeler [60]	**Remains of taruca** (*H. antisensis*) occurred together with those of guanaco (and still seen together nowadays).
(a-II) Fossil sites and their analyses	
Observations:	
1936 Fuenzalida Villegas [61]	Fossil huemul, site Hacienda Chacabuco at 33° S (p. 99).
1994 Moreno et al. [62]	Huemul in Central Chile, site Quereo at 30° S (p. 499).
2011 Labarca and Alcaraz [63]	Fossil **huemul** found at 31° S.
2017 Iriarte et al. [64]	Fossil **huemul** found in Coquimbo region, at 31° S (p. 23).
(b) Direct observations of huemul since 1900 related to tree-less steppe and ecotones	
Observations:	
1900 Steffen [65]	Expedition crew: for weeks we subsisted from huemul meat; farther east among baren hills and undulating ground of the Patagonian pampa (steppe), **huemul alternate with guanaco** (p. 200).
1902 Prichard [66]	**Guanaco co-occur with huemul**, I killed a huemul and a guanaco with consecutive shots (p. 68); bones together of guanaco and huemul (p. 132); tracks of guanaco and huemul in steppe (p. 133); saw huemul in steppe by River de Los Antiguos (p. 145); I had just shot a guanaco, when a huemul buck dashed past me within twenty yards (steppe, p. 240); huemul seen east of Lake Buenos Aires some 70 km from forests, the Natives said that earlier they were more numerous in that region (p. 249).
1914 Sievers [67]	Huemul also occur in Patagonian plains (pg. 76); huemuls are not often in steppe areas, and guanaco also occurs in mountains (p. 266).
1943 Harrington [68]	Natives use of skins was for toldo tents, clothing, bags, war protection, balloons to cross rivers, etc.; the use of skins went down due to diminishing fauna, some nearly totally exterminated as with the huemul (p. 80, 85).
1977 Povilitis [69]	Observed **huemul and guanaco** in the same areas.
1988 Goni [70]	In the steppe area of Meseta del Aguila, **guanaco were mixed with huemul** according to settlers, and in the past.
1997 Velásquez [71]	Extant **huemul occur with many guanaco**; a **group of four huemuls was feeding together with a group of 11 guanacos**; in those areas he observed males with shed antler, and had also found shed antlers.
1998 Velásquez [72]	Extant **huemuls occur with many guanacos**, and some remain continuously as **residents in ecotonal valley bottoms**.
2006 Cramer [73]	1902: in steppe-ecotone area by Lago Pueyrredon, they hunted an ostrich, **saw guanaco, and then shot four huemuls** (p. 327).
2008 Guineo et al. [74]	There was **EXTANT huemul overlap with guanaco**, and prior documentation of groups of **huemuls and guanacos feeding together in local steppe areas**; since 2006 **huemuls have expanded towards drier part of Torres where guanaco is, likely due to an expanding huemul population.**

Table 1. *Cont.*

(b) Direct observations of huemul since 1900 related to tree-less steppe and ecotones	
2010 Mirabelli [75]	**Huemul male was documented in steppe area of National Park Perito Moreno**; this occurred some 20 years after livestock removal.
2013 Wittmer et al. [76]	Area dominated by **steppe had abundant guanaco**, but 350 **kill sites of radio-collared pumas had remains of guanacos and huemul.**
2016 Christie and Pardinas [77]	Three **huemuls were seen in steppe area at 90 km from the nearest forests.**
2018 Vidal et al. [78]	**Extant re-introduced adult huemuls and their fawns** remained at the bottom of the **valleys shared with the guanaco** and never climbed the mountains surrounding the Breeding Center and their final home ranges.
2023 CONAF [79]	Huemul in Parque Nacional Torres del Paine, steppe, at 50°52′17″ S, 72°46′42″ W; 50°52′37″ S, 72°44′8″ W (p. 4).
(c) Behavioral and ecological observations relevant to huemul ecology	
Observations:	
1925 Krieg [10]	**Huemul is osteologically downright identical to taruca** (northern huemul), such that they are likely only subspecies (p. 596).
2012 IUCN Huemul Task Force [80]	In **1993 it was shown to be erroneous to claim that the huemul was a deer of the mountains** (p. 3302).
1994 Frid [81]	**28% of area used by huemul was flat valley**, dominated by **graminoids and herbs**; in **spring**, they were not seen in forest, **and mainly in flat grassland bottoms; males nearly exclusively remained in flatlands.**
1999 Cofre and Marquet [82]	**Huemul** use forests, Andean steppe, and **Patagonian steppe**; huemul are a habitat generalist; in Chile, huemul received one of the highest Conservation Priority Index (p. 57, 60).
2002 Mendoza et al. [83]	Huemul skull morphology: very close to red deer and axis deer; all classified as **mixed-feeder** whose diet portion of **grass can be from 25 to 75%** (p. 236).
2005 Galende et al. [84]	Reported **many species of Graminae determined in the huemul diet.**
2007 Prothero and Foss [85]	Some deer, including huemuls, are mixed feeders incorporating significantly grass in the diet; none of the cervid evolved into a grazing specialist (p. 301).
2016 Corti [86]	Fecal **diet** analysis of huemul in the 'San Miguel' lot of the Forestal Mininco: **34.9% grasses,** and **11.5% herbs.**
2017 Iriarte et al. [64]	Chile: plants often have **low selenium and iodine levels, affecting livestock, and in areas with huemul** (p. 49–50).
2022 Vynne et al. [87]	**Huemul** use forests, **Low Monte**, Chilean **Matorral**, Andean steppe, and **Patagonian steppe** (their Supplementary Table S4).
2023 van Beest et al. [88]	Bioavailability of key elements influences wild herbivore performance; **higher levels of trace minerals Cu, Se, and Mo was positively linked to annual calf recruitment.**

Table 2. Data interpretations stemming from historical direct observations.

Type of Direct Observation	Source
Deer were seen by Atlantic coast, Peninsula Valdes, Port Desire, from Santa Cruz River down to the Magellan Strait; Natives used to hunt deer as far as the Patagonian coast.	1779 de la Piedra [89] 1789 Malaspina (2004) (p. 218) [90] 1837 Viedma (p. 68) [91] 1899 Moreno (p. 266) [92] 1917 Cooper (p. 6) [93]

Table 2. *Cont.*

Type of Direct Observation	Source
Guanaco and deer on Tierra del Fuego.	1839 Fitzroy [94] 1841 Lacroix (p. 48) [95] 1887 Lista (p. 12) [96] 1987 Hershkovitz (p. 85, only deer) [97] 2016 Christensen (p. 156) [98] 2019 Vietri and Godino (p. 100) [99]
Both deer and dogs of Natives were seen.	1788 Vargas Ponce (p. 317) [100] 1837 Viedma (p. 68) [91]
Deer were used by Natives for skins, meat, furniture, toldo tents, floor rugs, utensils made of several skins of deer, leather jackets made of 10–12 layers of deer skin, such that not even a sword or a dagger can penetrate; using so many huemul skins, the Natives were named "Huemuls"; Araucanian Natives had deer as their most important hunting goal; the skins were used commercially, including for the Chilean military.	1788 Vargas Ponce (p. 343) [100] 1837 Viedma (p. 80) [91] 1871 Cunningham (p. 143) [101] 1899 Coppinger [102] 1900 Fonck (pp. 85, 283, 303, 387) [103] 1915 Latcham (p. 246) [104] 1917 Cooper (pp. 5, 192) [93] 1946 Schmieder (pp. 789, 849) [105] 1963 Emperaire (pp. 93–95, 106) [106] 2010 Cruz [107] 2020 Raimilla [108]
Natives wait for huemuls near the river sides, and with many dogs are able to kill some with sticks or with stones; dogs to hunt deer and guanaco; huemuls are very tame, and boleadoras could be used to kill them; once Natives depopulated an area of prey, they moved to another site; today with the help of horses, Natives can hunt even more effectively using boleadoras; they pursued huemuls till these tried to swim to another island, then they approached them in canoes and speared them with a harpoon; I was fed a casserole containing meat of a huemul fawn shot with a pistol.	1788 Vargas Ponce (p. 340) [100] 1839 Fitzroy [94] 1909 Martin (p. 307) [109] 1917 Cooper (p. 216) [93] 1917 Kölliker et al. (p. 119) [110] 1945 d'Orbigny (pp. 708, 709) [111] 1963 Emperaire (pp. 93–95, 106, 124) [106] 2011 Aguilera [112]
Natives sometimes travel 750 miles to the north as they have many horses (6–7 per man), to go hunting along the foothills.	1839 Fitzroy [94]
Guanaco readily take to water and swim from island to island; they were common in high mountains before being overhunted.	1839 Fitzroy [94] 1877 Reed (p. 540) [113] 1917 Kölliker et al. (p. 190) [110]
Many large herds of deer were seen on the plains eastward of several inlets, in open plains covered with luxuriant grass; herds of huemuls and also guanaco.	1839 Fitzroy (p. 310) [94] 1899 Stange (p. 17) [114]
Natives looked for explorers, ships, and colonists to trade huemul skins for tobacco and alcohol; in steppe areas there was high hunting pressure by Natives and 60 tons of ostrich feathers were traded each year in Argentina.	1871 Cunningham (p. 349) [101] 1915 Latcham (p. 246) [104] 1917 Cooper (p. 5, 192) [93] 1924 Wickenburg (p. 94) [115]
Gauchos moving cattle/mules down to winter ranges often had huemuls mixed in the herds, then killed them to eat; in winter huemuls prefer to graze in low grassland with good, green grass (migration).	1877 Reed (p. 541) [113] 1938 Dir. Parques Nac. Argentina [116] 1940 Cabrera and Yepes (p. 271) [117] 1945 de Agostini (p. 184) [118] 1985 Povilitis [119]
Huemuls still occurring in northern Chile (31° S, 34° S).	1877 Reed [113] 2020 Raimilla [108]

Table 2. *Cont.*

Type of Direct Observation	Source
Huemul seen and hunted in the steppe, and then shot guanaco in that area; huemul some 630 km from nearest forest; bones of guanaco, huemul and rhea in a settlement; Patagonian pampa offers plenty of meat sometimes by huemuls that often venture even into the steppe areas; huemuls also choose as refuge small depressions that are formed in the pampa under the bushes; in steppe we shot five huemuls, then a couple of ostriches; in a large grass meadow there was a band of fifty huemuls grazing in the middle of it; in winter huemuls descended together with guanaco down to Nirihuau valley, where they were all feeding mixed with cattle and sheep; huemuls are now rarely found in the steppe.	1879 Moreno (pp. 209, 213, 219) [120] 1884 Roa (p. 186) [121] 1893 Hudson (pp. 38, 210, 212) [122] 1899 Coppinger [102] 1929 Steffen (pp. 231, 248) [123] 1931 Barrette & Barrett (pp. 172, 173) [124] 1935 Latcham (p. 24) [125] 1946 Schmieder (pp. 789, 849) [105] 2010 Cruz [107]
Hunting by Natives resulted in huemuls now only remaining at very high elevations; in remote valleys; before they existed in valleys but already rare and rapidly disappearing; without efficient measures, they will soon be on the list of extinct species; in winter huemuls went down to valleys and even to foothills, but to get away from humans they concentrate more and more in high mountains where only snow and hunger moves them down; huemuls were systematically hunted wherever they occurred; huemul is one of our species urgently needing government protection.	1900 Fonck (p. 282) [103] 1917 Kölliker et al. (p. 119) [110] 1933 Cabrera [126] 1936 Birabén & Hylton Scott (p. 157) [127] 2020 Raimilla [108] 2020 Sierpe [128] 2021 Novaro and Walker [129]
Huemuls in areas with guanaco; Laguna Guanaco should have been called Laguna Huemul since we saw those there; in northern Biobio huemul and guanaco were exterminated recently; we hunted a guanaco and a huemul to feed our group; recent shed antlers on hill in steppe area, where there are many guanaco.	1900 Fonck (p. 283) [103] 1909 Martin (p. 689) [109] 1929 Steffen (p. 150) [123] 1943 Osgood [130]
Cabins of colonists often had wood structures of chairs, beds and shacks covered with huemul skins, and rifles hanging on their walls; to feed their livestock and dogs, colonists made many trails through forests or burnt down a lot to better utilize these areas and to go higher up into mountains, thus only a small remnant of the previously large populations of huemuls became refugees in inaccessible high mountains and remote lake corners; to see huemuls nowadays requires one to climb high mountains far from human settlements; huemuls have lost prime winter range to livestock and human occupation, but recent zooarchaeological data implicitly endorsed this crucial role that huemuls' seasonal movements play.	1917 Kölliker et al. (p. 201) [110] 1952 Franke (p. 14) [131] 2021 Novaro and Walker [129]

2. Materials and Methods

We systematically reviewed the historical literature about this species to expand upon the information on the documented past distribution and habitat use, and thus improve understanding of the flexibility and phenotypic plasticity of huemuls. This updated review was based on literature searches provided by Swisscovery and ISI Web-of-Knowledge and using appropriate published taxonomic terminology. Thus, in our systematic review, we searched for synonyms of the huemul's scientific name in the literature, which included terms such as *Hippocamelus bisulcus*, *Equus bisulcus*, *Equo bisulco*, *Cervequus andicus*, *Camelus equinus*, *Lama bisulca*, *Auchenia huemul*, *Auchenia huamel*, *Cervus andicus*, *Cervus antisensis*, *Cervus chilensis*, *Cervus leucotis*, *Capreolus leucotis*, *Capreolus huamel*, *Furcifer huamel*, *Furcifer chilensis*, *Furcifer andicus*, *Furcifer antisensis*, *Xenelaphus leucotis*, *Xenelaphus bisulcus*, *Huamela leucotis*, *Creagroceros chilensis*, *Cariacus chilensis*, *Mazama bisulca*, *Odocoileus bisulcus*, and *Hippocamelus dubius* [22]. Furthermore, old literature cited in historical reports was accessed in libraries containing such old original documents. In addition, the bibliographic review revealed direct historical observations, and archaeological as well as fossil data. Then, we reviewed the topographic and phytogeographic characteristics of Argentine Patagonia and evaluated the potential ability of the steppe ecosystem of supporting large herbivores by mapping the current distribution and numbers of cattle, sheep, horses and guanacos (*Lama guanicoe*) in this Patagonian landscape. Additionally, we mapped the historical records of

huemul observations [13,22–27] upon the geohydrological landscape of the steppe region, and compiled a list of edible vegetation with their recorded consumers to further evaluate this environment's ability to support medium to large-sized herbivores.

3. Results

3.1. Archaeological and Fossil Evidence

The newly obtained literature based on material from archaeological sites and their analyses provides several conclusions. Records obtained from various sites describing the occurrence of huemul (13 reports, see details in Table 1) show that these were located in steppe ecosystems, 20–160 km to the east of the nearest forests. Two reports mentioned huemul sub-fossils by the Atlantic coast. Various of these new-found records corroborate reports of the co-occurrence of huemul's archaeological remains with that of guanaco at the same sites (16 reports). Past reports on huemul skins indicate that their hair provides much buoyancy, which explains the exceptional swimming ability of the huemul, and thus their presence on many island sites (eight reports) should not come as a surprise. Ten reports described huemul remains at Tierra del Fuego archaeological sites. However, besides the huemul, according to one report, the Lesser Rhea (*Rhea americana*) also went extinct on Tierra del Fuego, which was likely due to another example of the impact of humans causing historical extinctions on islands [132]. Instructively, in 1860 there were an estimated 3000 hunter-gatherers (Ona natives) on the eastern part of Tierra del Fuego, described as large and powerful "foot" natives without canoes [133–135]. As nomads, they hunted guanacos using dogs, and had no permanent villages. Being effective hunters, it would be expected that their impact on easy prey like huemul led to its extermination. In fact, when colonists caused the Onas to retreat southwards, it resulted in guanacos disappearing rapidly—even though they are much more difficult to hunt, and thus causing a decline of the tribe to some 100 people by 1917 [134]. Another study showed that huemul hunting intensity increased over time, likely due to the increasing human population (Tabel 1, [46]), while a further study (Table 1 [35]) outlined how in Patagonia, huemuls had retreated over time from east to west to remain only by the Andean Mountain range. Regarding the past northern extent of its distribution, four studies (Table 1) report on fossil remains found in Chilean sites around 30–33° S, thus, lending support to three other studies mentioned earlier [22]. Additional reports based on direct observations during historical times provide further information (details in Table 2), such as that huemuls were still seen at the Atlantic coast at the Península Valdés, Port Desire, and along the coast down to the Strait of Magellan (five reports), and also mentioned that they were observed on Tierra del Fuego (six reports).

3.2. Evidence from Hunting Activities (Newly-Found Reports in Table 2)

A core issue is the degree of confidence huemuls exhibit, basically being fearless of the presence of humans, and thus, facilitating being hunted. Indigenous people were reported to systematically hunt huemuls wherever they occurred, often using many dogs (six reports), using only clubs and rocks (two reports) or lassos and boleadoras (three reports). Once the colonists arrived, indigenous people were reported to frequently having had access to rifles (three reports) impacting the huemul population even further. The intense hunting and use of huemuls by humans were described regarding their quality as food and materials (12 reports). The skins were used for clothes, tents and utensils, with war jackets made out of 10–12 layers of deer skins. The skins were also regularly traded by natives mainly for tobacco and alcohol. The intense hunting pressure in the Patagonian steppe was described for the late 19th century, when indigenous people traded 30–70 tons of Patagonian rhea feathers (South American ostrich) each year: this corresponded to some 132,000–308,000 rheas [136]. Remarkably, the huemul was listed as one of the commercially important species traded and utilized by humans internationally, as published in London in 1883 [137]. Regarding the distribution, huemuls were seen and sometimes hunted in steppe

areas, and frequently observed with guanaco nearby (21 reports). On three occasions, old reports mentioned seeing large herds of huemuls and bands of up to fifty individuals.

3.3. Huemul Observations since the 20th Century

Relevant data include more recent observations of the huemul distribution (see new-found details in Table 1). Huemuls were reported in tree-less steppe and ecotonal environments, up to 90 km from forests (13 reports). Further, some accounts reported that huemuls remained residents of the ecotonal valley floor in Tamango, Chile (Table 1, [72]). The co-occurrence of huemuls and guanacos, including feeding in mixed groups in 1997, was also well documented (11 reports).

More recent data on the behavior and ecology of the huemul can help our understanding of the historical information. For instance, in 1993, based on 102 old reports, Díaz concluded that it is erroneous to claim that the huemul was a deer of the mountains [24]. Frid showed that huemul spent substantial time in flat grassland valleys, especially during spring, with males remaining all year in those low flat lands nearly exclusively [81]. Galende et al. found eleven species of grasses in the huemul's diet [84]. While some populations had grass species making up to 16% of their diet [26,27], Corti determined 35% of graminoids in the diet composition of another population [86,138]. The sister species, taruca (*Hippocamelus antisensis*), have been shown to have a diet preference containing even up to 70% grass species at certain sites [139]. Moreover, the huemul's craniodental morphology closely resembles that of the red (*Cervus elaphus*) and axis deer (*Axis axis*), which are classified as mixed-feeders (i.e., grazers and browsers), and whose diet composition can range from 25 to 75% of grass species [83,85]. These accounts of the diet and the skull morphology studies support the huemul's to use non-forested habitats, namely scrub-grasslands (Low Monte), brush land (Matorral), and Andean and Patagonian steppes [82,87]. However, a critical characteristic of the Patagonian steppe is the fact that besides grass species, it also contains many edible woody species (see below).

3.4. Distribution of Biomes in Argentine Patagonia and Their Herbivore Carrying Capacity

Regarding the phytogeographic characteristics, Argentine Patagonia is bordered by the Andes Mountains on the west, the Atlantic Ocean on the east, and extends south to include Tierra del Fuego Island. The Patagonian steppes and 'cold' semi-desert occupy most of the relief, including vast plains, plateaus and mountain ranges on the east of the continental divide of the 'Southern Cone', with a mean annual temperature of 12 °C [140]. The Patagonian biome also includes flat and extensive territory of vegetation, and can be differentiated into two major phytogeographic provinces [141,142]: (1) the Monte province, which covers a small part of northern Patagonia (east of the isotherm of 13 °C, between 36–44° S), and is dominated by a shrub steppe; and (2) the Patagonia province, which makes up most of Argentine Patagonia, borders the southern side of the Monte province and extends past the continent to include the northeastern part of Tierra del Fuego. These plains of southeastern Patagonia and northeastern Tierra del Fuego also contain xerophytic brush [133]. The sub-Andean region is represented by steppes dominated by perennial grass species, while to the east there are steppes containing perennial grass species, as well as many shrub species [141].

Importantly, the Patagonian steppe grasslands are very diversified, both physiognomically and floristically. This high heterogeneity refutes the common perception of Patagonia being only a vast grassland desert reaching down the Southern Cone [141,143]. Vegetation types range from semi-deserts to humid prairies with a large variety of shrub and grass species [133,141]. Productive prairies and meadows (mallines) are distributed throughout the region and are generally associated with rivers, creeks, valley bottoms, or local springs, with higher water availability [141]. Furthermore, the hydrological system of Argentine Patagonia provides connectivity and corridors reaching the Atlantic Ocean (Figure 1), with a mean annual precipitation not exceeding 200–300 mm [140]. Many grass and shrub species are endemic and highly edible to livestock and wildlife (Supplementary Table S2).

Moreover, woody plants constitute a vital food reserve for native herbivores like guanacos that inhabit the steppe, with nutritional qualities of 13 woody species, first described in 2017 [140].

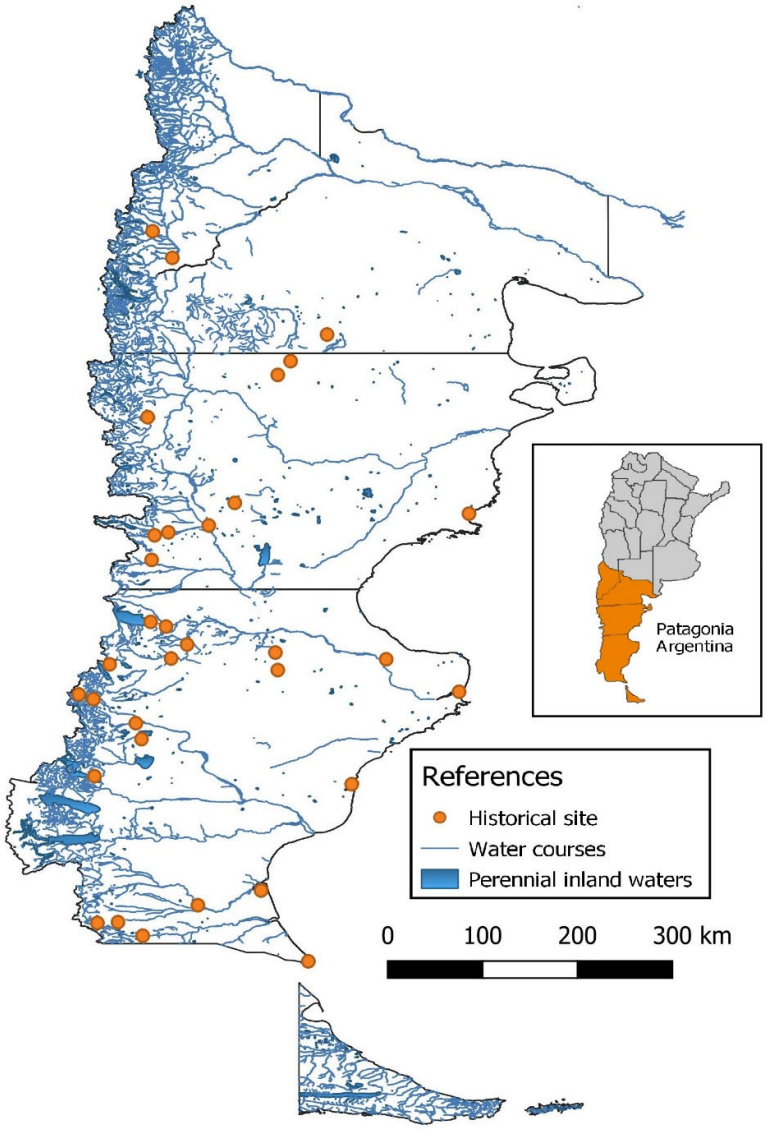

Figure 1. Historical sites of huemul in relation to main water courses in Argentine Patagonia: endorheic lakes and lagoons and courses stretching to the Atlantic. [www.ign.gob.ar/NuestrasActividades/InformacionGeoespacial/CapasSIG (accessed on 1 October 2023)].

These regional qualities of the Patagonian steppe grasslands corroborate the extensive distribution and biomass of herbivores (Figure 2), although the livestock pressure was found to be an order of magnitude greater than that observed in natural ecosystems with similar primary productivity [141,143]. These regional patterns of primary productivity are matched by strong patterns of livestock biomass and, as a result, the proportion of the aboveground net primary productivity (ANPP) consumed by herbivores. Hence, the ANPP and livestock biomass in Patagonia, southern Argentine had been analyzed, the latter based on official censuses data [143]. The least productive zones had an ANPP of 597 kg/ha/yr, supporting 64 kg/km^2 (live weight) of wild herbivores in natural ecosystems, and 637 kg/km^2 of livestock in pastoral ecosystems. The most productive zones (meadows/mallines by water courses, valley bottoms) had an ANPP of 5970 kg/ha/yr, supporting 200 kg/km^2 of wild herbivores in natural ecosystems, and 3200 kg/km^2 of livestock in pastoral ecosystems [143]. In comparison, another cold-temperate grassland in

Yellowstone National Park (mean annual precipitation of 500 mm, mean annual temperature of 3 °C) has an ANPP of 1890 kg/ha/yr, that supports 3700 kg/km^2 of wild herbivore biomass [144]. In essence, this productivity of Patagonia—particularly in relation to its hydrology, is well expressed by maintaining the substantial biomass of ungulate herbivores, and thus also supports the records of prior huemul presence.

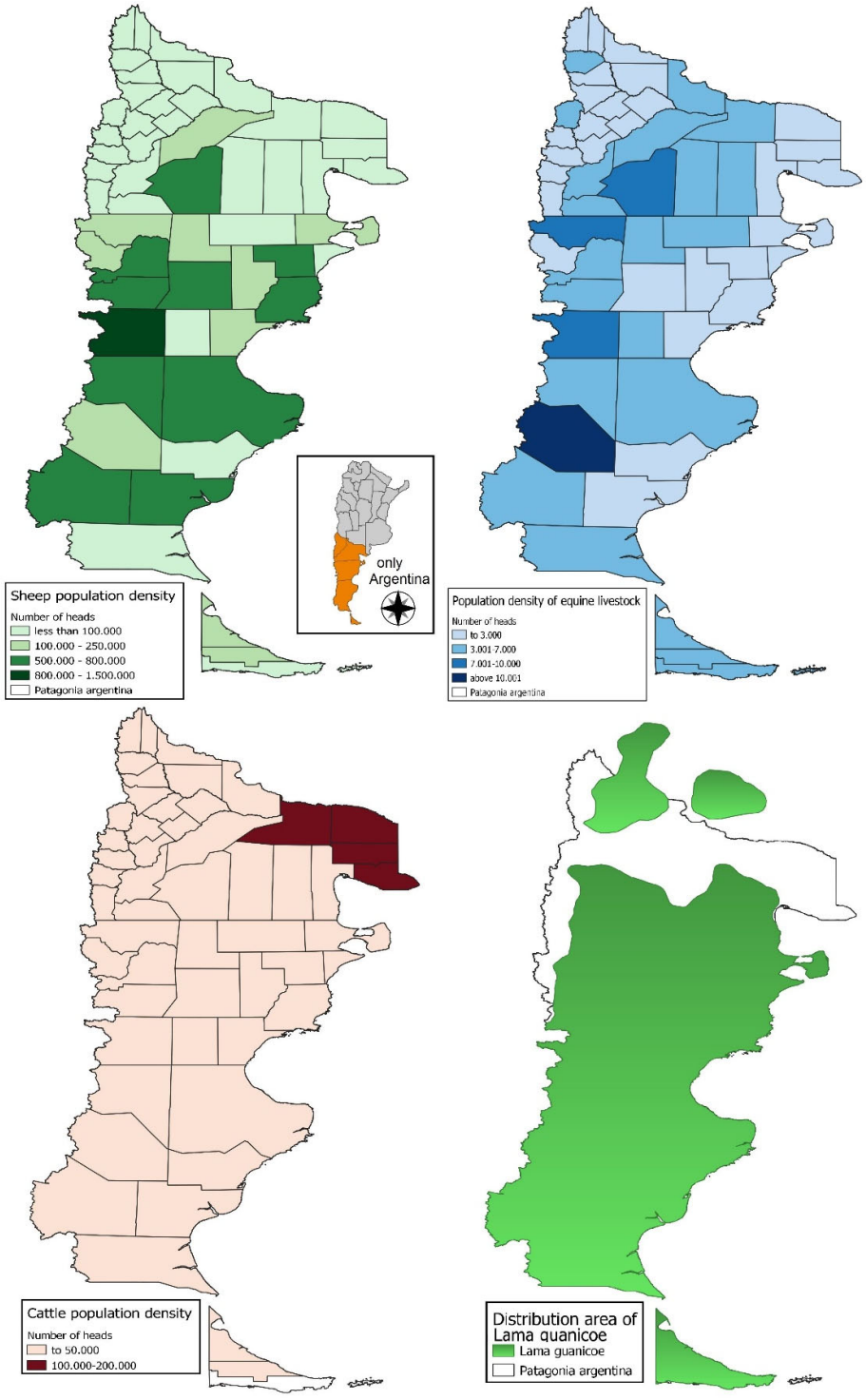

Figure 2. Distribution in Argentine Patagonia of domestic sheep [145], horses [146], cattle and wild guanaco [147]. Population densities are indicated for domestic livestock (totals per sector). Cattle: www.argentina.gob.ar/senasa/mercados-y-estadisticas/estadisticas/animal-estadisticas/bovinos/bovinos-y-bubalinos-sector-primario (accessed on 1 October 2023).

3.5. Relevant Background of Huemul Ecology

The huemul has been classified as a mixed feeder [83,85] and, also as a user of non-forested areas [82,87]. This is corroborated by its anatomy showing limb adaptations to open unforested habitats [29], and having spotless fawns, as with the taruca [148–150]. This coincides with the sympatric findings of it with the guanaco, as recorded in archaeological sites and by historical and current observations. Being effective swimmers (with the aid of their buoyant hollow hair, a morphological characteristic of cervids), huemuls commonly use water to escape from predators, or to move to better feeding or breeding areas. Moreover, this adaptive behavior would explain its frequent occurrence on many islands. The Tierra del Fuego Island—which still harbors guanacos today—stands only at 3.7 km from the continent at the narrowest stretch. Why could not the huemul have easily reached this island in the past? The proximity of this island to the continent and frequent sightings of huemuls crossing the ocean and Andean lakes during current times support corresponding archaeological and historical observational data of its past presence on many islands, including Tierra del Fuego. In comparison, other cervids commonly swim long distances [151]. For instance, white-tailed deer (*Odocoileus virginianus*) from the oceanic islands were documented to swim at least 11 km [152], red deer some 17 km [153], and mule deer (*Odocoileus hemionus*) some 25 km [154].

Both huemul and taruca are listed as migratory by the IUCN [155], which can be expected to occur in seasonal environments, such as in Patagonia and the Andes mountains [156,157]. This explains the well-documented migrations by guanaco and the transhuman migration of all livestock from summer ranges down to winter ranges [158]. All plants in temperate and mountainous regions are seasonally variable in their nutritional quality and quantity, which drives the seasonal migrations of browsers, mixed feeders and grazers alike [157]. This evidence certainly confirms earlier documentation of huemul migrations, including that of them descending in winter together with guanaco and feeding in groups with cattle and sheep in mountain valleys [125].

The crucial questions regarding the extant locations of remaining huemul subpopulations are regarding how it affects population dynamics [159]: do these sites qualify as 'source areas'? The loss of migratory traditions for numerous huemul subpopulations [22] certainly indicates an important loss of accessing high quality or prime habitat sectors, that are much needed during the winter months in the lowlands and that may sustain viable source populations.

4. Discussion

4.1. The Ease of Hunting Huemul

Without a doubt, huemuls were much easier to hunt than feral cattle, simply using pistols and even only a knife (Figure 3) [66,160,161]. This also applied to native hunters who were able to kill huemul with clubs, rocks, and lances [100,106,162]. As the native people's existence was based on wild game, they were efficient hunters, and easy prey would have been extirpated locally.

The very shy guanaco, which can run very rapidly (65 km/h), was hunted with bow and arrow (at 20–30 m), and was able to sustain the Ona natives over thousands of years [135], but in such areas, easy prey like huemul would have been likely eliminated early on. For some areas, it is well documented that past hunting of huemuls was also aimed at trading their products, including skins which reached Europe. Thus, if past hunting resulted in strong declines and local extinctions of guanacos (by 91–98% [129]), although much more difficult to hunt than huemuls, it is likely that huemuls were locally extirpated even faster. Similarly, the human colonization of the Andean valleys in modern times added additional pressures, which further exasperated the impact, and probably caused further local eliminations of huemul within decades.

Figure 3. Open habitats used by extant huemul in rolling or flat landscapes, far from forests. (**a1**–**a7**) Huemul documented in areas of Chalten (Argentina), Torres del Paine and O'Higgins (Chile); (**b**) Rio Cochrane (Chile) showing their inherent confidential behavior towards humans; (**c**) A gaucho about to kill a confidential huemul using a knife, registered by Onelli in 1904 using time-consuming hyalotype photo; (**d**) confidential huemul photographed in the 1920s by A. Grosse; (**e**,**f**) Princeton expeditions, late 1800s, hunting confidential huemul as far as 200 km from forests.

Likely due to rapid extirpations and the nomadic behavior of the early indigenous people, ancient kill and butchering sites or middens (prehistoric trash dumps) containing huemul remain undescribed. The first encounters with Ona natives on Tierra del Fuego showed them to principally live by hunting guanaco, but with such a speedy nomadism that hardly any signs were left at kill and camp sites to allow documenting any patterns [135]. This makes archeological data even more fragmentary, thus making it extremely difficult to interpret prehistoric dynamics [135], and therefore, obfuscates any early harvesting and use dynamics of huemul. Similarly, Fiedel and Haynes (2004) found no descriptions of kill sites east of the Great Plains of North America, where large mammals, like elk, deer, bear, and woodland bison, were utilized by Paleo-Indians during the past 12,500 years [163]. Regarding the huemul use by the natives, the study of the 'Cerro Casa de Piedra' cave in Patagonia provided human coprolites containing hair of huemul and guanaco [54]. However, they found only a total of six coprolites in the cave in layers covering over 4000 years of occupation by human groups (five humans would have produced about 1400 tons of feces). Thus, the sample frequency is so minuscule that it would not allow quantitative analysis of prey use. Further, this evidence pointed out that early humans fed on huemuls, however no conclusion can be made if these huemuls were hunted or scavenged as carcasses. Similarly, other sites produced so few huemul bone fragments deposited across long time periods, that these do not allow quantitative analysis regarding population dynamics [164]. Hunter-gatherers frequently had hunted their prey to local or regional extinction which would be more likely with prey having a weak defense behavior toward such hunters [165,166]. Borrero (2008) acknowledged that so far there had been a bias in surveys in Patagonia that focused on caves representing more permanent sites [167]. Transient hunting camps and movements are thus under-represented and difficult to document anyway [135,163]. This way, efficient hunting may have caused local prey extirpations without leaving many traces. Undoubtedly, more archaeological insight about early humans would be expanding such beneficial knowledge.

4.2. Past Distribution and Abundance of Huemul

Huemuls and guanacos were mentioned to have occurred on Chiloé Island as part of its fauna [36,168,169]. Moreover, huemul specimens had been collected there and are stored at the Museum of Comparative Zoology, Harvard University (code: Mamm BOM-1766 22635072) [170]. To the north, the island is separated by a mere 2 km from the continent, while to the east the closest intermediary islands are 11 km away, thus explaining the arrival of both herbivores via swimming. Likely, human hunting pressure on such islands resulted in these local extirpations [132].

Eight sources mention the most northern samples stemming from Chilean sites at around 30° S (Tables 1 and S1). Furthermore, archaeological sites from this current review provide additional cases of huemul remains found in steppe areas, including some at 160 km from the nearest forests. Moreover, there are also extant huemuls observed 90 km from the nearest forests [77].

From the completed dataset in the present study, combined with the previous ones [22], it is clear that direct historical observations of huemuls occurred near the Atlantic coast in areas such as Península Valdés, Port Desire, and down to the Strait of Magellan; these are corroborated by some archaeological findings.

Similarly, in historical observations and archaeological findings mention huemul Tierra del Fuego (Table 1 and Table S1). An instructive re-discovery regards the small Yahgan natives (around 1.5 m tall) who inhabited a specific sector of the southwestern shores of Tierra del Fuego Island [37,133]. As semi-nomads, they traveled among small nearby islands using their small canoes, and subsisting chiefly from the ocean. The missionary Thomas Bridges completed an extensive dictionary by 1879, that registered the Yahgan language based on 32,000 words [133]. A staggering fact is that they used wording to indicate that they cast or shed something "as deer cast or shed their anthers" [37] (p. 609). They did not reach the northern continental zone with their canoes, yet such specific

biological knowledge requires substantial interactions with huemul, the only deer which could have occurred on Tierra del Fuego Island.

Then, there are many archaeological and historical records of the co-occurrence of guanaco and huemul, which frequently were found in unforested areas (see Figure 2 for guanaco distribution). In addition, there are also observations of extant cases, like mixed groups of guanacos and huemuls feeding together in the watershed of Rio Pillanleufu and Cochrane, both in Chile (F. Vidal, pers. comm.), and huemuls using open and flat areas (Figure 3). Furthermore, the world's most comprehensive information source, the IUCN's Red List of Threatened Species, made several important observations. Accordingly, in 2016 Black-Decima, Corti, Díaz et al. concluded for huemul that temperate and subantarctic grasslands and shrublands are all suitable and of mayor importance for them, while Andean wetlands and temperate deserts were marginal habitats [155]. Moreover, they referred to two areas where livestock removal had resulted in huemuls recolonizing those lowlands and even entering steppe areas [155].

Regarding the past abundance of huemul, De Agostini (1945) stated that thousands of guanacos and huemuls grazed in the plains and in brushy areas, but that huemul "is now close to extinction due to the merciless hunting that has been done on it", i.e., as the reason why they remain only in high mountains [118]. Notably, the fact that huemul skins were exported to Europe from both Argentina and Chile, and being listed in an 1883 book about commercially important species, indicate that it was an accessible, abundant and economically important species. Furthermore, several historical sources (e.g., 1839, 1902, 1931, 1936) mention still seeing large herds and bands of fifty and 100 huemul (Tables 1 and S1).

4.3. Herbivore Carrying Capacity in Patagonia

Several historical reports (Tables 1, 2 and S1) indicate that huemuls had been present in several sites far from forests (Figure 1). These historical sources do not provide quantitative data about past huemul abundance nor density. However, the past and current presence of wild and domestic herbivores in these Patagonian plains support the historical presence of huemuls. Specifically, many areas of Patagonia without forests provide habitat supporting large populations of ungulates such as guanaco, cattle, sheep, and horses [171,172]. Distribution maps show sheep occurring throughout most of these areas, whereas cattle presence is more restricted, but still substantial [173]. For instance, extensive sheep ranching in arid Patagonia started late in the 19th century, reaching 50 million heads [129], aside from more than 200,000 cattle and millions of native guanacos (Figure 2). This capacity of these plains to sustain a large biomass of wild and domestic ungulates is based on the immense geohydrological system containing several rivers that empty into the Atlantic Ocean (Figure 1). These valleys result in around 5% of the area being classified as productive wet meadows (mallínes), considered to represent oases for wildlife [171]. As sheep and/or cattle commonly occur with cervids in other parts of the world, such as *Odocoileus* in the Great Plains, the huge biomass of livestock and guanacos supported by the Patagonian plains supports the historical co-occurrence of huemuls.

4.4. The Origin and Need to Conserve Migration

Numerous historical accounts (Tables 1, 2 and S1) refer to seasonal migratory movements by huemuls, and their use of valley bottoms and wintering grounds in the foothills. None of the extant subpopulations of huemuls are known to still migrate, and a refuge population studied recently was shown to remain year-round on high-elevation summer ranges, resulting in severe health problems [22]. Similarly, living year-round on high-elevation summer ranges has been shown to have disastrous consequences for other ungulates including with respect to micro and macro elements [144]. A recent review of ungulate migrations [8] highlights the evolution and benefits of migration, and the myriad of ecosystem benefits from migratory herbivore populations. The smallest migratory species weigh around 20 kg like the roe deer (*Capreolus capreolus*), whereas medium-sized ungulates like the huemul often migrate the longest distances. In temperate regions, the arrival of snow

frequently triggers autumn migrations. Partial migration is also common, where some winter range environments allow residency during the whole year, and another fraction of the population migrates to distant habitats during the summer.

4.5. Significance for Future Conservation Measures

It is essential to develop conservation strategies to revert the current lack of recovery and ever increasing risk of extinction of huemuls, which are also considered to be the most highly endangered cervids of the Americas. Although their potential distribution has been misjudged, and even refuted, due to the lack of recognizing ample supportive evidence, the present study supplies additional solid evidence to affirm that this species is adapted to a vast array of environmental conditions. The evidence in this study of historical data reveals a much higher phenotypic plasticity in this species than previously acknowledged, which allows for novel approaches to aid in their recovery.

Acknowledging the more realistic adaptability of this species, a strategic conservation plan from a landscape ecology approach should integrate the habitats utilized by them during historic times. This requires the recognition and incorporation of the spatial phenomena, known as source-sink habitat dynamics, and the process by which a species might populate new areas, including those considered to be sink habitats. We must acknowledge that habitats predominantly in use today by huemuls have not resulted in positive population growth, and as such present us with a conservation challenge. It would be to this species' advantage to create a paradigm shift from solely focusing on protecting them in their currently used habitat type (sink and marginal habitats) to providing them with a chance to survive once again in the more productive lowlands (source habitat), where habitat conditions can provide them with the essential dietary nutrients lacking in the upper elevations of many currently used areas. This study supports the impetus to conduct the powerful shift away from this non-productive paradigm that has highly influenced huemul conservation efforts in the last half century.

One conceivable conservation strategy falls under an adaptive management approach that would aim to reintroduce huemuls to historical sites considered to represent their source habitat. Concern must be taken for past threats and their potential current impact. Given that ranching practices of the past century have substantially diminished throughout Patagonia, dogs and humans do not pose the same threat as before, besides the increased awareness of the modern day Argentinean society of the need to protect the natural environment. An additional advantage is the reduced development of huemul antlers, as they have never attracted typical modern hunters aiming to collect large trophy antlers. Additionally, much stricter controls are now enforced, given the huemul's prominent federal legal status as one of four Natural Monuments in Argentina. A number of extensive ranches that could be considered for this reintroduction program cover terrain from the cordillera to the lower valleys, and include ecotonal, riparian and steppe habitats; moreover, several of these properties no longer practice ranching. Thereby, this removes the main concern of herding dogs being a potential threat. Prior to reintroductions, the chosen area would have to be evaluated for potential impact from feral dogs, illegal hunting, and abundance of pumas, their principal natural predator. All potential threats would need to be taken into consideration when selecting the optimal site for a reintroduction. An adaptive management program would have to include monitoring for threats before and after the reintroduction, along with a predator control component. Nonetheless, up until the last decade, the Torres del Paine National Park had been the only place known to have a growing huemul population. They expanded towards the drier eastern grassland areas, but exposed to one of the highest reported puma density [174]. Regarding competition from exotic and wild ungulates, the main objective would be to assure that these populations are maintained well below their carrying capacity, thus preserving enough resources for huemul populations to thrive [174]. However, to avoid any potential impact, particularly during the early stages of the reintroduction, only sites that remain outside the current distributional range of exotic ungulates, or have very low densities

should be selected. Furthermore, a management program should include removal of any exotic deer dispersing into the area. Population growth parameters would need to be recorded and monitored to determine if the reintroduced population was responding positively to its new environment, and management would then have to be adapted accordingly. Furthermore, the spatial behavior should be monitored to document the process of repopulating new areas, dispersions, and development of migratory behavior.

5. Conclusions

To evaluate the ecological and biological characteristics of huemuls revealed by the reliable historical data compiled in this study, it is important to understand how the rare huemul situation might have come to exist. How did this cervid species came to be the only one recorded globally to live year-round as a refugee species in its summer home range? It is essential to realize that the huemul's rare, instinctive docile behavior towards humans—though not towards other predators, such as canids or felids—is very likely the root cause behind the accelerated reduction in their distribution. Although barely documented, their so-called 'tameness' exposed them to rapid extirpation wherever humans arrived. This anthropogenic process resulted in individuals surviving only in remote areas, and frequently in mountain summer ranges. Through this process, and by taking full advantage of their inherent phenotypic plasticity, they were able to survive a little bit longer despite their dire circumstances. Huemuls have shown striking resilience and adaptability, as exemplified when they survived captures and very long transportation trips, such as to New Zealand in 1870, and France and then England in 1881, or when they were raised and bred for several years in subtropical Buenos Aires in the 1930's [175]. However, as these extant refuge areas of the last remaining huemuls are lacking in essential minerals, the overall health of the species has been affected to the point of preventing any population recoveries. As a mixed-feeder, based on their craniodental morphology and having spotless fawns, shows them to be well suited for open habitats such as the Patagonian plains, an environment which supports a large biomass of wild and domestic herbivores. Instructively, the US National Research Council pointed out in 1991 that huemul used grassland areas in southern Chile and Argentina [176]. Accepting historical data and several biological aspects that clearly reveal their ample phenotypic plasticity and adaptability is an essential component in developing conservation strategies that can successfully revert the current lack of recovery and increasing risk of extinction. One possible conservation strategy involves an adaptive management approach that aims to reintroduce huemuls to historical sites considered to represent their source habitat. Given their reproductive potential, it would not take very long to corroborate if such populations have a positive population growth.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/conservation3040036/s1, Table S1: Key data selected from historical sources used previously; Table S2: Common plant species of the Argentine Patagonian steppe and forage properties related to domestic livestock and native wildlife. References [177–232] are cited in Supplementary Materials.

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