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Loss of Migratory Traditions Makes the Endangered Patagonian Huemul Deer a Year-Round Refugee in Its Summer Habitat

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Abstract: The huemul (*Hippocamelus bisulcus*) is endangered, with 1500 deer split into >100 subpopulations along 2000 km of Andes. Currently occupied areas are claimed-erroneously, to be critical prime habitats. We analyzed historical spatiotemporal behavior since current patterns represent only a fraction of pre-Columbian ones. Given the limited knowledge, the first group (n = 6) in Argentina was radio-marked to examine spatial behavior. Historically, huemul resided year-round in winter ranges, while some migrated seasonally, some using grasslands >200 km east of their current presence, reaching the Atlantic. Moreover, huemul anatomy is adapted to open unforested habitats, also corroborated by spotless fawns. Extreme naivety towards humans resulted in early extirpation on many winter ranges—preferentially occupied by humans, resulting in refugee huemul on surrounding mountain summer ranges. Radio-marked huemul remained in small ranges with minimal altitudinal movements, as known from other subpopulations. However, these resident areas documented here are typical summer ranges as evidenced by past migrations, and current usage for livestock. The huemul is the only cervid known to use mountain summer ranges year-round in reaction to anthropogenic activities. Losing migratory traditions is a major threat, and may explain their presently prevalent skeletal diseases, reduced longevity, and lacking recolonizations for most remaining huemul subpopulations.

Keywords: *Hippocamelus bisulcus*; conservation policy; historical distribution; human impact; migration; nutritional ecology; refugee species

1. Introduction

The Patagonian huemul (*Hippocamelus bisulcus*) is considered an endangered Odocoiline deer by the International Union for the Conservation of Nature [1], with Argentina having only an estimated 350–500 individuals left and split into 60 or more groups, and Chile having around 1000 remaining that are split into approximately 40 groups. Moreover, these groups are fragmented along some 2000 km of Andean mountains [2] and represent a numerical reduction of over 99% of the original population size [3]. Their social organization including social and sexual segregation, is very plastic as in other cervids, and likely highly influenced by population density [4]. The huemul have been negatively affected mainly by past overhunting, but also loss and fragmentation of habitat, malnutrition, diseases, dogs, and possibly by the introduction of alien wild and domestic ungulate species [1]. Unrestricted killing in the past to acquire valued products was one of the main factors that resulted in widespread population declines and the endangered status of this species (reviewed in Supplementary File S1). Extremely naive and tolerant of human presence [5], huemul can be easily killed at a close distance by the simple use of rocks, clubs or knives (Figure 1). This unique docile behavior towards humans has resulted in their local extirpation, especially in those areas used by indigenous people and early colonists (Supplementary File S1). However, past over-harvesting has not only resulted in local extirpation, but we hypothesize that it also eliminated their migratory traditions.

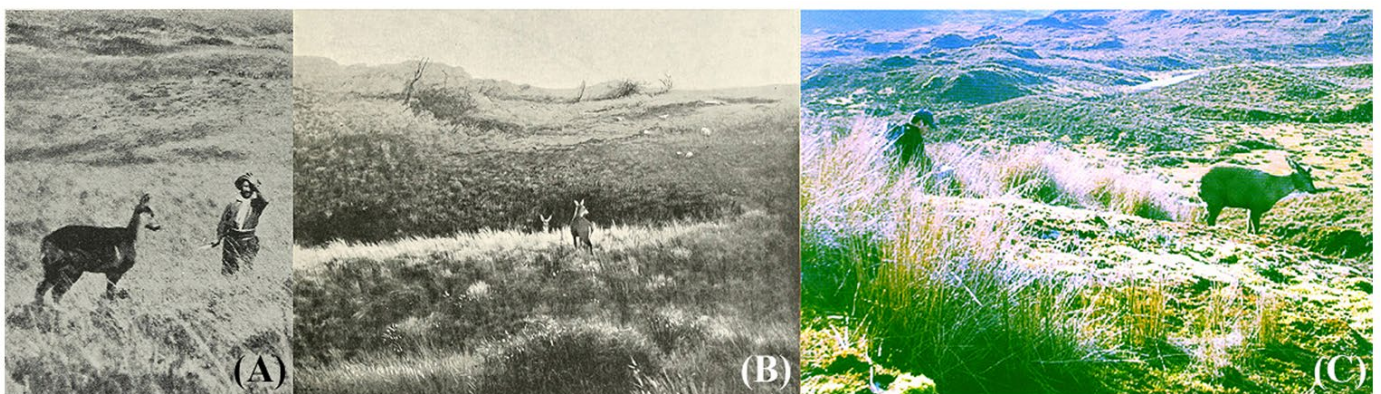


Figure 1. Huemul are well-known for their use of steppe grassland and lack of fear of humans. (A) gaúcho putting to death a huemul using a knife, photographed by Onelli in 1904, see Supplementary File S1, (B) huemul walking away after having sniffed the leg of Prichard in 1902, see Supplementary File S1, (C) a more recent close encounter near Cochrane, Chile.

Although extant groups of huemul persist along the seasonal Andean Mountain range, none have been shown to still exhibit migratory behavior [6]. Seasonal migration allows a species to capitalize on spatiotemporal variation in resources and being a plastic behavior, also results in colonization of new areas. Among cervids, year-round resident populations on winter ranges in seasonal mountain environments are the norm, as well as the eventual development of a portion of that population that migrates altitudinally [7,8]. Migratory cultural behavior is transmitted vertically from mother to young, whereas dispersal is innate and by random diffusion that is predetermined genetically, but may also occur secondarily in response to environmental conditions [9]: thus, preserving cultural traits like migrating are considered important, especially for endangered species [10–13] (Supplementary File S2).

Most extant huemul subpopulations thus tend to exist today in remote mountain areas that have been unattractive for human settlement because of climatic conditions,

topography, remoteness or having otherwise little value for agriculture or forestry [14,15]. Modern mainstream interpretations commonly consider areas of extant subpopulations as representing prime habitat in which the huemul evolved [2,16]. There is a common misconception that these areas represent their natural ecological niche, rather than recognizing that the huemul may have been isolated by anthropogenic activities to persist only in such suboptimal habitat that was less accessible to humans, and effectively has become a refugee species by being forced to contract its range and lose its migratory behavior [17–20]. The huemul continue to be described as “mountain deer adapted to Andes mountains”, “found only in the Andes”, “high-altitude species”, “mountain deer with unmistakable mountaineer anatomy”, “at 2000–3000 m asl of Andes”, “commonly in high-altitude regions that are also rocky and steep”, and “a forest deer” [6,21–24]. This unfounded assumption has led to the characterization of the huemul as predominately a browser and a non-migratory species. This has influenced the course of huemul conservation and the approaches taken over the past four decades [25]. Historical evidence of past huemul distribution is commonly depreciated by calling these “anecdotal accounts”, thus disregarding all such data, including those from reputable scientific explorers of the Patagonian region during the last two centuries (reviewed in Supplementary File S1).

Securing adequate sample sizes of field data is difficult with rare and endangered species that live in remote refuge areas as occurs with huemul [6]. The current pattern of habitat use by many isolated huemul subpopulations, including the few remaining huemul reported here from Shoonem Park, and the revealed differences with the documented historical patterns, highlights the central urgency to achieve a valid diagnosis of the causes and consequences of becoming a year-round refugee in areas which qualify as seasonal summer ranges [20].

For the present study, we (1) provide a summary of an extensive literature review of historical records of this species that we conducted in order to examine the evidence of huemul occurrences in the treeless landscape of Patagonia and their seasonal movement patterns; then (2), we provide new information on seasonal habitat use by the first group of huemul ever radio-collared in Argentina as a means to then compare current patterns with historical ones; (3) we evaluate the process of migration and occupation of new habitat areas by wild cervids to put into perspective our findings regarding the behavioral change between past and current movement patterns and habitat use by huemul; and finally, (4) we discuss the implications of huemul having lost migratory traditions and the consequences of being forced to live year-round in a refugia which formerly represented only a seasonal summer habitat, and the secondary problems that have arisen as a result.

2. Materials and Methods

2.1. Systematic Literature Review

To better understand the flexibility and phenotypic plasticity of huemul through the lens of their overall usage of habitats in Argentina, we gleaned the literature on historical habitat use by this species, and then evaluated processes involved in the migration, dispersal, and occupation of new habitat areas among other wild cervids. A comprehensive review (2021–2022) was based on the broad literature access provided by Swisscovery (<https://slsp.ch>, accessed on 4 April 2022), including the ISI Web-of-Knowledge and their 17 external databases, by searching for huemul and other related deer species to assemble actual and historical data on huemul occurrences, and compare this to distribution patterns of other cervids. The systematic search about huemul included *Hippocamelus bisulcus* and its synonymy [26,27], that is the various historic taxonomic terms used for this species, like *Equus bisulcus* (Molina, 1788), *Equo bisulco* (Leuckart, 1816), *Cervequus andicus* (Lesson, 1842), *Camelus equinus* (Treviranus, 1803), *Lama bisulca* (Fisher, 1829), *Auchenia huemul* (Smith, 1827), *Auchenia huamel* (Hamilton, 1842), *Cervus andicus* (Lesson, 1842), *Cervus antisensis* (Burmeister, 1879), *Cervus chilensis* (Gay and Gervais, 1846), *Cervus leucotis* (Giebel, 1855), *Capreolus leucotis* (Gray, 1849), *Capreolus huamel* (Gray, 1850), *Furcifer huamel* (Gray, 1850), *Furcifer chilensis* (Sclater, 1883), *Furcifer andicus* (Lesson, 1850), *Furcifer antisensis* (Wagner,

1855), *Xenelaphus leucotis* (Gray, 1872), *Xenelaphus bisulcus* (Prichard, 1902), *Huamela leucotis* (Gray, 1872), *Creagroceros chilensis* (Fitzinger, 1873), *Cariacus chilensis* (Brooke, 1879), *Mazama bisulca* (Lydekker, 1898), *Odocoileus bisulcus* (Trouessart, 1898), and *Hippocamelus dubius* (Leuckart, 1816). Additional older literature cited in historical accounts was accessed by visiting key libraries containing such old original documents. Given the absence of other cervids in Patagonia, except the extremely small pudu (*Pudu puda*), and clear physical differences to guanaco (*Lama guanicoe*), the past documentation of a cervid identified with any of the taxonomic synonyms for huemul were taken as valid data.

Moreover, assessing the validity of a given data point for representing evidence was based on the physical description of the observed animal, their drawings or their photographs, which basically prevented any biased data point. The key sources about historical habitat use—including spatiotemporal, are reviewed in Table 1, Supplementary File S1, and displayed in Section 4.

Table 1. Selection of historical reports about huemul: distribution between the Andean Mountains and the Atlantic Ocean, coexistence with guanaco, group sizes, migratory-resident behavior, and hunting.

Date	Author(s)	Observations of Presence	
1521 and 1598	after Eastman	1915	By Atlantic ports of San Julian and Desire, Atlantic
1793	Pennant	By Port Desire, Atlantic Coast	
1833	MacDouall	By Gregory Bay, open area, 100 km from the nearest forest	
1835	Roulin	By Port San Julian, Atlantic Coast	
1863	Cox	Year-round resident populations on winter ranges, coexisting with guanaco	
1864	Claraz	Many guanacos coexisting with equally as many huemul in lowlands	
1871	Musters	Harvested huemul in open, treeless areas	
1875	Günther	Between Andean Mountain foothills and Patagonian mesas, reaching the Atlantic Coast	
1880	Behm	Seen in open area far from forests while hunting 45 km east of Chilean border	
1892	Philippi	Large groups during seasonal migration to lower areas	
1898	Lydekker	Migration down to the open grassland plains where they remain during winter	
1900	Steffen	His team ate huemul for weeks, working in open grasslands of foothills: coexistence with guanaco further east	
1901	Burmeister	Eighteen huemul (2 groups) in open grasslands, 220 km from nearest forest	
1902	Prichard	Groups with more than 100 huemul coexisting with guanaco during winter in valleys	
1903	Church	Grassland plains were the home of guanaco, huemul and ostriches	
1903	Hatcher	Harvesting huemul in the open 100 km from the nearest forest	
1904	Anonymous	The governor hunted huemul far east of continental divide 270 km from forests (includes photo)	
1905	Onelli	Near Choiquenilahue and between Senguier and Chubut rivers, 120 km from forests	
1911	Neveu-Lemaire	Reported winter migration down to valleys	
1923	Osgood	Harvesting huemul in steppe grasslands far from forest, coexisting with guanaco	
1925	von Colditz	Harvesting several huemul in steppe grasslands far from forest	
1929	Gigoux	Reported seasonal migration and formation of large herds in winter	
1936	Giai	Reported seasonal migration and formation of 50 or more huemul in winter	
1940	Krieg	Year-round resident huemul in low valleys	
1945	Agostini	Many guanacos and equally as many huemul in open grasslands	
1949	Grosse	Seasonal migrations and large herds in low valleys	
1962	Liebermann	Seasonal migrations in winter down to protected valleys and foothill areas	
1969	Kolliker Frers	Reported huemul still occurred in Patagonian open grasslands until 1850s	

2.2. Radiotelemetry

We studied the huemul in the Protected Park Shoonem (44°51' S, 71°48' W; 167 km² with elevations ranging from 850–2060 m asl), located on the eastern slopes of the southern Andes. The studied watershed contains Fontana and La Plata lakes, which are surrounded by tall mountains (Figure 2). Within the sub-Antarctic zone, the site containing huemul around lake La Plata is covered by old-growth, dense forests predominately of deciduous lenga beech trees (*Nothofagus pumilio*), which occur from the lake level (930 m) up to about 1300 m, with the uppermost lenga forming chaparral [28]. The seasons are defined as winter from June to August, and summer from December to February. The mean winter temperature is −3 °C with winter precipitation between 300–400 mm, principally as snow (Figure 2), while the total annual mean precipitation is 2000 mm [29]. Most Andean environments are characterized by harsh climatic conditions, extensive deep snow cover in

winter, and contrasting altitudinal levels such that it results in guanaco migrating toward low altitudes when the snow cover is too deep to survive [30,31].

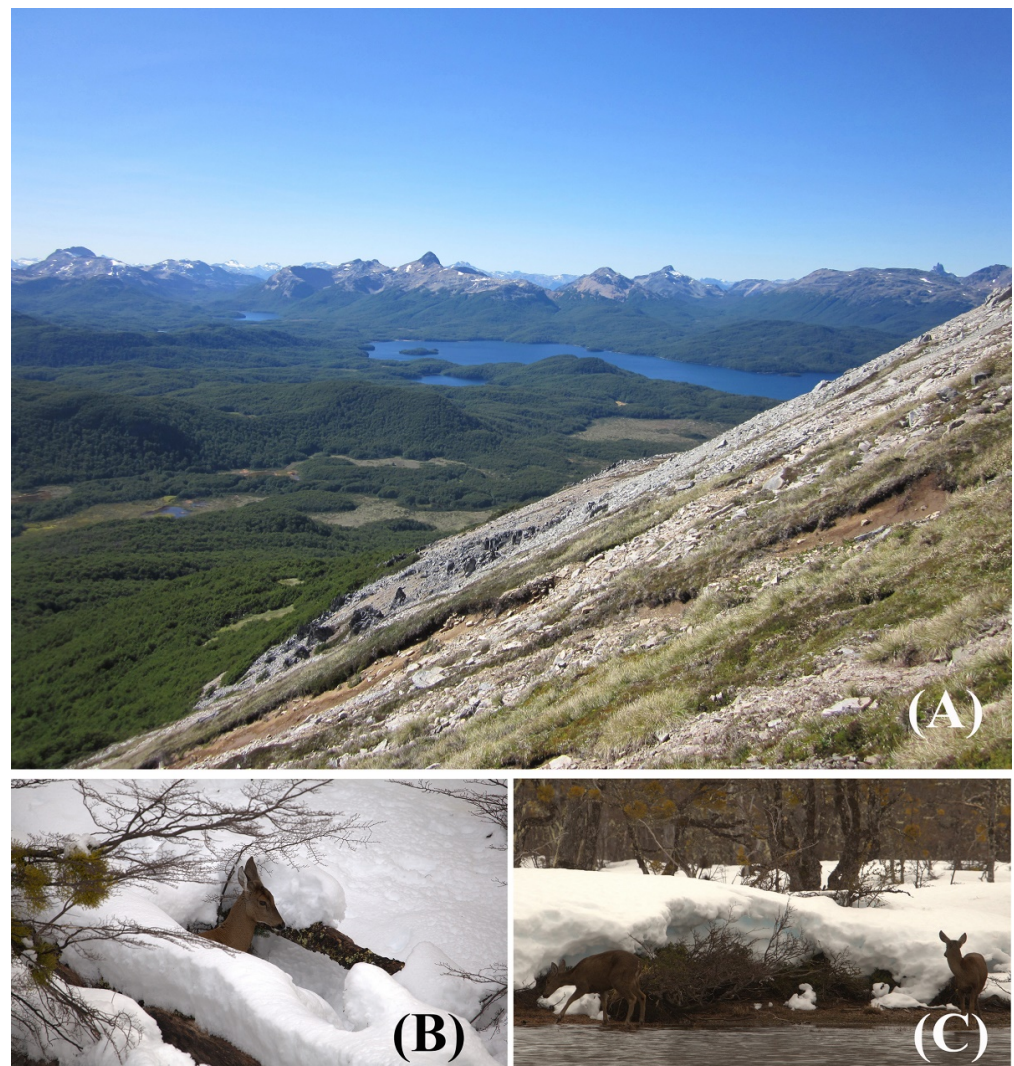


Figure 2. (A) Protected Park Shoonem (only its western part: $44^{\circ}51' S$, $71^{\circ}48' W$), owned by the village of Alto Rio Senguier, province of Chubut. The view is of the western portion of Lake La Plata, with the surrounding mountains physically defining the watershed of the river Senguier and serving as a refuge area for huemul. The edge of the lake provides the lowest elevation accessed by huemul during winter, (B) snow conditions frequently result in huemul using open water for their displacements, (C) photos taken in September 2017.

During the winter of 2017, adult huemul (3 females, 3 males) were immobilized by darting (permit Disp. Nr. 22/2017-DFyFS-MP, Province of Chubut). To minimize risks, a DanInject JM SP25 rifle allowing continuous pressure adjustment, and a mounted scope containing a laser range finder, were used to dart the animals. Medetomidine and ketamine, reversed by atipamezole are considered very safe for cervids [32] induction and reversal are fast (2 min or less), there is generally an ample tolerance for various concentrations, and highly concentrated drugs allowed the use of small darts, thus minimizing trauma. Moreover, changes in pulse and respiratory rates are minimal [33]. The time of induction was noted, the animal was kept in lateral recumbency, eyes were covered, the pulse, respiratory rates, and temperature were monitored, the general health condition was examined, and after blood collection and placing the radio collar, the reversal was applied.

Individuals were fitted with VHF radio transmitters (Sirtrack Ltd., Havelock North, NZ, USA; Telonics Inc., Mesa, AZ, USA) with several capable of transmitting signals for up to 10 years, a time window exceeding the average life span of deer in this area [34]. During the winter of 2021, the VHF radio collar was replaced with a satellite unit (Lotek, Newmarket, ON, Canada) on one male. We monitored the radio-collared individuals regularly to determine if they were alive or dead, and then located them using the telemetry equipment to allow us to make observations regarding their physical state, group composition and other biological data, and to record their general locations, or their precise GPS locations based on visual observations or triangulations [35]. The altitude above sea level (asl) of each location was determined via Google Earth. Given the behavioral responses of the animals and the reduced frequency of visual encounters, the method was considered to be acceptable regarding animal welfare. Confirmations via radio signals as to whether an individual was dead or alive were determined repeatedly (2 times per week usually), and covered every month of the study period (August 2017 to April 2022), and were accomplished more frequently than location determinations. Non-statistical techniques for range analysis were used to calculate home range sizes based on the determined locations, using a minimum concave polygon (MCP) approach. This choice was made in order to specifically exclude the lake surfaces, and thus to ensure that such areas not used by collared individuals were not included in home range calculations [35–39]. However, the present analysis emphasized only the documented maximal space use, independent of the frequency of usage as an indication of probability density surface [40]. Although a small number of precise locations may result in a reduced estimate of the home range size, the sampling over a large time period, as in this study, compensates by repeatedly covering all seasons [41]. Moreover, even crudely estimated home range sizes have led to insights into animal behavior and ecology [41], and this information is fundamentally important for managing and maintaining viable populations [6]. The home range sizes determined here may not allow comparisons to other studies, but among the present cases. The coverage of precise and general locations during all seasons of several years was considered sufficient to evaluate potential migratory movements. These were defined as follows: resident, the distance between centroids of seasonally used areas is less than 3 km; migrant, the distance between centroids of seasonally used areas is more than 3 km with repeated seasonal return [38,42], or the elevational separation is >500 m [43]. The perimeter lengths of the home ranges, the largest linear distance of displacements, and patterns of winter and summer locations—particularly elevational shifts (asl), were also calculated and compared regarding sex and seasons. Although the quantity of locations is limited and covers several years, inter-annual site fidelity is common among cervids and thus permits a description of seasonal habitat use patterns [44]. Descriptive statistics were used to summarize the data and to describe the samples [45]. Hence, means and standard errors were computed, and compared by sex and season using independent *t*-test. Lastly, the VHF data from a male collected over 48 months was compared to satellite data from his new collar, covering 8 months. Additionally, opportunistic observations of unmarked deer were recorded by date and location and used to document spatiotemporal habitat use patterns in this population.

3. Results

3.1. Historical Distribution

Based on the broad literature review, a total of 130 historical records were found covering the years 1521 until 1915, and a further 190 records covering the years up to 1990. Publications since 1990 about huemul numbered 129, which is about 3.7% compared to the quantity of publications about red deer (*Cervus elaphus*), indicating the scant modern research activity concerning huemul.

Considering historical observations and records in the Protected Park Shoonem, huemul formerly occurred also much farther east of this watershed, following the water course and diminishing elevations. For example, numerous specimens were collected

Fig

in a scientific expedition near the shore of Lake Fontana [46] some 35 km further east of currently extant huemul, and huemul were sighted in mountains some 180 km east of the present study population [47] (Section 4). The literature review resulted in numerous additional localities with historical evidence of huemul presence based on hunting collections, shed antlers, and archeological samples, as well as observations of residency and seasonal migratory behavior ($n = 54$, Table 1, Supplementary File S1). The historical distribution reached some 680 km further north of the currently northern-most and isolated population [48–50]. The historical distribution depicted in Section 4 is an approximation based on historical sites and at a scale that does not indicate potentially inhabitable areas [51]. However, most of this area contains guanaco [52] and allows livestock production [53], which thus serves to indicate that these areas also would sustain huemul. Historically used sites further east drop some 265 m in elevation for every 100 km towards the Atlantic coast, whereas annual precipitation drops from a maximum of 2000 mm at the continental divide to 400 mm at 100 km east, and down to 180 mm at another 150 km further east [5,54].

3.2. Extent of Altitudinal Movements

The six VHF radios of collared huemul resulted in 89 precise locations (mean = 14.83, SE = 2.6, range 6–24, Figure 3, Appendix A), whereas general surveys allowed additional confirmations of their seasonal presence ($n = 935$). The satellite unit placed on the male provided over 1675 additional location points over an 8-month period, corroborating the prior data based on his VHF radio. The coastline along the lake turned out to be the lowest elevation (930 m) used in the study area and thus represents the lower extent of the altitudinal gradient upon which movements were recorded, as none of the huemul moved further east and down the watershed during winter.

The elevations used during summer did not differ between males and females ($t = 2.03$, $p = 0.056$), and ranged between 930–1153 m asl ($n = 37$, mean = 1013.86 m, SE = 8.97). During winter, the elevations used also did not differ between males and females ($t = -1.52$, $p = 0.101$), and ranged between 930–1164 m asl ($n = 29$, mean = 969.03 m, SE = 10.27). The minimal elevational difference between the lowest summer and highest winter location for five huemul averaged a mere 36.2 m (SE = 21.06, range 11–119 m), with the highest elevations recorded in summer. One female though had a difference of 223 m, but with the highest elevation recorded during a mild winter, rather than during previous summers. However, these elevational usages are minimal and indicate residential behavior, as corroborated by general telemetry surveys every month, which numbered 37 to 239 observations per animal with a mean (\pm SE) of 150.17 (\pm 40.06; $n = 935$). Year-round average elevations for males (mean = 979.53 m, SE = 7.36, range 966–992 m asl) were similar to those of females (mean = 1001.59 m, SE = 5.8, range 991–1011 m asl).

When comparing mean elevations in summer versus winter, these did not differ ($t = -2.042$, $p = 0.055$) for females (summer: 1050 m, SE = 31.82; winter: 976.42 m, SE = 16.87), whereas for males (summer: 1006.76 m, SE = 8.85; winter: 948.02 m, SE = 5.26) they differed slightly ($t = -6.87$, $p = 0.02$), although their absolute maximal altitudinal difference was only 159 m. Overall, the maximal annual elevational displacements by these six huemul across all months of the study period averaged only 149.5 m (range 74–229 m). Moreover, marked, and also many unmarked individuals, were located at the shore of the Lake La Plata (930 m asl) in every month of the year (Figure 3). Additional huemul signs (tracks, feces, bones) were recorded up to 1250 m asl, even though surveys were conducted up to 100 m above the treeline which is at 1300 m asl, corroborating earlier observations that there is little use above the treeline [3,28].

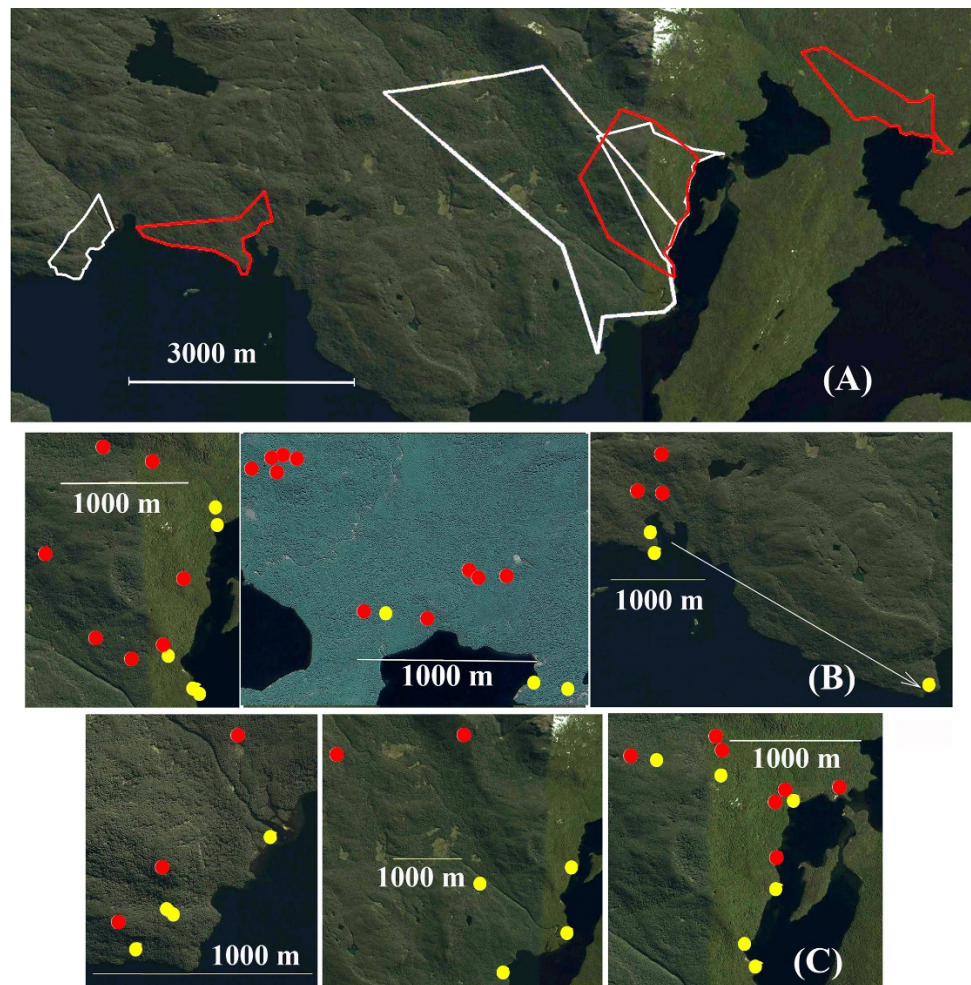


Figure 3. (A) Annual home ranges of 3 male (red) and 3 female (white) huemul in the Protected Park Shoonem. Precise locations in winter (yellow) and summer (red) of 3 male (B), and of 3 female huemul (C). Arrow indicates one unusual displacement in late winter, which ended in death by starvation.

3.3. Extent of Horizontal Movements and Size of Annual Home Ranges (MCP)

Because individuals were marked in separate capture events in different areas, they all were considered to belong to different social groups. However, subsequent observations revealed that the home ranges of two females slightly overlapped, the home range of a male overlapped those of these two females (Figure 3a), and they were also sighted together. The longest horizontal displacement recorded within the habitually used yearly home ranges averaged 2133 m (SE = 448) among the six huemul. Two exceptional movement distances were not included in these data: a male with a home range not exceeding 1.6 km in dimension based on 14 months of data, suddenly left it in early spring, to move along the edge of the lake to a new site 4.7 km away (Figure 3b). There he died shortly after from starvation/malnutrition, and with severe bone pathology having negatively affected his foraging behavior [55]. One female (2–3 years old) moved 2.13 km after the capture event, but then returned shortly afterward to remain in a defined home range not exceeding 1.1 km in dimension. The perimeter length of yearly home ranges among 5 huemul averaged 5032 m (SE = 738), with an additional home range of a female having 11 km of perimeter. Since horizontal movements were recorded every month between August 2017 and April 2022, their magnitudes indicate the absence of migratory movements. This is in agreement with the absence of sightings of huemul (live, dead, shed antlers) further down the watershed for many decades.

The home range sizes reported here are a reflection of the sampling frequency of VHF radios allowing precise fixes, but covering all seasons and several years. The mean size of annual home ranges (MCP, representing minimal values) did not differ between males and females ($t = -0.56674$, $p = 0.300589$), averaging 159.33 ha (SE = 64.52). The home range size of one female was estimated at 464 ha and resulted from moving several kilometers to also use another flat area. In the one case, where the VHF collar was replaced with a satellite radio, the former technique determined a home range of 68 ha with a maximal displacement of 2147 m ($n = 24$), while the latter resulted in 190 ha with a maximal displacement of 2500 m ($n = 1675$). However, the 190 ha consisted of areas used at the end of winter and the beginning of summer, amounting to 163 ha and 147 ha, respectively, with an 80.5% overlap (Appendix A).

3.4. Processes of Migration and Geographic Expansion to New Habitat by Wild Cervids

Past over-harvesting not only resulted in the extirpation of local huemul subpopulations, but we hypothesize that it also eliminated their migratory traditions. Considering this loss, recognizing the processes involved in migratory traditions among cervids plays a key role in better understanding the consequence of losing such behavior [10].

Among cervids living in seasonal environments, including *Odocoelines*, a newly (re)colonized area initially has deer behaving as residents, whereby migratory behavior is non-existing. It also occurs even if the translocated animals stemmed from populations being migratory in their original site [12]. Only after multiple decades (up to 90 years for *Alces*) and increasing local population density, have translocated populations increase their propensity to start migrating again [12]. While deer movements are shaped by the distribution of resources for fine-scale foraging, this will eventually also include broad-scale migrations [56].

Regarding migration behavior, the multi-generational process to encounter and adopt movement corridors that allow green-wave surfing [56] plays an important role in the foraging strategy of *Odocoelines*, and the access to plant green-up along the migratory route is an additional key foraging benefit of migration [57]. Migration behavior thus not only refers to using fixed seasonal ranges, but also provides important foraging value while deer move along these corridors following the green wave (spring green-up), thereby enabling a prolonged exposure to high-quality forage and hence more energy [57].

Fundamental and primary mechanisms for ungulate migration involvement are non-genetic processes of social learning and cultural transmission [12]. Moreover, spatial memory of the migration route had an extraordinary influence on migration, affecting movements manifold stronger than tracking spring green-up or autumn snow depth [56], and was characterized by strong fidelity [13,44,58]. Such spatial memory along with resource tracking allowed deer to repeatedly use the same migratory routes of 820 km round-trip [56,59]. Consequentially, the loss of migratory traditions will thus expunge generations of knowledge about the locations of high-quality forage and likely suppress population abundance [10,12], and leave pockets of potential habitat unoccupied because of the lost memory of viable migratory routes [13]. For instance, *Odocoelines* were shown to have little to no plasticity in terms of whether or where they migrated: resident deer remained residents, and migrant deer remained migrants, regardless of age, reproductive status or number of years monitored ([13,60]; Supplementary File S2). Certainly, some individual plasticity does occur and explains the development of new movement patterns including recolonizations [8,61].

For seasonal environments, Fretwell theorized in 1972 [17] how species would select habitats. Accordingly, under natural conditions, wild cervids tend to occupy all available habitats by doing best in source areas, so named for allowing positive population growth. Animals dispersing from source areas will also start to occupy suboptimal areas, including sink areas, so named because the local recruitment rate achieved there does not compensate for the local losses. There, populations are only maintained by replacement with newly arriving dispersers from source areas. Similarly, initial populations establishing themselves

in source areas are year-round residents. Some dispersers, particularly in mountains at seasonal latitudes, will eventually move altitudinally to establish new summer ranges, and then return to their original winter area, thereby rejoining that resident population [62]. Thus, over several generations, basic plasticity becomes apparent, resulting in partial migration (coexisting resident and migratory individuals), changes in timing and routes, and also changes at the individual level [8]. Moreover, established migratory traditions can override signals of habitat quality and predation risks, such that deer can pass the best summer habitats to remain in the worst habitat at much further distance [13,58], or cross several mountain ranges to get to traditional winter-summer areas (Supplementary File S1). Similarly, when the culturally transmitted migratory behavior is interrupted after offspring lose their migratory mother, for instance, they will adopt resident behavior (Supplementary File S1). These well-documented processes of migratory behavior of cervids thus support the same hypothesized behavior among huemul, and the fact that it can be eradicated by over-killing, for instance.

Various observations show that the dispersal of adult or juvenile animals naturally connects source and sink areas [63]. Yet, source-sink population dynamics may change if dispersal is somehow constrained, e.g., by rapid anthropogenic changes in landscapes resulting in animals no longer making optimal habitat selection decisions as acquired by cultural transmission [64,65].

A comprehensive review by Xu et al., (2021) [8] revealed that many wild ungulates exhibit substantial migratory plasticity resulting in partial migration, and changes in migratory paths or localities. Their study revealed 127 migration change events in direct response to natural and human-induced environmental changes across 27 ungulate species. In addition to the suite of ecological processes playing a role which they described, we report here for the first time that the huemul is the only example of an ungulate in seasonal habitat having changed its behavior to become year-round residents in typical seasonal summer range habitat.

4. Discussion

4.1. Historical Spatial Habitat Use

The weight of evidence indicates that local extirpations of huemul resulted from overhunting by early humans and their dogs, which was exacerbated by huemul's lack of anti-human behavior [66,67] (Supplementary File S1; Figure 1). Nonetheless, several historical accounts between the years 1521–1925 still mentioned huemul subpopulations — with some even considered numerous, extending from the Andean ecotonal foothills to the Patagonian mesas, and even reaching as far east as the Atlantic coast (Figure 4, Table 1). A huemul was harvested in 1904 at a site 270 km east of the continental divide, which is 225 km east of the eastern-most currently living huemul [25]. This hunt by the governor of Chubut was documented photographically [68]. Additionally, huemul were described to co-occur with guanaco in areas even reaching the Atlantic coast (Supplementary File S1).

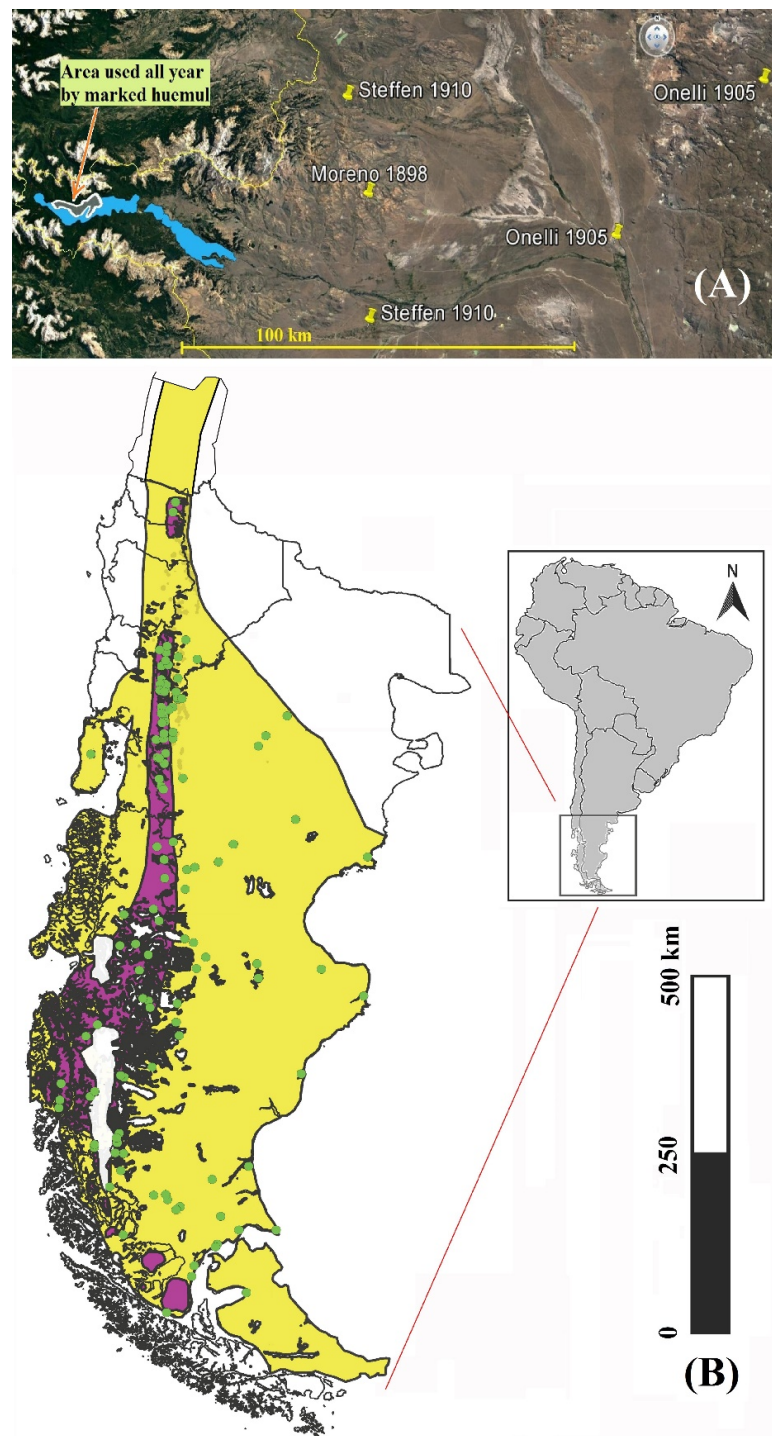


Figure 4. (A) Historical and current spatial distribution of huemul in the Protected Park Shoonem. The blue polygons show lakes Fontana and La Plata. The current year-round range (grey polygon outlined in white) is at the upper elevational margin of summer ranges and near the Andean continental divide, compared to historically used areas (indicated by yellow ticks) [47,69,70]. Distances traveled to summer ranges in the past are well within common seasonal movement distances for similar cervids like *Odocoileus*. (B) Historical distribution (yellow); current distribution (purple: Jimenez et al. [71]), unsuitable areas (internal white zones indicating bare ice fields, rocky slopes without vegetation, or lakes), and historical locations (green dots), based on reports by naturalists, shed antlers, and archeological samples (Supplementary File S1).

The historical accounts of huemul also occurring far from forests are further corroborated by their osteology: analyses of rear limb ecomorphology indicate huemul are adapted to open habitat (unforested) areas [72,73]. The perceived short stature thus was not due to short limbs but to a thick coat of long hair (up to 19.5 cm long, Source: Shoonem Foundation collection) that concealed the leg length, thus creating a misperception [74]. Moreover, huemul limb morphology does not overlap with species considered mountain specialists, but falls within the range of other cervids, with some populations of *Rangifer* spp. and even *Odocoileus virginianus* having much shorter legs than huemul: these findings contradict the long-standing assertion that attributed the apparent short stature of huemul to be an adaptation to mountainous terrain [74,75]. Moreover, stable isotope analyses of archeological samples reveal that huemul's diet from open environments cannot be differentiated from that of steppe guanaco [76]. Lastly, the cryptic pattern of fawns does not coincide with huemul having evolved in forested habitats. Camouflage appears to be the single most important evolutionary force in explaining why most cervids have spotted fawns: this crypsis provides the strongest protection in forests as a likely mechanism by which fawns could escape detection by predators [77]. Yet very few cervid species, including huemul, have non-spotted fawns, which is to be expected if natural selection acted on the species principally in open habitat areas [77]. Consequently, Webb (2000) proposed the cervid tribe Rangiferini, which includes the northern *Rangifer* and the southern *Hippocamelus*, the former using extensive open tundra and steppe [78]. Hence whereas historic data confirms a reduction in distributional range of huemul, together with anatomic data it also indicates the loss of migratory traditions (see below).

4.2. Historical Seasonal Habitat Use

The hypothesis that the huemul was once migratory like other cervids in seasonal environments, is corroborated by historical observations. Thus, in the past, huemul frequently were year-round residents in valleys and other low elevation winter ranges, while some migrated between summer and winter ranges, and formed large winter groups of more than 100 individuals [66,79–82]. Current habitat use by huemul in the Protected Park Shoonem certainly represents only a small fraction of the watershed reported to have been used historically [45,46] (Figure 4). Additionally, old shed antlers, which are not related to a harvested animal, have been collected in historically used temperate grasslands, including a few sites near the Atlantic Ocean some 300 km east of Andean summer ranges. Analyses of aboriginal use of huemul showed that hunting occurred in grassland summer ranges, together with guanaco [83,84]. Moreover, it should be noted that even very early on (e.g., 1847, 1873, etc.) it was recognized that huemul already had regionally disappeared and remained mainly in high and inaccessible areas [31], which already were interpreted as being refugee areas (Supplementary File S1), though this perspective was lost in recent decades.

Similarly, bighorn sheep (*Ovis canadensis*) were overhunted, and lost their traditional seasonal migrations resulting in many sedentary herds and associated seasonal deficiencies due to low forage quality, which was considered the ultimate cause of declining herds, and one of the largest problems challenging their long-term persistence [85]. Sika deer (*Cervus nippon*) in Japan also respond strongly to hunting and disturbances, and their seasonal migrations aim toward safer areas to avoid hunting and culling, besides being warmer and less snowy in winter. Sika deer are avoiding hunting areas representing the most suitable foraging sites (e.g., pastures), to move to safer sites even with poor forage, like forested areas with hunting prohibited [86].

4.3. Contemporary Spatiotemporal Habitat Use in the Protected Park Shoonem

The pattern of seasonal habitat use was very similar among both sexes. Areas used during harsh winters occurred at the lowest possible local elevation (lake shores), but these are also regularly used during the remainder of the year. Conversely, during the mild winter of 2021, one female used an elevation even higher than in any summer since 2017. This explains the very reduced minimal yearly elevational displacement

(mean = 36.2 m). Moreover, given that unmarked and some marked huemul were observed year-round at lake level, it appears most or all marked huemul used the shoreline during the summer as well. In comparison, huemul further north (Los Alerces National Park) [87] had a similar elevational displacement between average summer and winter locations of merely 200 m, which were classified as seasonal shifts. Moreover, these small seasonal elevational differences and distances, plus their presence at all elevations during the whole year, hence indicate that these huemul are non-migratory [6]. Huemul studied in Chile over several years in three different areas showed that winter and summer range usage largely overlapped, with an insignificant mean elevational displacement of about 200 m, and thus were considered non-migratory [88]. After reintroducing huemul around 1980 to Torres del Paine National Park, some family groups remained in low-elevation areas year-round, while other individuals eventually adopted a pattern of using areas somewhat elevated (up to 150 m higher) in summer, and descending to those lower areas mainly during winter, which was also considered as non-migratory [89–91]. Lastly, huemul in periglacial refuge areas by the Pacific coast also had limited elevational displacement as the treeline there is only at about 400 m asl. These huemul were non-migratory; they favored the flat and open grassland habitat, where twice as many fecal pellet groups were found as compared to those in forested hillsides [14].

Maximal horizontal movements were also very limited within the year-round habitually used home ranges of huemul in our study population at Shoonem Park. The longest movement (4.7 km) was made by a male in early spring, maybe induced by advanced disease, which terminated in his death from starvation shortly after (Figure 3b). In the study by Gill et al. [88], individuals considered non-migratory rarely moved more than 5 km, and the mean distance moved between summer and winter areas was 552 m (range 44–1219 m). In contrast, the reintroduction of seven huemul in the years since 2016 in the Los Rios region (Chile) revealed that exploratory movements of one male during the first month following his liberation included two excursions that reached 10 and 18 km in length, occurring in opposite directions, and that extended beyond his eventual home range (F. Vidal unpubl. data). The other animals moved less before establishing a home range. All released animals were born in the breeding center Huilo Huilo, they were radio-collared and released next to the center, and were permanently surveyed thereafter. It revealed that these adults and their fawns remained in the valley bottoms shared with the guanaco, and they never climbed the mountains that surround the center and their final home ranges (F. Vidal unpubl. data). The dispersal events and subsequent habitat use by these huemul so far are the first-ever documented cases, and they illustrate the movement potential of huemul, their all-year resident behavior in valley bottoms near riparian habitat with the best grass availability, which thus helps explain their historical distributions and movements, in concordance with the behavioral capacity of other *Odocoileus*.

The short movements displayed by huemul studied here explain the small year-round home ranges, averaging 167 ha (SE = 64.6), albeit possibly an underestimation. Year-round mean home range sizes in Tamango (Chile) were 318 ha, and similar between non-migratory females and males [88]. For huemul reintroduced to Torres del Paine National Park, year-round home range sizes as determined during a 10-year study varied between 269–336 ha [90]. In comparison, although similar-sized mule deer (*Odocoileus hemionus*) are typically migratory in the Rocky Mountains, resident deer on winter ranges utilized a continuous year-long home range, displacing only some 1300 m between seasons, and shifting to just slightly higher elevations in summer [60,92].

The huemul studied here clearly were year-round residents within a single and well-defined area, which was also corroborated by numerous antlers shed in that area. These resident huemul used an area that would be typical summer range habitat within this seasonal mountainous region, but is unsuitable for year-round inhabitancy due to nutritional limitations as evidenced by prevalent pathology [5,34,93] and lack of recovery of this population (Supplementary File S2). Moreover, solely between the early 1900s till the 1960s

93 the snow line rose by about 100–200 m in many parts of the Andes [94], which likely plays a role in this study area and the concomitant performance of this study population.

88, 91 One of the very few huemul subpopulations known to be recovering, that resulted from the reintroduction to Torres del Paine National Park, where valley bottoms function as source areas, has resulted in huemul spatially expanding to eastern grassland areas [89,91]. This suggests that the absence of recolonizations of additional areas by most other extant huemul groups is because their current habitats do not qualify as source areas. Thus, the absent population growth with simultaneous low densities, results in very few or no dispersers, and thus explains the recorded lack of recolonization. For instance, whereas initial colonists of low valleys reported unearthing old, shed antlers when first plowing [95], the very rare contemporary huemul disperser entering that valley usually ends up dying [96]. Additionally, the continuing extinction of numerous such groups localized in remote refugee areas have been documented [97]. This coincides with observations that whereas dispersing adults or juveniles naturally connect source and sink areas, this has not been registered among the remaining extant huemul groups.

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4.4. Implications of Having Lost Migratory Traditions

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104 Areas used by extant resident huemul at high elevations are considered to represent summer ranges, thus constituting an ecological trap. This is substantiated by red deer introduced to former huemul winter ranges: initially, they behaved exclusively as resident deer, remaining on the winter range year-round. However, after several decades of population growth, a segment of the herd became migratory [5]. Importantly, guanaco are also known to use high mountains and forests, with corresponding seasonal migrations to low elevation winter ranges [90,98], with displacement distances reaching 70 km [99,100]. Moreover, guanaco were also drastically overhunted like huemul, but in contrast, have largely been eliminated from their prior mountainous distribution [31,52,101–103]. Notably, since colonial times, past and current livestock producers practice transhumance by herding their animals out of the Shoonem Protected Park before winter, as is the practice in other similar watersheds both in Argentina and Chile, in order to move them to areas considered appropriate winter ranges [104]. Odocoelines of similar body size were shown to avoid areas with >40 cm of snow [105], which may explain the use by huemul of the lake shores in the Protected Park Shoonem during peak winter, where snowpacks are considerably reduced along the beaches (Figure 2). However, this year-round residency in a seasonal area classified as a summer range can result in health problems due to dietary deficiencies.

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109, 110 Historical remarks already considered the use of summer and winter ranges as a determinant of huemul health. Given the low density of herbivores in most areas of extant huemul, protein and energy supplies are considered adequate and cannot explain the prevalent disease pattern or the lacking population recovery (Supplementary File S2). Health issues have now been corroborated by the high prevalence of skeletal pathologies in huemul spread over a large geographical region [106], including nearly 90% of individuals reported in this study, which qualifies these huemul as refugees (Supplementary File S2). Nutritional deficiencies were hypothesized to account for the high incidence of bone disease [107]. For one, valley bottoms tend to have soils enriched in minerals due to the topographic effect and accordingly, huemul reported here as residents in a summer range suffer from acute geochemical stress [101]. Moreover, huemul were shown to be deficient in essential micronutrients (Se, Cu, Mn) which coincides with their skeletal problems [55,108,109], and low average life span [34]. This is similar to situations in bighorn sheep [85] (Supplementary File S2), and likely explains the unusual reactions of huemul to other diseases due to their compromised metabolic and immune systems [55]. In contrast, migratory mammalian herbivores partially living in resource-poor environments travel farthest to fulfill their resource needs [110,111].

By eliminating sedentary subpopulations on winter ranges and consistently removing the last dispersing huemul, the remaining animals exhibit the aberrant behavior of becoming tied year-round to refugee areas that qualify as seasonal summer ranges. This artificial

19/111 anthropogenic elimination of migratory traditions has resulted in most extant huemul remaining in suboptimal Anthropocene refugia [19,112]. Clearly, the resident behavior reported here for huemul taking place on a seasonal summer range is not the norm for cervids that use winter ranges either as residents or seasonal migrators.

4.5. Implications for Conservation

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81 To base conservation strategies for huemul on its modern distribution is erroneous due to being an artifact, as has been recognized for other ungulates [18,85,109] (Supplementary File S2). Remarkably, Grzimek in 1973 [82] already recognized that huemul have been exterminated in most historical areas, such that they only survive in a few small mountain refuge areas (“bis auf wenige winzige Rückzugsgebiete ausgerottet”). Moreover, it is essential that the “shifting baseline syndrome” be overcome [113], that is repeating old, unfounded and outdated interpretations, like huemul being a “mountain deer”, being short-legged, non-migratory, etc., which qualify as stereotyping and compromising conservation efficacy [20]. As shown with published fake information, these are cited many times, over long periods, and have even caused an impact on human health [114]. 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, as has been modeled for huemul based on the extant distribution (e.g., Riquelme et al.) [2]. This risk is especially large when the species has been limited to suboptimal habitat for numerous decades [17], even centuries, as has occurred with resilient huemul. Acknowledging historical species ranges

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17, 19, 20, 114–117 is thus important for recovering endangered species [17,19,20,115–118] (Supplementary File S2). Most important for non-recovering subpopulations is the need to differentiate if extant subpopulations live in a marginal or natural sink area, or in an artificial ecological trap, since the latter two will drive a local subpopulation to become extirpated. Moreover, sedentariness on seasonal summer ranges by loss of migratory culture may be one of the largest problems challenging the long-term persistence of most huemul subpopulations, as has been determined for bighorn sheep populations (Supplementary File S2). Illustratively, the rare case of a growing huemul subpopulation after its reintroduction in Torres del Paine National Park, with resident groups in valley bottoms, is expanding into grassland areas where they overlap with guanaco [89,95]. Similarly, huemul reintroduced in the Los Rios region (Chile) became residents in valley bottoms together with guanaco (F. Vidal unpubl. data). To recover endangered huemul, Kauffman et al. [118] recently pointed out the importance to consider their historical distribution and migratory tradition. Moreover, it is critically important to recognize the length of time required to reestablish migratory behavior as shown in different cervids, which needed 12 or more generations to reinitiate migratory behavior, once a critical density among residents was attained (Supplementary File S2). A key requirement will be the conservation of “migratory routes”, a target essentially already projected in Argentina, by huemul being declared a Natural Monuments by federal and provincial laws [119]. An additional tool is declaring new areas containing migratory routes as a Natural Monument according to Category III of the IUCN. Importantly, the preservation of migratory routes also allows fundamental ecological processes to continue (food webs, nutrient cycling) [120], besides their function to assure the survival of species dependent on seasonal migration [10,118].

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Differentiating between the proximate and ultimate causes of mortality is necessary to understand the population dynamics of ungulate populations. Particularly the interaction between predation and malnutrition as a cause of mortality is difficult to disentangle without manipulative experiments or other means of assessment [121]. Therefore, to experimentally test the refugee interpretation, it is highly recommended that huemul be reintroduced into habitats proposed to be critical source areas and with minimal modern anthropogenic threats, to monitor their habitat-specific fitness, while using animals in the currently inhabited refuge areas as controls [10,17,20,119]. Reverting the artificial situation would require creating resident subpopulations of huemul in formerly used winter ranges (Figure 4). Furthermore, instead of waiting until reaching densities that

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promote the natural emigration and re-establishment of migratory traditions, this process could be accelerated by training young animals via imprinting to acquire a migratory pattern, as has been done successfully with other ungulates [122,123]. Once winter ranges are repopulated, along with positive recruitment rates, the expansion to unoccupied ranges, i.e., neighboring winter and summer ranges, can occur. Available evidence supports the hypothesis that a major factor behind the current failure of many huemul subpopulations to recover numerically and spatially is the current absence of their members in suitable winter ranges. Repopulating such areas would in time also allow reconnections between the currently isolated subpopulations, concordant with the common pattern among other cervids in seasonal regions, which consists of mixed group compositions on both summer and winter ranges. In this way, a winter range frequently receives migratory members from several distinct summer ranges, while a summer range will receive members from distinct winter ranges [58,60,124–126], and thus contributes to gene pool diversity.

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A lesson learned from this study, of general application to conservation biology, is that it can be a fatal mistake to define the “area of habitat” (AOH according to Brooks et al.) [127] for an endangered species on the basis of its current distribution. This distributional range is often not the same environmental space that was once occupied by the species under natural conditions (from source to sink habitats) but is instead a refuge where it was displaced by the human footprint, and frequently is nutritionally insufficient to sustain its populations. Unfortunately, the ‘protected area paradox’ [15,19,128], which is widespread and applies to huemul, has facilitated the provision of protection in less productive habitats and has resulted in ineffectual attempts to conserve huemul in suboptimal habitats (i.e., as refugee species) where the subpopulation barely persists at extremely low densities and with compromised health issues.

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5. Conclusions

Making a leap towards conceptualizing what constitutes the fundamental factors preventing recovery of most subpopulations could release the huemul from its current imperilment. Many winter ranges historically used by all-year residents and also by migratory huemul apparently have turned from source to sink areas, mainly because of human predation in the past, and currently due to a lack of dispersers, due to the abundance of humans, dogs, automobile traffic, and agricultural land conversion. Among cervids in seasonal mountain areas, the huemul appears to be the only one that has mostly year-round resident subpopulations in what would be considered a typical summer range, and thus can be classified as an unfortunate refugee species, stuck in an ecological trap. To our knowledge, this is the first published account of a cervid species afflicted by these circumstances. Several huemul refugee subpopulations are known to be severely afflicted with disease resulting from concomitant micronutrient deficiencies, which explains their short life spans, and absence of both population growth and spatial expansion. Major steps towards reverting the prevailing absence of recovery over the past decades will be their reintroduction to historic winter source areas and the subsequent encouragement and fostering of reestablishing the migratory tradition. Additionally, a numerical and spatial recovery will also result in reconnecting the currently isolated subpopulations. The distributional retraction of the huemul and the extirpation of numerous local and isolated populations, including islands such as Tierra del Fuego and Chiloé, clearly show that without strong assistance from novel conservation technologies it will be difficult to prevent the extinction of this endemic deer in Patagonia.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/conservation2020023/s1>. File S1: Compendium of the Review about the Huemul Distribution in Patagonia: Past and Present; File S2: Compendium: Review of Consequences for Ungulates when losing Migratory Traditions. References [129–304] are cited in Supplementary Materials File.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Spatial behavior of huemul during summer and winter (precise locations based on VHF radio collars), in the Protected Park Shoonem, Chubut, Argentina, between August 2017 and April 2022.

Cases	Total Data Points (N)			Minimal Separation (m)		Vital Status	
	Summer	Winter	Spring/Fall	Horizontal	Altitudinal	Capture	Dead
female 1	3	6	4	122	68	2017	unknown
female 2	2	3	1	2140	143	2017	2018
female 3	8	7	5	0	0	2017	alive
male 1	3	3	5	423	38	2017	2018
male 2	7	7	1	89	71	2017	2020
male 3	14	4	6	0	0	2017	2022

Table A2. Scale of the spatial behavior of Male 3 (satellite radio collar) at the end of winter, and the autumn of 2022.

	GPS Fix * (n)	Area (ha)	Perimeter (m)	Overlap	Seasonal Displacement
(a) Aug 13–Sept 30	437	163	5760	76 %	490 m more south than (b)
(b) Oct 1–Dec 10	405	147	4810	85%	235 m more north than (a)
(c) Dec 11–Mar 7 2022	833	158	5440		no changes
Total survey	1675	190	6610		

* these are precise points with DOP of 2 or less.

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Compendium of the Review about the Huemul Distribution in Patagonia: Past and Present

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1. Process of occupying habitat areas by wild cervids

Habitats allowing positive population growth are classified as source areas. Cervids and other ungulates introduced or re-introduced to source areas frequently expand their range along additional source areas. Once the animal density increases, dispersers will eventually also inhabit marginal areas, and even sink areas, where losses are only replaced with additional incoming dispersers (Pulliam, 1988). In a similar manner, the initial populations established in source areas are all-year residents. Possibly due to increasing population density, some dispersers in seasonal latitudes will move altitudinally to establish new summer ranges, yet return to their original winter area, and thereby re-joining that resident population. This was shown to have occurred with red deer (*Cervus elaphus*) recolonizing the Swiss National Park (Haller, 2002), and exotic red deer introduced to Patagonia in areas formerly used by huemul (Flueck and Smith-Flueck, 2011). There might exist some special cases where a winter range is inhabitable during summer, such that there are no resident animals and all of them participate in the migration (e.g. Mysterud et al., 2011). This might be more related to wet/dry seasons rather than seasonal altitudinal migrations in cold-temperate regions. It takes generations to evolve migratory behavior as a cultural trait (Putman and Flueck, 2011; Festa-Bianchet, 2018; Jesmer et al., 2018). The young of migrating mothers follows them to migrate to winter ranges, and back to summer ranges the following spring (Jakopak et al., 2019). However, a mother dying on the winter range commonly results in the young remaining there as a resident (Flueck, 1989; Thirgood, 1995; Via et al., 1995; Avital and Jablonka, 2000; McClure et al., 2005). Recolonization generally occurs by moving to new winter ranges, and after arriving to such an area, its initial use is as residents (Haller, 2002; Flueck and Smith-Flueck, 2011), and only after several generations does migratory behavior become established to use surrounding summer ranges (Festa-Bianchet, 2018). Traditional migratory patterns even lead to bypassing better areas and to remain in inferior habitat, even by traversing several mountain ranges (Moser, 1962; Flueck, 1989).

Consequently, during the last glaciation huemul occurred in grasslands to the east of the Andes mountains, and once glaciers started to retreat, they began to occupy the Andes range and eventually passed to the western side (Flueck and Smith-Flueck, 2011). Many areas of the Andes were inhabited and used within a migratory pattern, which later has been eliminated through anthropogenic impacts (see below). These processes resulted in most extant huemul remaining as year-round resident populations in summer ranges with various consequences as shown in the accompanying paper.

2. Historical spatial habitat use by huemul

Before the first explorers arrived and initiated the first documentation of features in Patagonia, the situation of huemul had already been modified. For one, early humans (indigenous and colonists) and their hunting dogs affected the huemul distribution. In addition, the unusual lack of anti-human behavior of huemul (see below) intensified the effect by resulting in local extinctions. Most importantly, the first descriptions of huemul by several early naturalists already noted this phenomenon (Gay, 1847; Philippi, 1892; Steffen, 1895; Onelli, 1905; Gigoux, 1929).

2.1. Lack of anti-human behavior

In terms of fearlessness, Osgood (1923) was able to throw rocks at huemul a few meters away; indigenous people killed them with just rocks, clubs or lasso (Onelli, 1905; Housse, 1953; Díaz and Smith-Flueck, 2000; Tonko, 2008); and in open grasslands, a team member could approach a huemul and kill it with just a knife, while first allowing the head explorer to take a time-consuming hyalotype photo (Onelli, 1904). Prichard (1902b) described how after shooting a huemul standing in a group, the other members still came closer, so that eventually he could harvest a whole group. This fearlessness was corroborated during the first-ever capturing of six huemul in Argentina: the time between spotting the animal and placing a capture dart ranged from 32 to 73 minutes, and still allowed to place the dart from distances ranging only from 10 to 23 m. The huemul simply ignored the people preparing themselves for darting (Flueck and Smith-Flueck, 2018). Although huemul apparently can reduce their tolerance towards humans, the process was certainly too slow in the past, when the aim was to harvest huemul (Prichard, 1902b; Goss, 1983).

2.2. Historical efficiency of hunting huemul

Past densities in areas easily accessed by humans can also be deduced from the reported hunting efficiency. For instance, Juan Ladrillero reported in 1558: 'and then we went up to the place known as the Deer Point, where in just one hour two of our men shot fifteen of them with the arquebus' – and this being weaponry less accurate than bow and arrow (Diaz and Smith-Flueck, 2000). Prichard (1902a) summarized that he could have very easily shot ten huemul in a day, based on his whole team living from huemul for many weeks during work. Equestrian precolonial humans rarely hunted huemul in the forests as horses and boladores were useless there, however, they killed huemul out in the open foothills, lowlands or open valleys (Falkner, 1774; de la Cruz, 1836; Prichard, 1902a; von Colditz, 1925; Gigoux, 1929; Grosse, 1949; Housse, 1953; Liebermann, 1962; Iglesias, 1965; Kolliker Frers, 1969). Boladores are devices with weights on the ends of interconnected cords, used to capture animals by entangling their legs. Once the use of feral and controlled livestock became common, huemul - driven down by snow to lower forests, valley bottom and further out to open flats, were then much persecuted by gauchos or native people and their dogs (Gay, 1847; Prichard, 1910; von Colditz, 1925; Gai, 1936; Housse, 1953; Kolliker Frers, 1969; Miller et al., 1973; Torrejon, 2001). Every native hunter in Patagonia had at least a dozen dogs, to accompany them on hunting trips by horseback (Onelli, 1904; von Colditz, 1925).

2.3. Anthropophobia by huemul and other cervids

Under natural conditions, cervids are exposed to numerous predators, mainly felids, canids, ursids, raptors and humans. Large predators of felids, canids and humans commonly elicit an anti-predator responses, by the deer becoming alerted and if needed, by fleeing. Under special conditions like captive breeding, cervids may become predator-naïve, or when an exotic predator has been introduced. Commonly, a basic level of anti-predator behavior is always present, like red deer (*Cervus elaphus*) introduced to Patagonia, being able to adapt to the new predator puma (*Felis concolor*) (Flueck and Smith-Flueck, 1993). Another example is a bedded newborn Black-tailed deer fawn (*Odocoileus hemionus columbianus*) which increases the pulse and respiratory rate when first approached by a human, and when mobile later on, retains a distance even when the tamed mother feeds off the hand of a person. Thus, general anti-predator behavior does not have to be learned, and anthropophobia is typically exhibited even during an animal's first encounter with a human (Stringham and Rogers, 2017).

Studying wild Odocoilines, deer alerted shortly after a human started to approach, with approach distances ranging from 70 to 1000 m (Lingle and Wilson, 2001). Similarly, different ways of approaching by a human resulted in the deer fleeing at a minimal distance of 60-90m, depending on the approach tactic (Stankowich and Coss, 2006; Stankowich, 2008).

In contrast, huemul are naive regarding humans, in a unique way among cervids. In actuality, one or more people frequently can get very close to huemul, including in areas where the animals likely never had seen a human. Moreover, huemul will walk towards humans to very close distances: such cases are documented repeatedly with photos and videos. For instance, finding a group of 4 huemul in a remote part of a Chilean National Park, a video of 5 minutes shows how this group approaches and a female eventually sniffs the leg of the person, and then moves on slowly (Flueck, unpubl). Very young fawns also walked directly up to people (Flueck, unpubl.). It corroborates a similar experience by Prichard (1902a) when a huemul walked away after having sniffed his leg, or the gaucho putting to death a huemul using a knife, photographed by Onelli (1904). This lack of anti-human behavioral response explains the historical efficiency of hunting huemul, thus preventing adaptive behavioral changes, and resulting in their local extermination.

2.4. Historical use of huemul products

The ease of hunting huemul was accompanied by the many useful products obtained. Instructively, early descriptions at contact with pedestrian hunter-gatherers referred to some as 'huemules', reflecting their clothes made from huemul skins (Steward, 1946; Torrejon, 2001). For one sole area it was estimated that two thousand huemul were killed per year, mainly to feed dogs, pigs, chickens, while skins were made into clothing and shelters for people and their domestic animals, or used for commercial trading (Giai, 1936; Liebermann, 1962; Iglesias, 1965; Kolliker Frers, 1969). Claraz (1864) stated that huemul hides had already been traded for over 50 years (i.e. 1785) through Carmen de Patagones via Buenos Aires to Europe (Cabrera and Yepes, 1940), through Valdivia (Philippi, 1873), while Behm (1880) mentioned the export site of Punta Arenas in Chile for hides, and in addition for male heads in velvet. Considered useful for its various products, the huemul was listed as early as 1883 as one of the commercially important species traded and utilized by humans (Simmonds, 1883). Then, to provide better protections, Chile proposed in 1902 to charge an export tax for huemul skin hides (Ramirez Morales, 1991).

When the Chilean Presidente José Joaquín Prieto decided in 1832 to place the huemul symbol in their National Flag, huemul had already become so unknown that the first Flag depicted huemul as a horse, based on the first description by Abbot Molina in 1782, naming it *Equus bisulcus* (now: *Hippocamelus bisulcus* Molina 1782). However, most relevant is the declaration of 1832 made by President Prieto: that huemul was already most rare, and how its good skin had been their valued material to make the corslets and war boots for their troops of soldiers (Donoso et al. 2017).

2.5. Historical comments about the concurrent problematic status of huemul

The ease of hunting huemul and the high interest in its products resulted in local extinctions in many sites. Therefore, it is not surprising that historically huemul was not only considered as having already disappeared or as being very rare (Vidaurre, 1782; Molina, 1809; Gay, 1847; Sclater, 1873; Philippi, 1857, 1892; Sclater, 1873; Prichard, 1910; Wolffsohn, 1910; von Colditz, 1925; Hauman, 1926; Latcham, 1935; Gai, 1936; Magne de la Croix, 1937; De Agostini, 1941; Ringuelet, 1946; Housse, 1953; Pefaur et al., 1968; Kolliker Frers, 1969; Miller et al., 1973), but was also considered to be close to extinction (Onelli, 1905; von Colditz, 1925; Dawilov, 1926; Gigoux, 1929; Grosse, 1949; Kolliker Frers, 1969). Moreover, as colonization had already advanced in other sites, and with it the disappearance of huemul, hunters in one such region were honored with a feather in their hats if still able to kill a huemul (Prichard, 1902a).

2.6. Historical reports about sites still containing huemul

Although locally exterminated in many areas early on, some historical accounts still mentioned huemul populations - with a few even considered numerous, between the Andean foothills and the Patagonian mesas, and even reaching all the way eastward to the Atlantic coast (Günther, 1875; Behm, 1880; Prichard, 1902a,b; Church, 1903; Hatcher, 1903; Onelli, 1905; Osgood, 1923; von Colditz, 1925; Gai, 1936; Santos Gollan, 1946; Housse, 1953; Liebermann, 1962; Kolliker Frers, 1969; Conway 2005). Reports from the 16-19th centuries mentioned huemul near ports of San Julian and Desire (e.g. Pigafetta 1521 and van Noort 1598, both cited in Eastman, 1915; Pennant, 1793; MacDouall, 1833; Roulin 1835). With time, naturalists found an even more reduced distribution, but still with some descriptions of huemul far from the Andean forest, including in the so-called 'Patagonian pampa' (Claraz, 1864; Musters, 1871; Burmeister, 1873; Moreno, 1898, 1899; Prichard, 1902a,b; Hatcher, 1903; Onelli, 1905; Steffen, 1897, 1900, 1910; Wolffsohn, 1910; Osgood, 1923; von Colditz, 1925; Gigoux, 1929). In these same reports, huemul were commonly found occurring in great numbers together with guanaco.

Moreover, indigenous people were reported to like and to be cooking huemul meat, hunted in steppe areas together with guanaco and ostrich (*Rhea pennata*) (Bürger, 1924; Aschero, 2010; Machon and Juarez, 2013). Even documented with photos is a huemul hunted by the governor of Chubut in 1904, at a site 270 km east of the continental divide (Anon., 1904).

Many of these historical reports of huemul distribution resulted from expeditions aimed at describing the landscape, hydrology and biology, such that there is much corroborating evidence in form of resulting huemul specimens deposited in numerous museum collections all over the world: Italy, France, Switzerland, Austria, Germany, Czechoslovakia, England, USA to name a few. Also corroborating the historic distribution are numerous shed antlers or huemul remains found in archeological sites (Onelli, 1905; Reichlen, 1959; Laming-Emperaire et al., 1972; Johnson, 1976; Silveira, 1979; Cardich and Miotti, 1983; Massone, 1984; Goni, 1988; Serret, 1990; Diaz, 1993; Re et al., 2005; Diaz et al., 2007; Carballo Marina et al., 2008; Paillan and Tello, 2012; Teta and Rodríguez, 2020).

Nonetheless, it is utmost important to recognize that the pre-Columbian anthropogenic impact on the huemul distribution was substantial, and resulted in corresponding initial reports of already severely modified circumstances. Thus, others have concluded that huemul and guanaco were already nearly extinct by the time of the first Spanish arrival, but still occurred in Coquimbo (Chile, at 30°S) as late as 400 years ago (Fig. 4b in the accompanying paper): this is 680 km further north of the extant and isolated northern-most population (Bahre, 1979; Saavedra and Simonetti, 1991; Moreno et al., 1994; Ale, 2014).

2.7. Paleobiogeography

The pre-Columbian distribution of huemul resulted likely from *Odocoileus* founders (Morejohn and Dailey, 2004), which dispersed through the Panama isthmus. Species which successfully passed this equatorial filter were generalists and predominantly savanna-adapted (Webb, 1978), and considering paleoclimatic conditions, *Hippocamelus* colonized southwards through continuous savanna habitat east of the Andes (Hoffstetter, 1963; Hershkovitz, 1969; Frailey et al., 1980; Markgraf and Kenny, 1997). The early presence of *Hippocamelus* species in South American plains, and its absence from Andean fossil records imply that the genus did not evolve in the Andes. The most probable scenario suggests that *Hippocamelus* first evolved elsewhere as suggested by lowland fossils (Paula Couto, 1953, 1979; Rusconi, 1967) as mentioned above. Glaciations kept *Hippocamelus* repeatedly away from the Andes, with fossils known from northeastern Brazil (8°9'S, 36°22'W), and from the rangeland plains of southeastern Brazil, Uruguay and Argentina (Castellanos, 1944; Magalhaes et al., 1992; Eisenberg, 2000; da Silva et al., 2006; Guérin and Faure, 2009; Anonymous, 2021). Hershkovitz (1972) thus recognized *Hippocamelus* as pastoral and only secondarily adapted to sylvan habitats.

During glaciations, the Andes were covered with ice even near the equator (Clapperton, 1993; Coltorti et al., 2007), and continuous sheets 1600-1800 m thick covered the Andes from about 33-56°S during the last glacial maximum (Flint and Fidalgo, 1969). Glaciers south of 42°S dipped into the Pacific and reached hundreds of kilometers into eastern Patagonia. There, only non-forested habitat existed, with Patagonia-like rangelands reaching far into Brazil, and much of South America was covered by savanna and rangelands (Marshall, 1988; Clapperton, 1993; Rasmussen, 1994; Markgraf and Kenny, 1997; Tatura et al., 2002; Rabassa and Coronato, 2009). Moreover, the sea level was 120-150 m lower than currently and the Atlantic coastline located >300 km east of the present coastline, which almost doubled the area of eastern, flat paleorangelands (Rabassa et al., 2011). Huemul thus persisted repeatedly in only non-forested habitats, which is the typical environment for the extant congeneric taruca (*H. antisensis*) (Flueck and Smith-Flueck, 2012a).

During glaciations, *Hippocamelus* persisted in eastern non-forested lowlands, and as mixed feeders, huemul are known to consume notable amounts of grass (Smith-Flueck, 2003; Prothero and Foss, 2007). Extant huemul ate 16% grass (Sierralta, 2003), while taruca had ~60% of grass in its diet (15 species, Gazzolo, 2006). Furthermore, besides Gramineae, Patagonian rangelands contain many shrubs, they maintain important green-grass production throughout winter, and deer are known to heavily use seed heads, further corroborating past distributions of huemul in non-forested habitat. Even smaller-sized cervids thrive exclusively in non-forested rangelands, like Pampas deer (*Ozotoceros bezoarticus*) or roe deer (*Capreolus capreolus*) (Pérez et al., 2008), and many *Odocoileus*, including *Odocoileus*, are versatile in foraging and successfully utilize rangelands, steppes and deserts besides closed forests (Putman and Flueck, 2011). Similarly, huemul also exhibit flexible feeding behavior, utilizing some 200 plant species (from modern studies), and many more if considering past distributions and exotic food received in zoos like in Buenos Aires (Flueck and Smith-Flueck, 2012b).

Once eastern Patagonia became free of ice, huemul were able to reach Andean habitat and, when deglaciation allowed, eventually cross the Andes through corridors which

had opened (Moreno et al., 1994). Faunal exchanges from the east occurred across low Andean passes, explaining the presence of huemul in late Pleistocene as far north-west as 30°S by the Pacific coast (Bahre, 1979; Saavedra and Simonetti, 1991; Moreno et al., 1994; Ale, 2014). With the last glacial retreat, forests spread from few western refuges, and eventually covered the southern Andes again, reaching their current extent only 2,000-3,000 years ago (Markgraf and Kenny, 1997; Rabassa and Coronato, 2009; Armesto et al., 2010).

The only congeneric, taruca - considered osteologically indistinguishable and possibly a mere subspecies by some (Wagner, 1855; Philippi, 1857; Dabbene, 1911; Krieg, 1925; reviewed in Diaz, 1995), currently utilize non-forested rangelands with high affinity to Patagonia (Fernández and Busso, 1997). However, taruca also have been displaced because of anthropogenic pressures, e.g. from *Prosopis* forests by the Pacific coast (Dabbene, 1911; Horkheimer, 1960; Sinclair, 2009). Although now mainly found above treeline, some populations are still found, even exclusively, in *Polylepis* and yungas forests, also due to continued hunting pressure (Aldenderfer, 1998; Tarifa and Yensen, 2001).

Paleobiogeography indicates that the ability to utilize non-forested rangelands was essential for the persistence of huemul (HersHKovitz, 1972; Webb, 1978), making the claim unrealistic that huemul are strictly a forest-dependent species.

3. Historical seasonal habitat use

3.1. Resident behavior of huemul

Not only were huemul described as year-round resident populations in valleys and on winter ranges, but also as having been there frequently together with guanaco, and even with numbers equivalent to guanaco (Cox, 1863; Claraz, 1864; Prichard, 1902a; Steffen, 1910; Krieg, 1940; de Agostini, 1945; Grosse, 1949).

Examples of current resident behavior at low elevations stems from a large island with mountains reaching 1830 m.a.s.l., and forests reaching the coast. All sightings and signs occurred between sea level and 200 m elevation, and on 0-15 % slopes: no huemul signs were recorded above the tree or shrub lines (Moreira-Arce et al., 2021)

3.2. Migratory behavior of huemul

In some cases, huemul grazed together with cattle or mules on high-elevation summer ranges, and then went down with the domestic animals when these were driven by gauchos from summer areas to low winter range lands (Philippi, 1892). Others have described huemul to descend to valleys and/or out into the grasslands during winter where they formed large groups of over 100 huemul (Moreno, 1898; Gay, 1847; Claraz, 1864; Sclater, 1875; Lydekker, 1898; Prichard, 1902a,b; Wolffsohn, 1910; Steffen, 1910; Neveu-Lemaire and Grandidier, 1911; von Colditz, 1925; Dawilov, 1926; Gigoux, 1929; Gai, 1936; Krieg, 1940; Grosse, 1949; Housse, 1953; Lieberman, 1962; Kolliker Frers, 1969; Ibar Bruce, 1973; Goss, 1983; Serret, 1990). Moreover, given that antlers are shed in late winter and have nothing to do with hunting, any antler findings can serve as an additional indicator of winter habitat use, by resident or migratory animals. As such, old shed antlers have been collected in historical winter ranges like temperate grasslands. For example, when first settling the large Rio Manso valley, a colonist reported finding old shed antlers while initially plowing riparian areas (Flueck and Smith-Flueck, 2012b). Then interestingly, prehistoric remains have been found in Patagonian grasslands and near the Atlantic Ocean (Ibar Bruce, 1973; Cardich and Miotti, 1983; Serret, 1990; Guineo et al., 2008; Fernandez et al., 2016), including a human-modified antler recently (Cruz et al., 2010). Hence, from very early on it was recognized that continued human pressure resulted in huemul remaining in high and inaccessible areas (Pennant, 1793; Gay, 1847; Philippi, 1892; Wolffsohn, 1910; Cabrera and Yepes, 1940; Ibar Bruce, 1973), which was interpreted as being refugee areas (Krieg, 1940; Housse, 1953; Liebermann, 1962; Kolliker Frers, 1969). Current habitat use by huemul in the Park Shoonem is certainly only a frac-

tion of the area reported to have been used historically (Moreno, 1898; Onelli, 1905; Steffen, 1910).

4. List of references for historical spacial data

The main paper provides a map showing the locations of historical presence of huemul, based on hunting, shed antlers, and archeological samples (n = 54, Figure 4). The following list of citations formed the basis of these locations:

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S2: Compendium: Review of Consequences for Ungulates when losing Migratory Traditions

Content:

Implications of having lost migratory traditions

1. **Nutritional ecology and seasonal migrations**
- 2 **Carrying capacity in migratory ungulates using summer and winter ranges**
3. **Fundamentals of migratory traditions**
4. **Implications for conservation**

Implications of having lost migratory traditions

Humans have achieved a very sophisticated and temporarily privileged status among mammals. Their capacity to domesticate wild animals for providing them with food, materials, labor, and hedonistic enjoyment, has produced a sustained growth of this forced symbiosis until reaching, as a whole, 97% of the current biomass of mammals in the world (Berger et al., 2020). On a planet with finite resources, this expansive anthropic artifact results in a consequence of the phenomenon, namely the numerical decrease of wild species, their habitats, the loss of culturally transmitted knowledge, and the retraction of animal spatial distributions towards refuge environments.

1. Nutritional ecology and seasonal migrations

As early as 1925 the naturalist von Colditz considered the commonly found simple forked antlers in huemul as a sign of some sort of degeneration, since older samples reached up to 5 tines per side. Additionally, huemul being prevented from accessing winter areas was suggested to affect huemul health by resulting in malnutrition (Liebermann, 1962). Similarly, in historical times the related *Odocoileus* spp. were largely extirpated from the mesquite savannas range of north-central Texas, where specimens had much superior antler development when compared to remaining extant animals in timbered areas, attributed to a combination of the favorable foraging conditions on historical ranges and low population densities (Wells and Stangl, 2003). As luxury tissue, antler development clearly serves to indicate the nutritional conditions experienced by the male (Bubenik and Bubenik, 1990). Similarly, Liebermann (1962) considered the areas that the huemul were forced to use in winter as inhospitable high elevations and stated that huemul “were pushed there and fatally lost their biological capital before they could adapt”. This was corroborated more recently with at least 88% of dead ($n=34$, Flueck and Smith-Flueck, unpubl.) and 86% of live huemul affected with skeletal pathologies, antler asymmetry, and spread over a large geographical region (Flueck and Smith-Flueck, 2008, 2017; Flueck, 2020). All these samples were collected from individuals living year round at high elevations coinciding with old-growth lenga forest habitats (*Nothofagus pumilio*), and representing summer range habitat. These unusual pathological conditions together with the altered spatiotemporal use of habitats further qualify huemul as a refugee species (Flueck and Smith-Flueck, 2006, 2011; Kerley et al., 2012).

The underlying cause of the extant disease pattern relates to the commonly described effect of topography and precipitation on micronutrients, such as leaching occurring on ridge land while adjacent valley soils maintain or increase concentrations (Ren et al., 1987). Extensive areas thus exhibit lower concentrations of minerals in plants at high rather than low altitude (reviewed in Flueck and Smith-Flueck, 2011), as shown in mountain goats (*Oreamnos americanus*) living at higher altitudes having lower levels of essential selenium than elk and deer remaining in lower areas (Fielder, 1986). This was

corroborated in areas with extant huemul where soils from those higher sites had deficient selenium levels, whereas soil levels in low valley bottoms were adequate (Flueck et al., 2014). Areas used by huemul during summer (and also during winter), are generally considered to represent summer ranges based on winter conditions and fertility, such that all livestock producers in these areas remove their animals before winter and move them to winter areas (Gonzalez and Tapia, 2017; Massara Paletto and Buono, 2020). Notably, since colonial times, past and current livestock producers move their animals out of the Protected Park Shoonem before winter, as is the practice in other similar watersheds both in Argentina and Chile, to move them to areas considered appropriate winter ranges (Ladio and Lozada, 2004). Similarly, red deer (*Cervus elaphus*) introduced to former huemul areas remained as residents for several decades before adopting migratory behavior, when they always returned to winter ranges in that season (Flueck and Smith-Flueck, 2011). Congruently, huemul reported in the accompanying paper to be year-round residents in a summer range were deficient in several essential micronutrients based on hair analysis (Flueck, 2020), which explains the prevalent bone disease and low average live span (Flueck, 2015; Flueck and Smith-Flueck, 2008, 2017). The high frequency of asymmetry of antlers and their deformed development in many subpopulations also indicate nutritional problems (Geist, 1998). Besides causing a rare bone disease in huemul, selenium deficiency also affects metabolic and immune systems, such that the unusual reactions reported to caseous lymphadenitis and putative parapoxvirus pathogens may relate to such deficiencies (Flueck, 2020). Bighorn sheep (*Ovis canadensis*) were also shown to have lost traditional seasonal movements by overhunting that resulted in many herds having associated seasonal nutritional deficiencies, and which was considered the ultimate cause of declining herds (Honest and Frost, 1942; Packard, 1946; Leopold et al., 1963; Risenhoover et al., 1988). Moreover, reviewing a global database of large migratory mammalian herbivores, Teitelbaum et al. (2015) found that animals living in resource-poor environments travel farthest to fulfil their resource needs, and also had increased home range sizes. However, this trait only works for certain resources, mainly levels of protein, energy, fibers, and salt. Low phosphorous and/or calcium also is noted and results in chewing of bones. Importantly however, deficiency of many essential trace minerals are not perceived by ruminants, for example copper or selenium deficiencies. Thus, while migratory ungulates may leave a summer range temporarily to access a salt lick on the winter range, trace mineral deficiencies do not elicit a response. Instructively, although many wild ungulate exhibit substantial plasticity regarding to migrate versus to remain resident, or changing migratory paths and localities (Spitz et al., 2018), huemul was the only example of having changed to become residents in typical summer ranges (Xu et al., 2021).

2. Carrying capacity in migratory ungulates using summer and winter ranges

Conventionally, habitat carrying capacity for ruminants is based on forage supplies of energy and protein (Van Soest, 1982). In this respect, such type of nutritional constraints for current low-density huemul appear improbable, considering equivalent habitats support high densities of exotic herbivores such as red deer, although the latter also access typical winter ranges (Flueck and Smith-Flueck, 2006). Today, ecotonal ranges formerly used by huemul produce 3000-5000 kg/km² of exotic ruminant biomass, equivalent to 40-60 huemul/km² if they would forage similarly, as would be expected from mixed feeders (Flueck, 2010). Currently no huemul exist anymore in extra-Andean Argentine Patagonia which supported up to 25 million sheep, 4 million cattle and 0.5 million horses (von Thüngen and Lanari, 2010). Krieg (1940) also suggested that forage, which supported a large quantity of exotic herbivores with superb body development, could not explain the few or absent huemul. However, an evaluation of habitat should be restricted to the limiting nutrients (Van Soest, 1982), which frequently are specific macro- and micronutrients, rather than protein and energy supplies. As Liebermann (1962) al-

ready observed: “everybody familiar with mountains knows that summer and winter ranges are different and separated vertically; with snow fall, huemul must descend, however, it was exactly the lower hill sides and fertile valleys which were settled by men and his livestock. If huemul find lower areas occupied by livestock and people, they need to remain in higher places, where they will suffer from malnutrition with consequences to their offspring, and being weakened they are more prone to disease and easier prey to natural predators”.

3. Fundamentals of migratory traditions

In seasonal mountain areas, winter ranges naturally contain year-round residents besides the migratory members that utilize upper elevation summer ranges (Adams, 1982; Peters et al., 2017; Gogan et al., 2019; Koprowski and Krausman, 2019; Xu et al., 2021). Ungulates dispersing or being translocated to winter ranges tend to remain as residents initially (Haller, 2002; Flueck and Smith-Flueck, 2011), and it can take 90 years, or 12 to 13 generations, for half of the descendants of translocated animals to become migratory (Festa-Bianchet, 2018). Moreover, eventually established migratory traditions are rigid enough such that deer may ignore excellent areas (Gogan et al., 2019), traverse them to spend the summer in much inferior habitat at 110 km from their winter range (Flueck, 1989). They may also disregard elevated predation risks besides signals of habitat quality (Sawyer et al., 2019; Flueck and Smith-Flueck, 2011), as shown by traversing several mountain ranges in order to use their traditional winter and summer ranges (Moser, 1962).

Migratory behavior (altitudinal and horizontal) takes generations to evolve and is passed down culturally (Putman and Flueck, 2011; Festa-Bianchet, 2018; Jesmer et al., 2018; Gogan et al., 2019). A seasonally migrating female commonly gives birth to the young in the summer range, and in autumn the young follows the mother to migrate to the winter range, and back to the summer range the following spring, with the animals exhibiting very high fidelity to migratory routes and seasonal ranges (Jakopak et al., 2019; Morrison et al., 2021). Instructively, if a mother dies on the winter range, the young most often remains there accompanying other resident animals (Flueck, 1989; Thirgood, 1995; Via et al., 1995; Avital and Jablonka, 2000; McClure et al., 2005). A winter range rarely is inhabitable during summer such that all animals migrate away, but it occurs on ranges with wet/dry seasons.

The process leading to such partially migratory populations was also evidenced with European red deer introduced to winter ranges formerly used by huemul, where initially they remained all year as residents (Flueck and Smith-Flueck, 2011). After several decades, however, migratory behavior was adopted by some deer, and marked red deer migrated 24 linear kilometers (Flueck, 2005). This was also shown to have occurred with red deer recolonizing the Swiss National Park (Haller, 2002). Instructively, two occasions of reintroductions of huemul corroborate this basic pattern of recolonization behavior among cervids. Huemul were reintroduced to Torres del Paine National Park (Chile) between 1977-1980, with resident groups remaining in valley bottoms, and a subsequent expansion reached into grassland areas where they overlap with guanaco (Rau 2003, Guineo et al. 2008). Similarly, huemul reintroduced in the Los Rios region (Chile) became all-year residents in valley bottoms together with guanaco (F. Vidal unpubl. data).

Among cervids, using summer ranges and also accomplishing short visits during summer to access mineral licks on winter ranges (Brandborg, 1955; Mincher et al., 2008) are cultural migratory behaviors which are transmitted vertically (Adams, 1982; Nelson and Mech, 1999; Festa-Bianchet, 2018; Jesmer et al., 2018). These cultural traits in ungulates can go back 5000 to 6000 years ago (Andersen, 1991; Berger et al., 2006; Lyman, 2006), and are highly immutable (Sawyer et al., 2019). Preserving such cultural traits are considered important, especially for endangered species (Ryan, 2006; Jesmer et al., 2018).

Individuals of various ungulate species have been observed to briefly leave their summer range to make large excursions to winter ranges solely to use a mineral lick for a few hours to a few days, despite the increased risk from predation (reviewed in Flueck and Smith-Flueck, 2011). Many remaining huemul populations are tied year round to refuge areas on summer ranges because the residents on original winter ranges are extinct, and the few extant dispersers getting there are consistently being eliminated (Flueck and Smith-Flueck, 2011). Although a few recent sightings of huemul in ecotonal areas show that some do occasionally disperse from summer-range refuges, they do not establish reproductive populations as they can not survive in valleys settled by humans, inevitably being hunted, or killed by dogs or road traffic (Flueck, 2018). While migration and summer jaunts to mineral licks are learnt behaviors, dispersal is innate, being an emigration of individuals by random diffusion that is predetermined genetically and is not in response to environmental conditions (Howard, 1960). Odocoelines had little or no plasticity in terms of whether or where they migrate: resident deer remained residents, and migrant deer remained migrants, regardless of age, reproductive status or number of years monitored (Gogan et al., 2019; Sawyer et al., 2019). However, some individual plasticity does occur which explains the development of new movement patterns including recolonizations (van de Kerk et al., 2021; Xu et al., 2021).

The spacial capacity of migration among Odocoelines has been shown to reach distances up to 104 km (Gogan et al. 2019), up to 264 km (Sawyer et al. 2016), and even up to 410 km (Kauffman et al. 2020). This implies that huemul also can migrate substantial distances, and it corroborates the historical accounts referring to migrating huemul.

Therefore, the resident behavior reported for huemul that takes place on a summer range, not a winter range as is the norm for cervids, is an artefact of anthropogenic elimination of the migratory tradition resulting in the extirpation of all huemul in historical winter ranges.

4. Relevant case: a fossil deer suffering from bone pathology

The study of bones from a fossil deer endemic to Crete island revealed many pathological lesions (Lyras et al., 2019), equivalent to those described in huemul (Flueck and Smith-Flueck 2008, 2011, 2017). Lyras et al. (2019) concluded that the fossil deer on this island were affected by severe metabolic bone disease from soil mineral deficiencies and possible overgrazing of the habitat. Similarly, many huemul populations have been described as persisting in artificial "islands" with concomitant bone pathology (Flueck and Smith-Flueck 2011).

5. Implications for conservation

To base management strategies on the extant distribution, when it is an artefact, is erroneous as was shown for bighorn sheep in North America (Honest and Frost, 1942), and ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*) in Europe (Yockney and Hickling, 2000; Phoca-Cosmetatou, 2004; Baumann et al., 2005). The name "alpine chamois" resulted from historic overhunting which nearly exterminated chamois in low lands, but which survived in Alpine refuges. However, modern translocations resulted in its recovery such that it expanded to forested areas even far from the Alps, such that now it is also recognized as "forest chamois" in areas clearly corroborated by archaeozoology (Baumann et al., 2005). Huemul is another species which has been limited to suboptimal habitat for many decades if not centuries. If in such cases the currently used habitats are identified as the conservation priority areas for the species in question (e.g. Riquelme et al., 2018), without recognizing that these represent a suboptimal portion, this then might present one of the largest risks for such refugee species (Kerley et al., 2012; Faurby and Araujo, 2018; Nüchel et al., 2018). Sedentariness in artificial settings is considered one of the largest problems challenging long-term persistence of bighorn sheep populations

(Risenhoover et al., 1988), and acknowledging historical species ranges is thus important for recovering endangered species (Laliberte and Ripple, 2004; Phoca-Cosmetatou, 2004; Cromsigt et al., 2012; Kerley et al., 2012; Lea et al., 2016; Faurby and Araujo, 2018). Yet, although little knowledge exists about natural movement patterns of South American deer, this is likely to be fundamentally important to maintain viable populations (Grotta-Neto and Duarte, 2019). Whereas natural sink areas are the norm to be surrounding well-performing populations in source areas, there is the need to differentiate the former from an artificial ecological trap, since the latter will drive a local population to extinction (Battin, 2004). Moreover, it is essential that the shifting baseline syndrome be overcome (Soga and Gaston, 2017): repeating old, unfounded and outdated interpretations, like huemul being a “mountain deer”, being short-legged, non-migratory, etc. As shown with published fake information, these get cited many times, over long periods, and even with causing impact on human health (Bar-Ilan and Halevi, 2021).

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