Article

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 the Andes. Currently occupied areas are claimed—errorneously—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 their presently prevalent skeletal diseases, reduced longevity, and lacking recolonizations for most remaining huemul subpopulations. Given the limited knowledge, the first group (n = 6) in Argentina was radio-marked to examine spatial behavior. Historically, huemul resided year-round in 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](image-url) **Figure 1.** Huemul are well-known for their use of steppe grassland and lack of fear of humans. (A) Gaucho with knife hunting a huemul, 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), *Cerequus andicus* (Lesson, 1842), *Camelus equinus* (Treviranus, 1803), *Lama bisulca* (Fisher, 1829), *Auchenia huemul* (Smith, 1827), *Auchenia huamel* (Hamilton, 1842), *Cereus 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,
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                   |
| 1901 Burmeister |                              | coexistence with guanaco further east                                                   |
| 1902 Prichard|                      | Eighteen huemul (2 groups) in open grasslands, 220 km from nearest forest               |
| 1903 Church  |                      | Groups with more than 100 huemul coexisting with guanaco during winter in valleys         |
| 1903 Hatcher |                      | Grassland plains were the home of guanaco, huemul and ostriches                          |
| 1904 Anonymous |                              | Harvesting huemul in the open 100 km from the nearest forest                            |
| 1905 Onelli  |                      | The governor hunted huemul far east of continental divide 270 km from forests (includes photo) |
| 1911 Neveu-Lemaire |                              | Near Choiquenialhue and between Senguer and Chubut rivers, 120 km from forests         |
| 1912 Osgood  |                      | 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 Shoone (only its western part: 44°51′ S, 71°48′ W), owned by the village of Alto Rio Senguer, 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 Senguer 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
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 \( (n = 54, \text{Table 1, Supplementary File S1}) \). 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 \( (n = 37, \text{mean} = 1013.86 \text{m, SE} = 8.97) \). 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 \( (n = 29, \text{mean} = 969.03 \text{m, SE} = 10.27) \). 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 \((\text{mean} = 979.53 \text{m, SE} = 5.8, \text{range} 991–1011 \text{m asl}) \) were similar to those of females \((\text{mean} = 1001.59 \text{m, SE} = 5.8, \text{range} 991–1011 \text{m asl}) \).

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 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 Odocoilies, 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 Odocoilies, 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 evolution 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, Odocoilies 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 ecozone 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 tacks) [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 \([66,69,79–81]\). 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 \([46,47]\) (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 \([82,83]\). 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 \([84]\). 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 \([85]\).

### 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) [86] 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 [87]. 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 [88,89,91]. 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. [87], 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 Odocoiline.

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 [87]. 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 [89]. 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 [60,90].

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 [5,34,92] and lack of recovery of this population (Supplementary File S2). Moreover, solely between the early 1900s till the 1960s
the snow line rose by about 100–200 m in many parts of the Andes [93], which likely plays a role in this study area and the concomitant performance of this study population.

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 [88,91]. 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 unearthig old, shed antlers when first plowing [94], the very rare contemporary huemul disperser entering that valley usually ends up dying [95]. Additionally, the continuing extinction of numerous such groups localized in remote refugee areas have been documented [96]. 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.

4.4. Implications of Having Lost Migratory Traditions

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 [30,97], with displacement distances reaching 70 km [98,99]. Moreover, guanaco were also drastically overhunted like huemul, but in contrast, have largely been eliminated from their prior mountainous distribution [31,52,100–102]. 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 [103]. Odocoilines of similar body size were shown to avoid areas with >40 cm of snow [104], 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.

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 [95], 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 [106]. 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 [105]. Moreover, huemul were shown to be deficient in essential micronutrients (Se, Cu, Mn) which coincides with their skeletal problems [55,107,108], and low average life span [34]. This is similar to situations in bighorn sheep [84] (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 [109,110].

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
anthropogenic elimination of migratory traditions has resulted in most extant huemul remaining in suboptimal Anthropocene refugia [19,111]. 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

To base conservation strategies for huemul on its modern distribution is erroneous due to being an artifact, as has been recognized for other ungulates [18,84,108] (Supplementary File S2). Remarkably, Grzimek in 1973 [81] 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 [112], 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 [113]. 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 is thus important for recovering endangered species [17,19,20,114–117] (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 [88,91]. 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. [117] 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 [118]. 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) [119], besides their function to assure the survival of species dependent on seasonal migration [10,117].

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 [120]. 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 [10,17,20,118]. 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
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 [121,122]. 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 [58,60,123–125], and thus contributes to gene pool diversity.

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.) [126] 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’ [15,19,127], 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.

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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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.

|         | 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.

References

1. Black-Decima, P.A.; Corti, P.; Diaz, N.; Fernandez, R.; Geist, V.; Gill, R.; Gizejewski, Z.; Jiménez, J.; Pastore, H.; Saucedo, C.; et al. Hippocamelus bisulcus. In The IUCN Red List of Threatened Species; International Union for Conservation of Nature and Natural Resources: Gland, Switzerland, 2016.
2. Riquelme, C.; Estay, S.A.; López, R.; Pastore, H.; Soto-Gamboa, M.; Corti, P. Protected areas’ effectiveness under climate change: A latitudinal distribution projection of an endangered mountain ungulate along the Andes Range. PeerJ 2018, 6, e5222. [CrossRef] [PubMed]
3. Smith-Flueck, J.M.; Flueck, W.T. Natural mortality patterns in a population of southern Argentina huemul (Hippocamelus bisulcus), an endangered Andean cervid. Zeits. Jagdwiss. 2001, 47, 178–188. [CrossRef]
4. Putman, R.; Flueck, W.T. Intraspecific variation in biology and ecology of deer: Magnitude and causation. Anim. Prod. Sci. 2011, 51, 277–291. [CrossRef]
5. Peters, W.; Hebblewhite, M.; Mysterud, N.; Heurich, M.; Kjellander, P.; Linnell, J.D.C.; et al. Migration in geographic and ecological space by a large herbivore. Ecol. Monogr. 2017, 87, 297–320. [CrossRef]
6. Xu, W.; Barker, K.; Shawler, A.; Van Scoyoc, A.; Smith, J.A.; Mueller, T.; Sawyer, H.; Andreozzi, C.; Bidder, O.R.; Karandikar, H.; et al. The plasticity of ungulate migration in a changing world. Ecology 2021, 102, e03293. [CrossRef]
7. Howard, W.E. Innate and environmental dispersal of individual vertebrates. Am. Midl. Nat. 1960, 63, 152–161. [CrossRef]
8. Bolger, D.T.; Newmark, W.D.; Morrison, T.A.; Doak, D.F. The need for integrative approaches to understand and conserve migratory ungulates. Ecol. Lett. 2008, 11, 63–77. [CrossRef]
9. Festa-Bianchet, M. Learning to migrate. Science 2018, 361, 972–973. [CrossRef]
10. Kesler, B.R.; Merkle, J.A.; Goheen, J.R.; Aikens, E.O.; Beck, J.L.; Courtemanch, A.B.; Hurley, M.A.; McWhirter, D.E.; Miyasaki, H.M.; Monteleth, K.L.; et al. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 2018, 361, 1023–1025. [CrossRef]
11. Sawyer, H.; Merkle, J.A.; Middleton, A.D.; Dwinnell, S.P.H.; Monteleth, K.L. Migratory plasticity is not ubiquitous among large herbivores. J. Anim. Ecol. 2019, 88, 450–460. [CrossRef]
12. Frid, A. Habitat use by the endangered huemul (Hippocamelus bisulcus): Cattle, snow, and the problem of multiple causes. Biol. Conserv. 2001, 100, 261–267. [CrossRef]
13. Joppa, L.N.; Pfaff, A. High and Far: Biases in the Location of Protected Areas. PLoS ONE 2009, 4, e8273. [CrossRef]
14. Quevedo, P.; Von Hardenberg, A.; Pastore, H.; Alvarez, J.; Corti, P. Predicting the potential distribution of the endangered huemul deer Hippocamelus bisulcus in North Patagonia. Oryx 2017, 51, 315–323. [CrossRef]
15. Kerley, G.I.H.; Kowalczyk, R.; Crome, J.P.G.M. Conservation implications of the refugee species concept and the European bison: King of the forest or refugee in a marginal habitat? Ecography 2012, 35, 519–529. [CrossRef]
16. Faury, S.; Araujo, M.B. Anthropogenic range contractions bias species climate change forecasts. Nat. Clim. Change 2018, 8, 252–256. [CrossRef]
17. Nüschel, J.; Bocher, P.K.; Xiao, W.; Zhu, A.X.; Svenning, J.C. Snub-nosed monkeys (Rhinopithecus): Potential distribution and its implication for conservation. Biodiv. Cons. 2018, 27, 1517–1538. [CrossRef]
18. Brintell, J.A.; Lewis, R.N.; Elsner-Gearing, F.; Harvey, N.; Stanbrook, E.; Shultz, S. Species stereotypes as a result of unconscious research biases compromise conservation efficacy. Biod. Cons. 2021, 261, 109275. [CrossRef]
19. Redford, K.H.; Eisenberg, J.F. Mammals of the Neotropics: The Southern Cone, Volume 2, Chile, Argentina, Uruguay, Paraguay; The University of Chicago Press: Chicago, IL, USA; London, UK, 1992.
20. Aldridge, D.; Lopez, R.; Saucedo, C.; Viña, A.R. Los Ultimos Senderos del Huemul; Fundacion Huiiay: Santiago, Chile, 2007; ISBN 97895666667062.
23. Vila, A.R.; Saura, C.; Aldridge, D.; Ramilo, E.; Corti, P. South Andean Huemul Hippocamelus bisulcus (Molina 1782). In Neotropical Cervidology; Duarte, J.M., González, S., Eds.; FUNEP: Jaboticabal, Brazil, 2010; pp. 89–100.

24. González, S.; Barbanti Duarte, J.M. Speciation, evolutionary history and conservation trends of neotropical deer. Mammal. Nat. Neotrop. 2020, 27, 37–47. [CrossRef]

25. Escobar Ruiz, E.M.; Smith, J.M.; Flueck, W.T. El Huemul—Shoemem: Madera que se Mueve/re, 2nd ed.; Biblioteca Popular “Dr. Enrique Perea”: Alto Rio Senguerr, Argentina, 2020.

26. Diaz, N.I.; Smith-Flueck, J. The Patagonian Huemul. A Mysterious Deer on the Brink of Extinction; Literature of Latin America: Buenos Aires, Argentina, 2000.

27. Donoso, D.; Iriarte, A.; Segura, B.; Tirado, M. Antecedentes de Huemul (Capítulo 1). In El Huemul de Aysén y Otros Rincones; Iriarte, A., Donoso, D.S., Segura, B., Tirado, M., Eds.; Ediciones Secretaria Regional Ministerial de Agricultura de la Región de Aysén y Flora & Fauna Chile Ltd.: Aysen, Chile, 2017; pp. 13–61.

28. Smith-Flueck, J.M. La Ecología del Huemul (Hippocamelus bisulcus) en la Patagonia Andina de Argentina y Consideraciones sobre su Conservación. Ph.D Thesis, Universidad Nacional del Comahue, Bariloche, Argentina, 2003; pp. 1–361.

29. Sauter, T. Revisiting extreme precipitation amounts over southern South America and implications for the Patagonian Icefields. HydroL. Earth Syst. Sci. 2020, 24, 2003–2020. [CrossRef]

30. Puig, S.; Rosi, M.I.; Videla, F.; Mendez, E. Summer and winter diet of the guanaco and food availability for a High Andean migratory population (Mendoza, Argentina). Mammal. Biol. 2011, 76, 727–734. [CrossRef]

31. Kölliker, A.; Kühn, F.; Reichert, F.; Tomsen, A.; Witte, L. Patagonia. Resultado de las expediciones en 1910 a 1916; Sociedad Científica Alemana: Buenos Aires, Argentina, 1917; Volumes 1 and 2.

32. Citino, S.B.; Bush, M.; Grobler, D.; Lance, W. Anesthesia of boma-captured Lichtenstein’s hartebeest (Signocerus lichtensteinii) with a combination of thiafentanil, medetomidine and ketamine. J. Wildl. Dis. 2002, 38, 457–462. [CrossRef] [PubMed]

33. Muller, L.I.; Osborn, D.A.; Doherty, T.; Keel, M.K.; Miller, B.F.; Warren, R.J.; Mille, K.V. Optimal Medetomidine Dose When Combined with Ketamine and Tiletamine-zolazepam to Immobilize White-tailed Deer. J. Wildl. Dis. 2012, 48, 477–482. [CrossRef] [PubMed]

34. Flueck, W.T.; Smith-Flueck, J.M. Age-independent osteopathology in skeletons of a south American cervid, the Patagonian Huemul (Hippocamelus bisulcus). J. Wildl. Dis. 2008, 44, 636–648. [CrossRef] [PubMed]

35. White, G.C.; Garrott, R.A. Animal home ranges and territories and home range estimators. In Research Techniques in Animal Ecology: Controversies and Consequences; Boitani, L., Fuller, T., Eds.; Columbia University Press: New York, NY, USA, 2000.

36. Harris, S.; Cresswell, W.J.; Forde, P.G.; Trewella, W.J.; Woollard, T.; Wray, S. Home-range analysis using radio tacking data: A review of problems and techniques particularly as applied to the study of mammals. Mammal. Rev. 1990, 20, 97–123. [CrossRef]

37. Börger, L.; Franconi, N.; de Michele, G.; Gantz, A.; Meschi, F.; Manica, A.; Lovari, S.; Coulson, T. Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. 2006, 75, 1393–1405. [CrossRef]

38. Zweifel-Schielly, B.; Kreuzer, M.; Ewald, K.C.; Suter, W. Habitat selection by an Alpine ungulate: The significance of forage characteristics varies with scale and season. Ecoscraphy 2009, 32, 103–113. [CrossRef]

39. Kropil, R.; Smolko, P.; Garaj, P. Home range and migration patterns of male red deer Cervus elaphus in Western Carpathians. Eur. J. Wildl. Res. 2015, 61, 63–72. [CrossRef]

40. Kie, J.G.; Matthiopoulos, J.; Fieberg, J.; Powell, R.A.; Cagnacci, F.; Mitchell, M.S.; Gaillard, J.M.; Moorcroft, P.R. The home-range concept: Are traditional estimators still relevant with modern telemetry technology? Philos. Trans. R. Soc. B 2010, 365, 2221–2231. [CrossRef]

41. Powell, R.A. Animal home ranges and territories and home range estimators. In Research Techniques in Animal Ecology: Controversies and Consequences; Boitani, L., Fuller, T., Eds.; Columbia University Press: New York, NY, USA, 2000.

42. Bunningfeld, N.; Börger, L.; van Moerter, B.; Rolandson, C.M.; Dettki, H.; Solberg, E.J.; Ericsson, G. A model-driven approach to quantify migration patterns: Individual, regional and yearly differences. J. Anim. Ecol. 2011, 80, 466–476. [CrossRef]

43. Spitz, D.B.; Hebblewhite, M.; Stephenson, T.R.; German, D.W. How plastic is migratory behavior? Quantifying elevational movement in a partially migratory alpine ungulate, the Sierra Nevada bighorn sheep (Ovis canadensis sierrae). Can. J. Zool. 2018, 96, 1385–1394. [CrossRef]

44. Morrison, T.A.; Merkle, J.A.; Hopcraft, J.G.C.; Aikens, E.O.; Beck, J.L.; Boone, R.B.; Courtemanch, A.B.; Dwinnell, S.P.; Fairbanks, W.S.; Griffith, B.; et al. Drivers of site fidelity in ungulates. J. Anim. Ecol. 2021, 90, 955–966. [CrossRef]

45. Marshall, G.; Jonker, L. An introduction to descriptive statistics: A review and practical guide. Radiography 2010, 16, e1–e7. [CrossRef]

46. Anchorena, A. Descripción Gráfica de la Patagonia y Valles Andinos; Compañía Sudamericana de Billetes de Banco: Buenos Aires, Argentina, 1902.

47. Onelli, C. El huemul. Su patria: Su vida. Rev. Jardín Zool. Buenos Aires 1905, 1, 370–374.

48. Bahre, C.J. Destruction of the Natural Vegetation of North-Central Chile; University of California Publications in Geography: Berkeley, CA, USA, 1979; Volume 23, pp. 1–117. ISBN 0-520-09594-4.

49. Saavedra, B.; Simonetti, J.A. Archaeological evidence of Pudu pudu (Cervidae) in central Chile. Z. Saeugetierkunde 1991, 56, 252–253.

50. Ale, A. A social economic formation of hunter-gatherers in the semiarid northern Chile: A revaluation of San Pedro Viejo of Picasca site. Zaranda Ideas 2014, 11, 67–88.
51. Merow, C.; Wilson, A.M.; Jetz, W. Integrating occurrence data and expert maps for improved species range predictions. *Glob. Ecol. Biogeogr.* 2017, 26, 243–258. [CrossRef]

52. Travaini, A.; Zapata, S.C.; Bustamante, J.; Pedrana, J.; Zanón, J.I.; Rodriguez, A. Guanaco abundance and monitoring in Southern Patagonia: Distance sampling reveals substantially greater numbers than previously reported. *Zool. Stud.* 2015, 54, 23. [CrossRef]

53. De Gea, G. *El Ganado Lanar en la Argentina*, 2nd ed.; Universidad Nacional de Rio Cuarto: Rio Cuarto, Argentina, 2007; ISBN 978-950-655-448-1.

54. Ubaldi, J.A.; Angeles, G.R.; Gentili, J.O.; Geraldi, A.M.; Melo, W.D.; Carbone, M.E. *Geotecnologías del sur Argentino. Casos de Estudio*; Departamento de Geografía y Turismo (TIC), Universidad Nacional del Sur: Bahía Blanca, Argentina, 2014.

55. Flueck, W.T. Nutrition as an etiological factor causing diseases in endangered huemul deer. *BMC Res. Notes* 2020, 13, 276. [CrossRef]

56. Merkle, J.A.; Sawyer, H.; Monteith, K.L.; Dwinnell, S.P.; Fralick, G.L.; Kauffman, M.J. Spatial memory shapes migration and its benefits: Evidence from a large herbivore. *Ecol. Lett.* 2019, 22, 1797–1805. [CrossRef]

57. Aikens, E.O.; Kauffman, M.J.; Merkle, J.A.; Dwinnell, S.P.H.; Fralick, G.L.; Monteith, K.L. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecol. Lett.* 2017, 20, 741–750. [CrossRef]

58. Flueck, W.T. The effect of selenium on reproduction of black-tailed deer (*Odocoileus hemionus columbianus*) in Shasta County, California. *Ph.D Thesis, University of California, Davis, CA, USA, 1989.*

59. Kauffman, M.J.; Copeland, H.E.; Berg, J.; Bergen, S.; Cole, E.; Cuzzocreo, M.; Dewey, S.; Fatebert, J.; Gagnon, J.; Gelzer, E.; et al. *Ungulate Migrations of the Western United States;* Report 2020–5101; U.S. Geological Survey Scientific Investigations: Reston, VA, USA, 2020; Volume 1.

60. Gogan, P.J.P.; Klaver, R.W.; Olexa, E.M. Northern Yellowstone Mule Deer Seasonal Movement, Habitat Selection, and Survival Patterns. *West. North Am. Nat.* 2019, 79, 403–427. [CrossRef]

61. Van de Kerk, M.; Larsen, R.T.; Olson, D.D.; Hersey, K.R.; McMillan, B.R. Variation in movement patterns of mule deer: Have we oversimplified migration? *Mov. Ecol.* 2021, 9, 44. [CrossRef] [PubMed]

62. Haller, H. Der Rothirsch im Schweizerischen Nationalpark und dessen Umgebung. Eine alpine Population von *Cervus elaphus* zeitlich und räumlich dokumentiert. *Natl. Forsh. Schweiz* 2002, 91, 1–144.

63. Howe, R.W.; Davis, G.J.; Mosca, V. The demographic significance of ‘sink’ populations. *Biol. Conserv.* 1990, 57, 239–255. [CrossRef]

64. Remes, V.; Braunisch, V.; Bollmann, K.; Graf, R.F.; Hirzel, A.H. Living on the edge. Modelling habitat suitability for species at the edge of their fundamental niche. *Ecol. Model.* 2008, 214, 153–167. [CrossRef]

65. Goss, R.J. *Deer Antlers: Regeneration, Function and Evolution;* Academic Press: New York, NY, USA, 1983.

66. Tonko, J. Kaweskar travel narratives. *Onomazcin* 2008, 18, 11–47.

67. Anonymous. Excursión del gobernador del Chubut. *Caras Carotena* 1904, 7, 58.

68. Moreno, F.P. Apuntes preliminares sobre una excursion a los territorios del Neuquén, Río Negro, Chubut y Santa Cruz. *Rev. Mus. La Plata* 1898, 8, 200–459.

69. Caro, T. *Deer Antlers: Regeneration, Function and Evolution;* Academic Press: New York, NY, USA, 1983.

70. Barberena, R.; Méndez, C.; Mena, F.; Reyes, O. Endangered species, archaeology, and stable isotopes: Huemul (*Hippocamelus bisulcus*) isotopic ecology in central-western Patagonia (South America). *J. Archaeol. Sci.* 2011, 38, 2313–2323. [CrossRef]

71. Curran, S.C. Expanding ecomorphological methods: Geometric morphometric analysis of Cervidae post-crania. *J. Archaeol. Sci.* 2012, 39, 1172–1182. [CrossRef]

72. Curran, S.C. Exploring Eucladoceros ecomorphology using geometric morphometrics. *Anat. Rec.* 2015, 298, 291–313. [CrossRef]

73. Flueck, W.T.; Smith-Flueck, J.M. Ontological comparisons of archaeological skeletons: A case study on Patagonian huemul deer and its implications for conservation. *Anim. Prod. Sci.* 2011, 51, 327–339. [CrossRef]

74. Flueck, W.T. Functional limb anatomy in a refugee species: The endangered Patagonian huemul deer (*Hippocamelus bisulcus*). *Anat. Histol. Embryol.* 2021, 50, 411–416. [CrossRef]

75. Barberena, R.; Méndez, C.; Mena, F.; Reyes, O. Endangered species, archaeology, and stable isotopes: Huemul (*Hippocamelus bisulcus*) isotopic ecology in central-western Patagonia (South America). *J. Archaeol. Sci.* 2011, 38, 2313–2323. [CrossRef]

76. Caro, T. The adaptive significance of coloration in mammals. *BioScience* 2005, 55, 125–136. [CrossRef]

77. Webb, S.D. Evolutionary history of New World Cervidae. *In Antelopes, Deer, and Relatives;* Vrba, E.S., Schaller, G.B., Eds.; Yale University Press: New York, NY, USA, 2000; pp. 38–64.

78. Prichard, H.H. Field notes upon some of the larger mammals of Patagonia made between September 1900 and June 1901. *Proc. Zool. Soc. Lond.* 1902, 1, 272–277.

79. Gaià, A.G. Huemul, inofensivo venado de las soledades cordilleranas de la Patagonia. *Ciencia y Cultura* 1936, 6, 99–101.

80. Grzymek, B. *Grzimeks Tierleben: Enzyklopädie des Tierreichs—Säugetiere 3;* Neue Schweizer Bibliothek: Zurich, Switzerland, 1973.

81. Bürger, O. *Aus der Wildnis des Huemul. Erlebnisse und Abenteuer unter den Kolonisten und Indianern Chiles;* Verlag Deutsche Buchwerstätten: Dresden, Germany, 1924.

82. Goni, R.A.; Belardi, J.B.; Re, A.; Nuevo Delaunay, A.; Molinari, R.L.; Ferraro, L. Los grabados de la meseta del lago Strobel (Patagonia argentina) desde una perspectiva regional. *In Actas del Primer Simposio Nacional de Arte Rupestre*; Cusco Nov. 2004; Instituto Francais d’Etudes Andines: Lima, Peru, 2007; pp. 427–438.
84. Risenhoover, K.L.; Bailey, J.A.; Wakelyn, L.A. Assessing the Rocky Mountain Bighorn Sheep Management Problem. *Wildl. Soc. Bull.* **1988**, *16*, 346–352.

85. Nagaike, T. Bark Stripping by Deer Was More Intensive on New Recruits than on Advanced Regenerants in a Subalpine Forest. *Forests* **2020**, *11*, 490. [CrossRef]

86. Diaz, P.; Marqués, B.I.; Vila, A.R. Seasonal habitat use and selection of the endangered huemul deer (*Hippocamelus bisulcus*) in Patagonian Andes. *Mammal. Res.* **2013**, *77*, 371–380. [CrossRef]

87. Gill, R.; Sauceco, C.; Aldridge, D.; Morgan, G. Ranging behavior of huemul in relation to habitat and landscape. *J. Zool.* **2008**, *274*, 254–260. [CrossRef]

88. Guineo, O.; Guineo Garay, R.; Garay, G. Conociendo al Huemul de Torres del Paine; La Prensa Austral: Punta Arenas, Chile, 2008.

89. Garay, G.; Ortega, I.M.; Guineo, O. Social ecology of the huemul at Torres Del Paine National Park, Chile. *Anal. Inst. Patagon.* **2014**, *44*, 25–38. [CrossRef]

90. Webb, S.L.; Dzialak, M.R.; Houchen, D.; Kosiuc, K.L.; Winstead, J.B. Spatial ecology of female Mule deer in an area proposed for wind energy development. *West. N. Am. Nat.* **2013**, *73*, 347–356. [CrossRef]

91. Rau, J.A. Crecimiento poblacional de huemules del sur nativos y reintroducidos en la zona austral de Chile. In *4ta Reunión Chileno-Argentina sobre Estrategias de Conservación del Huemul*; Acosta-Jamett, G., Ed.; CONAF and CODEFF: Santiago, Chile, 2003; pp. 43–45.

92. Flueck, W.T.; Smith-Flueck, J.M. Troubling disease syndrome in endangered live Patagonian huemul deer (*Hippocamelus bisulcus*) from the Protected Park Shoonem: Unusually high prevalence of osteopathy. *BMC Res. Notes* **2017**, *10*, 739. [CrossRef] [PubMed]

93. Clapperton, C.M. The glaciation of the Andes. *Quat. Sci. Rev.* **1983**, *2*, 83–155. [CrossRef]

94. Flueck, W.T.; Smith-Flueck, J.M. Huemul heresies: Beliefs in search of supporting data. 2. Biological and ecological considerations. *Anim. Prod. Sci.* **2012**, *52*, 694–706. [CrossRef]

95. Flueck, W.T. Elusive cranial lesions severely afflicting young endangered Patagonian huemul deer. *BMC Res. Notes* **2018**, *11*, 638. [CrossRef]

96. Smith-Flueck, J.M.; Barrio, J.; Ferreyra, N.; Nuñez, A.; Tomas, N.; Guzman, J.; Flueck, W.T.; Hinojosa, A.; Vidal, F.; Garay, G.; et al. Advances in ecology and conservation of Hippocamelus species in South America. *Anim. Prod. Sci.* **2011**, *51*, 378–383. [CrossRef]

97. Franklin, W.L. Biology, ecology, and relationship to man of the South American camelids. In *The Biology of the Camelids*; Mares, M.A., Genoways, H.H., Eds.; Pymatuning Laboratory of Ecology, University Pittsburgh: Linesville, PA, USA, 1982; Volume 6, pp. 457–489.

98. Mueller, T.; Olson, K.A.; Dressler, G.; Leimgruber, P.; Fuller, T.K.; Nicolson, C.; Novaro, A.J.; Bolgeri, M.J.; Wattles, D.; DeStefano, S.; et al. How landscape dynamics link individual- to population-level movement patterns: A multispecies comparison of ungulate relocation data. *Glob. Ecol. Biogeogr.* **2011**, *20*, 683–694. [CrossRef]

99. Gelin, M.L.; Branch, L.C.; Thornton, D.H.; Novaro, A.J.; Gould, M.J.; Caragiulo, A. Response of pumas (*Puma concolor*) to migration of their primary prey in Patagonia. *PLoS ONE* **2017**, *12*, e0188877. [CrossRef]

100. Franklin, W.L.; Bass, F.; Bonacic, C.F.; Cunazza, C.; Soto, N. Management of Patagonian guanaco in the grazing agroecosystem of southern Chile. *Wildl. Soc. Bull.* **1997**, *25*, 65–73.

101. Bonavia, D. The South American Camelids: *An Expanded and Corrected Edition*; Monograph 64; Cotsen Institute of Archaeology Press, UCLA: Los Angeles, CA, USA, 2009; Available online: https://escholarship.org/uc/item/7xs9z2zs (accessed on 4 April 2022).

102. Schroeder, N.M.; Matteucci, S.D.; Moreno, P.G.; Gregorio, P.; Ovejero, R.; Taraborelli, P.; Carmanchahi, P.D. Spatial and Seasonal Dynamic of Abundance and Distribution of Guanaco and Livestock: Insights from Using Density Surface and Null Models. *PLoS ONE* **2014**, *9*, e85960.

103. Ladio, A.H.; Lozada, M. Summer cattle transhumance and wild edible plant gathering in a Mapuche community of northwestern Patagonia. *Hum. Ecol.* **2004**, *32*, 225–240. [CrossRef]

104. Poole, K.G.; Mowat, G. Winter habitat relationships of deer and elk in the temperate interior mountains of British Columbia. *Wildl. Soc. Bull.* **2005**, *33*, 1288–1302. [CrossRef]

105. Myburgh, J.; McGowan, K.; Davis, A. Veterinary Geology. In *Practical Applications of Medical Geology*; Siegel, M., Selinus, O., Finkelman, R., Eds.; Springer: Cham, Switzerland, 2021.

106. Flueck, W.T. Consideraciones acerca de la calidad nutritiva de habitat, hábitat óptimo, y evaluación de hábitat para huemul. In *4ta Reunión Chileno-Argentina Sobre Estrategias de Conservación del Huemul*; Acosta-Jamett, G., Ed.; CONAF and CODEFF: Santiago, Chile, 2003; pp. 30–34.

107. Landete-Castillejos, T.; Molina-Quilez, I.; Estevez, J.A.; Ceacero, F.; Garcia, A.J.; Gallego, L. Alternative hypothesis for the origin of osteoporosis: The role of Mn. *Front. Biosci. Elite Ed.* **2012**, *4*, 1385–1390. [CrossRef]

108. Gambín, P.; Serrano, M.P.; Gallego, L.; García, A.; Cappelli, J.; Ceacero, F.; Landete-Castillejos, T. Does Cu supplementation affect the mechanical and structural properties and mineral content of red deer antler bone tissue? *Animal* **2017**, *11*, 1312–1320. [CrossRef]

109. Bartlam-Brooks, H.L.; Beck, P.S.; Bohrer, G.; Harris, S. In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. *J. Geophys. Res. Biogeosci.* **2013**, *118*, 1427–1437. [CrossRef]

110. Teitelbaum, C.S.; Fagan, W.F.; Fleming, C.H.; Dressler, G.; Calabrese, J.M.; Leimgruber, P.; Mueller, T. How far to go? Determinants of migration distance in land mammals. *Ecol. Lett.* **2015**, *18*, 545–552. [CrossRef]
111. Monsarrat, S.; Jarvie, S.; Svenning, J.C. Anthropocene refugia: Integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world. *Philos. Trans. R. Soc. B* 2019, 374, 20190219. [CrossRef] [PubMed] [CrossRef]

112. Soga, M.; Gaston, K.J. Shifting baseline syndrome: Causes, consequences and implications. *Front. Ecol. Environ.* 2018, 16, 222–230. [CrossRef]

113. Armesto, J.J.; Manuschevich, D.; Mora, A.; Smith-Ramireza, C.; Rozzi, R.; Abarzú, A.; Peters, W.; Roettger, C.; et al. Mapping out a future for ungulate migrations. Limited mapped migrations hamper conservation. *Science* 2021, 372, 566–569. [CrossRef]

114. Aschero, C.A. Las escenas de caza en Cueva de las Manos: Una perspectiva regional (Santa Cruz, Argentina). In *Pre-Acts*; Talleres Gròs de Seis Ciervos Prehistòrics de Seis Ciervos Prehistòrics, 2010.

115. Cromsigt, J.P.G.M.; Kerley, G.I.H.; Kowalczyk, R. The difficulty of using species distribution modelling for the conservation of refugee species—The example of European bison. *Div. Distr.* 2012, 18, 1253–1257. [CrossRef]

116. Lea, J.M.D.; Kerley, G.I.H.; Hrabar, H.; Barry, T.J.; Shultz, S. Recognition and management of ecological refugees: A case study of the Cape mountain zebra. *Biol. Conserv.* 2016, 203, 207–215. [CrossRef]

117. Alpers, M.J.; Cagnacci, F.; Chamaille-Jammes, S.; Hebblewhite, M.; Hopcroft, J.G.C.; Merkle, J.A.; Mueller, T.; Mysterud, A.; Peters, W.; Roettger, C.; et al. Mapping out a future for ungulate migrations. Limited mapped migrations hamper conservation. *Science* 2021, 372, 566–569. [CrossRef]

118. Doughty, C.E.; Roman, J.; Faubry, S.; Wolf, A.; Haque, A.; Bakker, E.S.; Malhi, Y.; Dunning, J.B.; Svenning, J.C. Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. USA* 2018, 113, 868–873. [CrossRef]

119. Monteith, K.L.; Bleich, V.C.; Stephenson, T.R.; Pierce, B.M.; Conner, M.M.; Kie, J.G.; Bowyer, R.T. Life-history characteristics of mule deer: Effects of nutrition in a variable environment. *Wildl. Monogr.* 2014, 186, 1–62. [CrossRef]

120. Allred, W.J. Re-establishment of seasonal elk migration through transplanting. *N. Am. Wildl. Conf.* 1950, 15, 597–611.

121. Stiwe, M.; Nievergelt, B. Recovery of Alpine ibex from near extinction: The result of effective protection, captive breeding, and reintroductions. *Appl. Anim. Behav. Sci.* 1991, 29, 379–387. [CrossRef]

122. Adams, A.W. Migration. In *Elk of North America. Ecology and Management*; Thomas, J.W., Toweill, D.E., Eds.; Stackpole Books: Harrisburg, PA, USA, 1982; pp. 301–321.

123. Agassiz, L. The 1871–1872 Hassler expedition. In *Museum of Comparative Zoology; Occurrence Dataset*, Version 162.229; Morris, P.J., Ed.; Harvard University: Cambridge, MA, USA, 1872.

124. Brooks, T.M.; Pimm, S.L.; Akçakaya, H.R.; Buchanan, G.M.; Butchhart, S.H.M.; Foden, W.; Hilton-Taylor, C.; Hoffmann, M.; Jenkins, C.N.; Joppa, L.; et al. Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends Ecol. Evol.* 2019, 24, 977–986. [CrossRef]

125. Brown, C.G. Movement and migration patterns of mule deer in southeastern Idaho. *J. Wildl. Manag.* 1992, 56, 246–253. [CrossRef]

126. Stiwe, M.; Nievergelt, B. Recovery of Alpine ibex from near extinction: The result of effective protection, captive breeding, and reintroductions. *Appl. Anim. Behav. Sci.* 1991, 29, 379–387. [CrossRef]

127. Arntzen, J.C. Anthropocene refugia: Integrating history and predictive modelling to assess the space available for biodiversity in a human-dominated world. *Philos. Trans. R. Soc. B* 2019, 374, 20190219. [CrossRef] [PubMed] [CrossRef]

128. Behm, E. Reise im südwestlichen Patagonien von J.T. Rogers und E. Ibar, 1877, nebst den Tagebüchern von A. de Viedma 1782 und J.H. Gardiner 1867. *Petermanns Geogr. Mitteilungen* 1880, 26, 47–64.

129. Battin, J. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Cons. Biol.* 2004, 18, 1482–1491. [CrossRef]

130. Battin, J. When good animals love bad habitats: Ecological traps and the conservation of animal populations. *Cons. Biol.* 2004, 18, 1482–1491. [CrossRef]

131. Andersen, R. Habitat deterioration and the migratory behavior of moose (*Alces alces* L.) in Norway. *J. Appl. Ecol.* 1991, 28, 102–108. [CrossRef]

132. Aschero, C.A. Las escenas de caza en Cueva de las Manos: Una perspectiva regional (Santa Cruz, Argentina). In *Pre-Acts*; Talleres Gròs de Seis Ciervos Prehistòrics, 2010.

133. Baumann, M.; Babota, C.; Schibler, N. Native or naturalized? Validating alpine chamois habitat models with archaeozoological data. *Ecol. Appl.* 2005, 15, 1096–1110. [CrossRef]

134. Behn, E. Reise im südwestlichen Patagonien von J.T. Rogers und E. Ibar, 1877, nebst den Tagebüchern von A. de Viedma 1782 und J.H. Gardiner 1867. *Petermanns Geogr. Mitteilungen* 1880, 26, 47–64.

135. Berger, J.; Wangchuk, T.; Briceno, C.; Vila, A.; Lambert, J.E. Disassembled Food Webs and Messy Projections: Modern Ungulate Communities in the Face of Unabating Human Population Growth. *Front. Ecol. Evol.* 2020, 8, 128. [CrossRef]
140. Berger, J.; Steven, L.; Cain, S.L.; Berger, K.M. Connecting the dots: An invariant migration corridor links the Holocene to the present. *Biol. Lett.* **2006**, *2*, 528–531. [CrossRef]
141. Brandborg, S.M. *Life History and Management of the Mountain Goat in Idaho*; Wildlife Bulletin No. 2; Department of Fish and Game: Boise, ID, USA, 1955; 142p.
142. Bubenik, G.A.; Bubenik, A.B. *Horns, Pronghorns, and Antlers*; Springer: New York, NY, USA, 1990.
143. Burmeister, C.V. *Memoria Sobre el Territorio de Santa Cruz*; Imprenta La Nación, Ministerio de Agricultura de la República Argentina: Buenos Aires, Argentina, 1901.
144. Burmeister, H. The huemul. *Nature* **1873**, *9*, 82. [CrossRef]
145. Burmeister, C.V. Nuevos datos sobre el territorio Patagónico de Santa Cruz. *Rev. Museo Plata* **1893**, *4*, 227–256, 338–352.
146. Cabrera, A.; Yepes, J. *Mamíferos Sudamericanos*, 1st ed.; Compañía Argentina de Editores: Buenos Aires, Argentina, 1940; 370p.
147. Carballo Marina, F.; Manzi, L.M.; Campan, P.A.; Belardi, J.B.; Tiberi, P.; Belardi, J.B.; Manero, A.; Saenz, J.L. Distribución de cuencas y aporte a la preservación del patrimonio. In *Arqueología del Extremo sur del Continente Americano*; Borrero, L.A., Franco, N., Eds.; Editorial Dunken: Buenos Aires, Argentina, 2008; pp. 175–225.
148. Cardich, A.; Miotti, L. *Recursos Faunísticos en la Economía de los Cazadores-Recolectores de Los Toldos (Provincia de Santa Cruz)*. *Relaciones Soc. Argent. Antropol.* **1993**, *16*, 269–273.
149. Castellanos, A. Paleontología estratigráfica de los sedimentos neógenos de la Provincia de Córdoba. *Publ Inst. Fisiogr. Geol. 1944*, 23, 1–47.
150. Church, G.E. A traveller in Patagonia. *Nature* **1903**, *67*, 321–322. [CrossRef]
151. Clapperton, C.M. *Nature of environmental changes in South America at the Last Glacial Maximum*; *Palaeoecogr. Paleoclimatol. Palaeocool.* **1993**, *101*, 189–208. [CrossRef]
152. Claraz, M.G. Sur l’Equus bisulcus, de Molina. *Revue et Magasin de Zoologie Pure et Apliquee* **1864**, 241–248.
153. Coltori, M.; Abbazzi, L.; Ferretti, M.P.; Manzi, P.A.; Belardi, J.B.; Tiberi, P.; Manero, A.; Saenz, J.L. Distribución de cuencas y aporte a la preservación del patrimonio. In *Arqueología del Extremo sur del Continente Americano*; Borrero, L.A., Franco, N., Eds.; Editorial Dunken: Buenos Aires, Argentina, 2008; pp. 175–225.
154. Cardich, A.; Miotti, L. Recursos Faunísticos en la Economía de los Cazadores-Recolectores de Los Toldos (Provincia de Santa Cruz). *Relaciones Soc. Argent. Antropol.* **1993**, *16*, 269–273.
155. Castellanos, A. Paleontología estratigráfica de los sedimentos neógenos de la Provincia de Córdoba. *Publ Inst. Fisiogr. Geol. 1944*, 23, 1–47.
156. Cruz, I.; Munoz, A.S.; Caracotche, M. A huemul (*Hippocamelus antisensis*) y su rol en la Economía Andina. *Anales del Museo Nacional Buenos Aires* **1983**, *142*, 1–42.
157. da Silva, F.M.; da Silva Alves, R.; Franca Barreto, A.M.; Bezerra de S., G.M. Antecedentes sobre la historia natural de la taruca (*Hippocamelus antisensis*) y su rol en la economía Andina. *Anales del Museo de la Plata* **1993**, *16*, 189–208. [CrossRef]
158. da Silva, F.M.; da Silva Alves, R.; Franca Barreto, A.M.; Bezerra de S., G.M. Antecedentes sobre la historia natural de la taruca (*Hippocamelus antisensis*) y su rol en la economía Andina. *Anales del Museo de la Plata* **1993**, *16*, 189–208. [CrossRef]
159. Dawilov. *Coihue* *Magallania* **2007**, *27*, 35, 44–55.
160. de la Cruz, L. *Descripción de Los Territorios Patagónicos*; Ministerio de Agricultura de la República Argentina: Buenos Aires, Argentina, 1941.
161. De Agostini, A.M. *Antecedentes sobre la historia natural de la taruca (*Hippocamelus antisensis*) y su rol en la economía Andina. *Anales del Museo Nacional Buenos Aires* **1983**, *142*, 1–42.
162. De Agostini, A.M. *Antecedentes sobre la historia natural de la taruca (*Hippocamelus antisensis*) y su rol en la economía Andina. *Anales del Museo Nacional Buenos Aires* **1983**, *142*, 1–42.
163. Diaz, N.I. *Hippocamelus bisulcus* in Patagonia. *Z. Säugetierkunde* **1993**, *58*, 344–351.
164. Diaz, N.I. *Hippocamelus bisulcus* Molina, 1782: A historical perspective. In *The Patagonian Huemul, a Mysterious Deer on the Brink of Extinction*; Diaz, N.I., Smith-Flueck, J., Eds.; L.O.L.A.: Buenos Aires, Argentina, 2000; pp. 1–31.
165. Diaz, N.I.; Prieto, A.; Bahamonde, G. Guanacos tayacos: El lomo con la cordillera del oeste. *Estudios Geologicos* **2006**, *16*, 55–66.
166. Dabbene, R. La huemul de Bolivia y Perú, *Odocoileus* (*Hippocamelus*) antisensis (Orb.) y del avestruz petiso, *Rhea darwini* Gould en el N.W. de la República Argentina. *Aantes del Museo Nacional Buenos Aires 1911*, 14, 293–307.
167. Dawilov. *Coltura*; Gmo. van Woerden & Cia: Buenos Aires, Argentina, 1926; 103p.
168. de la Cruz, L. Descripción de la naturaleza de los terrenos que se comprenden en los Andes, poseídos por los Peguences; y los demás espacios hasta el río Chadileubu. In *Coleción de Obras y Documentos Relativos a la Historia Antigua y Moderna de las Provincias del Río de la Plata*; de Angelis, P., Ed.; Imprenta del Estado: Buenos Aires, Argentina, 1836; pp. 1–67.
169. De Agostini, A.M. *Andes Patagónicos: Viajes de Exploración a la Cordillera Patagónica*, 1era Versión; Imprenta Gotelli: Buenos Aires, Argentina, 1941.
170. De Agostini, A.M. *Andes Patagónicos: Viajes de Exploración a la Cordillera Patagónica Austral*; Talleres Gráficos Guillermo Kraft Ltda: Buenos Aires, Argentina, 1945; Volume 1, pp. 1–409.
171. Diaz, N.I. *Andes Patagónicos: Viajes de Exploración a la Cordillera Patagónica Austral*; Talleres Gráficos Guillermo Kraft Ltda: Buenos Aires, Argentina, 1945; Volume 1, pp. 1–409.
172. Diaz, N.I. *Antecedentes sobre la historia natural de la taruca (*Hippocamelus antisensis*) y su rol en la economia Andina. *Chungara* **1995**, 27, 45–55.
173. Diaz, N.I. Changes in the range distribution of *Hippocamelus bisulcus* in Patagonia. *Z. Säugetierkunde* **1993**, *58*, 344–351.
174. Diaz, N.I. *Hippocamelus bisulcus* Molina, 1782: A historical perspective. In *The Patagonian Huemul, a Mysterious Deer on the Brink of Extinction*; Diaz, N.I., Smith-Flueck, J., Eds.; L.O.L.A.: Buenos Aires, Argentina, 2000; pp. 1–31.
175. Diaz, N.I.; Prieto, A.; Bahamonde, G. Guanacos tayacos, huemules confiados: El limite occidental de los cazadores terrestres australes. *Magallania* **2007**, *35*, 133–138. [CrossRef]
176. Eastman, C.R. Beginnings of American natural history. *Amer. Museum J.* **1915**, *15*, 349–355.
177. Eisenberg, J.F. The contemporary Cervidae of Central and South America. In *Antelopes, Deer, and Relatives*; Vrba, E.S., Schaller, G.B., Eds.; Yale University Press: New York, NY, USA, 2000; pp. 189–202.
178. Falkner, T. A Description of Patagonia and the adjoining parts of South America: Containing an account of the soil, produce, the religion, government, and some particulars relating to Falkland islands; Hereford: London, UK, 1774; 144p.
179. Fernandez, P.M.; Cruz, I.; Bautista Belardi, J.; de Nigris, M.; Muñoz, S. La explotación del huemul (*Hippocamelus bisulcus*, Molina 1782) en la Patagonia a lo largo del holoceno. *Magallania* **2016**, *44*, 187–209. [CrossRef]
180. Fernández, O.A.; Buoso, C.A. Arid and semi-arid rangelands: Two thirds of Argentina. In *Proceedings from an International Workshop in Iceland*; Arnalds, O., Archer, S., Eds.; Rala Report no. 200; Agricultural Research Institute: Reykjavik, Iceland, 1997; pp. 41–60.
172. Fielder, P.C. Implications of selenium levels in Washington mountain goats, mule deer, and Rocky Mountain elk. *Northwest Sci.* 1986, 60, 15–20.

173. Flint, R.F.; Fidalgo, F. Glacial Drift in the Eastern Argentine Andes between Latitude 41°10' S. and Latitude 43°10' S. *Bull. Geol. Soc. America* 1969, 80, 1043–1052. [CrossRef]

174. Flueck, W.T. Spatio-temporal movements among red deer males, *Cervus elaphus*, introduced to Patagonia. In *XXVIth Congress of the International Union of Game Biologists; Pohlmeyer, K., Ed.; Hannover DSV-Verlag: Hamburg, Germany*, 2005; pp. 330–332.

175. Flueck, W.T. Exotic deer in southern Latin America: What do we know about impacts on native deer and on ecosystems? *Biol. Invasions* 2010, 12, 1909–1922. [CrossRef]

176. Flueck, W.T. Osteopathology and selenium deficiency co-occurring in a population of endangered Patagonian huemul (*Hippocamelus bisulcus*). *BMC Res. Notes* 2015, 8, 330. [CrossRef] [PubMed]

177. Flueck, W.T.; Smith-Flueck, J.M. Uber das in Argentinien angesiedelte Rotwild (*Cervus elaphus L.*, 1758): Verbreitung und Tendenzen. *Zeits. Jagdwiss.* 1993, 39, 153–160. [CrossRef]

178. Flueck, W.T.; Smith-Flueck, J.M. Predicaments of endangered huemul deer, *Hippocamelus bisulcus*, in Argentina: A review. *Europ. J. Wildl. Res.* 2006, 52, 69–80. [CrossRef]

179. Flueck, W.T.; Smith-Flueck, J.M. Huemul heresies: Beliefs in search of supporting data. 1. Historical and zooarchaeological considerations. *Anm. Prod. Sci.* 2012, 52, 685–693. [CrossRef]

180. Flueck, W.T.; Smith-Flueck, J.M. Radio marking the first group of endangered Patagonian huemul deer in Argentina. *J. Neotrop. Mammal.* 2018, 25, 461–465. [CrossRef]

181. Flueck, W.T.; Smith-Flueck, J.M.; Mincher, B.J.; Winkel, L.H.E. Soil selenium levels corroborate direct evidence of selenium deficiency in endangered Patagonian huemul deer (*Hippocamelus bisulcus*). In *Proceedings of the 8th International Deer Biology Congress; Ma, J., Zhang, M., Halbrook, R., Liu, B., Zhang, W., Eds.; Northeast Forestry University: Harbin, China*, 2014; pp. 52–53.

182. Frailey, D.; Campbell, K.E.; Wolff, R.G. Additions to the knowledge of *Hippocamelus, Ctenomys, and Myocastor* from the middle Pleistocene of the Tarija basin, Bolivia. *Occas. Papers Museum Nat. Hist. Univ. Kansas* 1980, 85, 1–14.

183. Flueck, W.T. Osteopathology and selenium deficiency co-occurring in a population of endangered Patagonian huemul (*Hippocamelus bisulcus*) diet during rainy season in Huascaran national park, Peru. In *Advances in Deer Biology; Bartos, L., Dusek, A., Kotrba, R., Bartosova, J., Eds.; Research Institute of Animal Production: Praha, Czech Republic*, 2006; p. 216.

184. Geist, V. *Deer of the World; Stackpole Books: Pennsylvania, PA, USA*, 1998; 421p.

185. Giguoux, E.E. El huemul. *Rev. Chilena Hist. Nat.* 1929, 23, 573–582.

186. Gonzalez, V.; Tapia, V. Manual bovino de carne. *Boletín INIA* 2017, 4, 1–73.

187. Goni, R.A. Arqueologia de momentos tardios en el Parque Nacional Perito Moreno (Santa Cruz, Argentina). In *Precirculados del IX Congreso Nacional de Arqueologia Argentina; Voss, W., Ed.; Imprenta de la Armada: Valparaiso, Chile*, 1973; pp. 1–164.

188. Gunther, A. Comments about Slater and *Cervus chilensis*. In *Proceedings of the Scientific Meetings of the Zoological Society of London; Messmer, M., Green, Reader and Dyer: London, UK*, 1875; pp. 44–46.

189. Hershkovitz, P. The recent mammals of the Neotropical region: A zoogeographic and ecological review. In *Evolution, Mammals, and Southern Continents; Keast, A., Erk, F.C., Glass, B., Eds.; State University New York Press: New York, NY, USA*, 1972; pp. 311–431.

190. Hershkovitz, P. The recent mammals of the Neotropical region: A zoogeographic and ecological review. *Quart. Rev. Biol.* 1969, 44, 1–70. [CrossRef]

191. Hofstetter, R. La faune pleistocène de Tarija (Bolivie). Note preliminaire. *Bulletin Museum National d’Histoire Naturelle* 1963, 35, 194–203.

192. Honey, R.F.; Frost, N.M. A Wyoming bighorn sheep study. *Wyoming Game Fish Depart. Bull.* 1942, 1, 1–127.

193. Horkheimer, H. *Vater und Sohn: Die Hesperian Tierwelt. Proceeding von dem 35. naturwissenschaftlichen Kongres; Pohlmeyer, K., Ed.; Hannover DSV-Verlag: Hamburg, Germany*, 1960; 314p.

194. Housse, P. *Animales Salvajes de Chile en su Clasificacion Moderna; Ediciones de la Universidad de Chile: Santiago, Chile*, 1953; 330p. [CrossRef] [PubMed]

195. Hügler, C.; Faure, M. The Cervidae (Mammalia, Artiodactyla) of the Upper Pleistocene/Lower Holocene deposits of the Serra da Capivara National Park Region (Piauí, Brazil). *Geobios* 2009, 42, 169–195. [CrossRef]

196. Günther, A. Comments about Slater and *Cervus chilensis*. In *Proceedings of the Scientific Meetings of the Zoological Society of London; Messrs. Longmans, Green, Reader and Dyer: London, UK*, 1875; pp. 44–46.

197. Hatcher, J.B. *Reports of the Princeton University Expeditions to Patagonia, 1886–1889. Vol. I: Narrative of the Expeditions. Geography of Southern Patagonia; E. Schweizerbart’sche Verlagshandlung: Stuttgart, Germany*, 1903; 314p.

198. Hauman, L. Arqueología de la Patagonia. *Boletín de la Sociedad Arqueológica de la Patagonia* 1969, 1, 1043–1052. [CrossRef]

199. Hesse, A. *Animalieu: A Classification of Animals and Their Costumes; Ediciones de la Universidad de Chile: Santiago, Chile*, 1953; 189p.

200. Ibar Bruce, J. *Aisen, Hombres y Naturaleza; Imprenta de la Armada: Valparaiso, Chile*, 1973; pp. 1–164.

201. Iglesias, R.E. El huemul. *Montañar* 1965, 7, 26–28.

202. Jakopak, R.P.; LaSharr, T.N.; Dwinnell, S.P.H.; Fralick, G.L.; Monteith, K.L. Rapid acquisition of memory in a complex landscape by a mule deer. *Ecology* 2019, 100, e02854. [CrossRef]

203. Johnson, L. Informe sobre una prospecció arqueològica en magallanes. *Ans. Inst. Pat. Punta Arenas* 1976, 7, 87–94.

204. Kolliker Frers, A. Das Waidwerk und die autochthonen Cerviden in Argentinien. In *Parque Diana; Vogel, C.A., Ed.; Stefan Schwarz Verlag: München, Germany*, 1969; pp. 25–31.
205. Koprowski, J.L.; Krausman, P.R. International Wildlife Management: Conservation Challenges in a Changing World; Johns Hopkins University Press: Baltimore, MD, USA, 2019; 248p.

206. Krieg, H. Biologische Reisestudien in Südamerika. V. Die chilenischen Hirsche. Zeits. Morphol. Ökol. Tiere 1925, 4, 585–597. [CrossRef]

207. Krieg, H. Als Zoologie in Steppen und Wäldern Patagoniens; Bayerischer Landwirtschaftsverlag: Muenchen, Germany, 1940; 197p.

208. Lacroix, F. Historia de la Steppe, Tierra de Fuego, e Islas Malvinas; Imprenta del Liberal Barcelones: Barcelona, Spain, 1841.

209. Laliberte, A.S.; Ripple, W.J. Range contractions of North American carnivores and ungulates. BioScience 2004, 54, 123–138. [CrossRef]

210. Laming-Emperaire, A.; Lavallée, D.; Humbert, R. Le site de Marazzi en Terre de Feu. Objets et Mondes 1972, 12, 225–244.

211. Latcham, R.E. Expedicion científica Macqueen al Aysen. Boletín del Museo Nacional 1935, 14, 7–31.

212. Leopold, A.S.; Cain, S.A.; Cottam, C.; Gabrielson, I.N.; Kimball, T.L. Wildlife Management in the National Parks. Am. For. 1963, 4, 32–35, 61–63.

213. Liebermann, J. Sobre la historia natural del huemul. Anal. Acad. Argent. Geogr. 1962, 6, 157–168.

214. Lingle, S.; Wilson, W.F. Detection and avoidance of predators in white-tailed deer (Odocoileus virginianus) and mule deer (O. hemionus). Ethology 2001, 107, 125–147. [CrossRef]

215. Lista, R. La Tierra del Fuego y sus habitantes. Boletin del Instituto Geografico Argentino 1922, 40, 117.

216. Lydekker, R. The Deer of all Lands: A History of the Family Cervidae, Living and Extinct; R. Ward: London, UK, 1898; pp. 1–329.

217. Lyman, R.L. Paleoecology in the service of conservation biology. Evol. Anthropol. 2006, 15, 11–19. [CrossRef]

218. Lyons, G.A.; Giannakopoulou, A.; Lillis, T.; van der Geer, A.A.E. Paradise lost: Evidence for a devastating metabolic bone disease in an insular Pleistocene deer. Intern. J. Paleopathol. 2019, 24, 213–226. [CrossRef] [PubMed]

219. MacDouall, J. Narratives of a Voyage to Patagonia and Terra del Fuego; Johns Hopkins; Technical Publication No. 10; The Colorado Game and Fish Department: Denver, CO, USA, 1962; 49p.

220. Makers, R.N. A year in Patagonia. J. Royal Geogr. Soc. London 1871, 41, 59–77. [CrossRef]

221. Magalhães, R.M.; Mello, M.G.; Bergqvist, L.P. Os cervidos pleistocenicos da regiao nordeste Brasileira. Boletin del Museo Nacional 1984, 14, 225–244.

222. Magalhães, R.M.; Mello, M.G.; Bergqvist, L.P. Os cervidos pleistocenicos da regiao nordeste Brasileira. Anais da Academia Brasileira de Ciencias 1992, 64, 149–154.

223. Magné de la Croix, P. El huemul. Caras y Cariates 1937, 40, 117.

224. Mansur, M.E.; Piquet, P. Evol. Anthropol. 217. Lyman, R.L. Paleozoology in the service of conservation biology. 2008, 15, 11–19. [CrossRef]

225. Mansur, M.E.; Piquet, P. Evol. Anthropol. 217. Lyman, R.L. Paleozoology in the service of conservation biology. 2008, 15, 11–19. [CrossRef]

226. Markgraf, V.; Kenny, R. Character of rapid vegetation and climate change during the late-Glacial in southernmost South America. In Past and Future Rapid Environmental Changes: Spatial and Evolutionary Responses to terrestrial Biota; Huntley, B., Ed.; Springer: Berlin, Germany, 1997; pp. 81–90.

227. Marshall, L.G. Land Mammals and the Great American Interchange. Am. Sci. 1988, 76, 380–388.

228. Massara Paletto, V.; Buono, G. Métodos de Evaluación de Pastizales en Patagonia Sur; Centro Regional Patagonia, Ediciones INTA: Buenos Aires, Argentina, 2020; 288p.

229. Massana-Donoso, M. Los paraderos tehuelches y proto-tehuelches en la costa del Estrecho de Magallanes. Anales del Instituto de la Patagonia 1994, 15, 27–42.

230. McClure, M.F.; Bissonnette, J.A.; Conover, M.R. Migratory strategies, fawn recruitment, and winter habitat use by urban and rural mule deer (Odocoileus hemionus). Eur. J. Wildl. Res. 2005, 51, 170–177. [CrossRef]

231. Miller, S.; Rottman, J.; Taber, R.D. Dwinding and endangered ungulates of Chile: Vicugna, lama, Hippocamelus, and Pudu. Trans. N. Am. Wildl. Natural Res. Conf. 1973, 38, 55–67.

232. Mincher, B.J.; Miconcynski, J.; Hnilicka, P.; Ball, R.D.; Houghton, T.X. Some aspects of geophagia in Wyoming big-horn sheep (Ovis canadensis). Eur. J. Wildl. Res. 2008, 54, 192–198. [CrossRef]

233. Molina, J.I. The Geographical, Natural, and Civil History of Chili; Longman, Hurst, Rees, and Orme: London, UK, 1809; Volume 1.

234. Moreno F.P. Explorations in Patagonia. Anais da Academia Brasileira de Ciencias 1922, 64, 149–154.

235. Moreno, P.I.; Villagran, C.; Marquet, P.A.; Marshall, L.G. Quaternary paleobiogeography of northern and central Chile. Rev. Chilena Hist. Nat. 1994, 67, 487–502.

236. Moser, C.A. The Bighorn Sheep of Colorado: A Review of Colorado’s Bighorn Sheep Studies; Technical Publication No. 10; The Colorado Game and Fish Department: Denver, CO, USA, 1962; 49p.

237. Mysterud, A.; Loe, L.E.; Zimmermann, B.; Bischof, R.; Veiberg, V.; Meisingset, E. Partial migration in expanding red deer populations at northern latitudes—A role for density dependence? Oikos 2011, 120, 1817–1825. [CrossRef]

238. Nelson, M.E.; Mech, L.D. Twenty-year home-range dynamics of a white-tailed deer matriline. Can. J. Zool. 1999, 77, 1128–1135. [CrossRef]
240. Neveu-Lemaire, M.; Grandidier, G. Notes sur les Mammifères des Hauts Plateaux de l’Amérique du Sud; Imprimerie Nationale: Paris, France, 1911; 127p.

241. Onelli, C. Trepando los Andes; Compania Sud-Americana de Billetes de Banco: Buenos Aires, Argentina, 1904; 297p.

242. Osgood, W.H. The journal of Wilfred Osgood: The Marshall Field Chilean Expedition of 1922-23. In Patterson, B.D. Field Museum of Natural History Bulletin 1983, 54, 28–33.

243. Packard, F.M. An ecological study of the Bighorn sheep in Rocky Mountain National Park, Colorado. J. Mammal. 1946, 27, 3–28. [CrossRef]

244. Paillan, J.T.; Tello, G.E. Los recursos naturales y culturales, 28 de Noviembre, Guer Aikie. In Santa Cruz: Su Importancia Turistica y Patrimonial; Informe Científico Técnico UNPA 4, ICT-UNPA-35-2012; Universidad Nacional de la Patagonia Austral: Rio Turbio, Argentina, 2012.

245. Paula Couto, C. Paleontologia Brasileira (Mamíferos); Instituto Nacional do Livro: Rio de Janeiro, Brasil, 1953.

246. Paula Couto, C. Tratado de Paleontozoologia; Academia Brasileira de Ciencias: Rio de Janeiro, Brasil, 1979.

247. Peñafiel, J.; Hermosilla, W.; DiCastri, F.; Gonzalez, R.; Salinas, F. Estudio preliminar de mamíferos silvestres chilenos: Su distribución, valor económico e importancia zoonótica. Rev. Soc. Med. Vit. 1968, 18, 3–15.

248. Pennant, T. History of Quadrupeds, 3rd ed.; B & J White: London, UK, 1793.

249. Perez, A.E.; Batres, D.A. Los otros cazadores. Explotación de cérvidos en la Localidad Araqueológica Meliquina, Parque Nacional Lanín, República Argentina. In Zoocarneologia hoy. Encuentros Hispano-Argentinos; Díez, J.C., Ed.; Universidad de Burgos: Burgos, Spain, 2008; pp. 89–107.

250. Philippi, R.A. Über den Guemul von Molina. Archiv für Naturgeschichte 1857, 23, 135–136.

251. Philippi, R.A. Zoología; Instituto Nacional do Livro: Rio de Janeiro, Brasil, 1896.

252. Philippi, R.A. El guemul de Chile. An. Museo Nat. Chile Primer Seccion Zool. 1892, 2, 1–9.

253. Phoca-Cogetmatatou, N. Site function and the ‘ibex-site phenomenon’: Myth or reality? Oxford J. Archaeol. 2004, 23, 217–242. [CrossRef]

254. Prichard, H.H. Through the Heart of Patagonia; D. Appleton and Co.: New York, NY, USA, 1902; 346p.

255. Prichard, H.H. Hunting Camps in Wood and Wilderness; William Heinemann: London, UK, 1910; 274p.

256. Prothero, D.R.; Foss, S.E. The Evolution of Artiodactyls; JHU Press: Baltimore, MD, USA, 2007.

257. Pulliam, H.R. Sources, sinks, and population regulation. Am. Naturalist 1988, 132, 652–661. [CrossRef]

258. Rabassa, J.; Coronato, A. Glaciations in Patagonia and Tierra del Fuego during the Ensenadan Stage/Age (Early Pleistocene-earliest Middle Pleistocene). Quaternary Intern. 2009, 210, 18–36. [CrossRef]

259. Rabassa, J.; Coronato, A.; Martinez, O. Late Cenozoic glaciations in Patagonia and Tierra del Fuego: An updated review. Biol. J. Linnean Soc. 2011, 103, 316–335. [CrossRef]

260. Ramirez Morales, F. Apuntes para una historia ecológica de Chile. Cuadernos de Historia 1991, 11, 149–196.

261. Rasmussen, P.C. Geographic variation in morphology and allozymes of south american imperial shags. N. Z. J. Zool. 1983, 10, 363–391. [CrossRef]

262. Re, A.; Delaunay, A.N.; Ferraro, L. Grabados en la meseta del lago Strobel (provincia de Santa Cruz, Argentina), el sitio laguna de las Playas. Rev. Soc. Med. Vet. 1968, 3–15.

263. Reichlen, H. Huemul in Fell’s Cave, Chile: Specimen MNHN-2M-MO-1988-211; Museum National d’Histoire Naturelle: Paris, France, 1959.

264. Ren, J.Z.; Zhou, Z.Y.; Pan, B.; Chen, W. Selenium distribution in four grassland classes of China. In Selenium in Biology and Medicine; Comb, G.F., Spall-holz, J.E., Levander, O.A., Oldfield, J.E., Eds.; AVI Books: New York, NY, USA, 1987; pp. 769–774.

265. Ringuelet, R.A. Temas de Ciencia Naturales; Museo de La Plata: La Plata, Argentina, 1946.

266. Rosas, Y.M.; Peri, P.L.; Herrera, A.H.; Pastore, H.; Pastur, G.M. Modeling of potential habitat suitability of Hippocametus bisulcus: Effectiveness of a protected areas network in Southern Patagonia. Ecol. Processes 2017, 6. [CrossRef]

267. Roulin, M. Mémoire pour servir a l’histoire du tapir: Et description d’une espece nouvelle (le tapir pinchaque) appartenant aux hautes régions de la Cordillere des Andes. Mémoires des Savans Etrangers 1835, 6, 5–112.

268. Rusconi, C. Animales Extinguidos de Mendoza y de la Argentina; Imprenta Oficial: Mendoza, Argentina, 1967.

269. Ryan, S.J. The role of culture in conservation planning for small or endangered populations. Conserv. Biol. 2006, 20, 1321–1324. [CrossRef]

270. Santos Gollan, J. Contribución al Conocimiento de los Mamíferos del Parque Nacional de Nahuel Huapi; Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires: Buenos Aires, Argentina, 1946; 66p.

271. Sawyer, H.; Middleton, A.D.; Hayes, M.M.; Kauffman, M.J.; Monteith, K.L. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 2016, 7, e01534. [CrossRef]

272. Schaller, G. Remarks on Cervus chilensis and Cervus antisiensis. J. Nat. History Ser. 4 1873, 11, 213–214. [CrossRef]

273. Schaller, G. On Cervus chilensis. Proc. Zool. Soc. Lond. 1875, 2, 44–47.

274. Serret, A. Observaciones Preliminares de Huemul, Hippocametus bisulcus, en el Lago Nansen del Parque Nacional Perito Moreno, Provincia Santa Cruz; Fundacion Vida Silvestre: Buenos Aires, Argentina, 1990; 23p.

275. Sierra, D. La microhistología de fecas para el estudio de dieta del huemul. In Huemul Ecology Research for Conservation Planning, Darwin Initiative ed.; Darwin Initiative: Cochrane, Chile, 2003.

276. Siewert, C. Un viaje a Patagonia. Boletin Inst. Geogr. Argentino 1896, 17, 363–391.
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 rejoining 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; Diaz 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; Giai, 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 an 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; Giai, 1936; Magné de la Croix, 1937; De Agostini, 1941; Ringuet, 1946; Housse, 1953; Pefaure 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; Giai, 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’ (Claraaz, 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 Rodriguez, 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 Odocoilines, including Odocoileus, are versatile in foraging and successfully utilize rangelands, steppe 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 tree line, 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; Wolflsohn, 1910; Steffen, 1910; Neveu-Lemaire and Grandidier, 1911; von Colditz, 1925; Dawilov, 1926; Gigoux, 1929; Giai, 1936; Krieg, 1940; Grosse, 1949; Housse, 1953; Lieberman, 1962; Kollerker 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; Wolflsohn, 1910; Cabrera and Yepes, 1940; Ibar Bruce, 1973), which was interpreted as being refugee areas (Krieg, 1940; Housse, 1953; Liebermann, 1962; Kollerker 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:

Agassiz, L. 1872. The 1871-1872 Hassler expedition. Occurrence dataset, version 162.229. doi.org/10.15468/p5rupv, accessed Oct 2020 In: (Ed. Morris PJ) Museum of Comparative Zoology. Harvard University, Cambridge, USA.

Ale, A. 2014. A social economic formation of hunter-gatherers in the semiarid northern Chile: a revaluation of San Pedro Viejo of Pichasca site. La Zaranda de Ideas 11:67-88.

Anchorena, A. 1902. Descripción gráfica de la Patagonia y valles andinos. Compania Sudamericana de Billetes de Banco, Buenos Aires.

Anonymous, 1904. Excursión del gobernador del Chubut. Caras y Caretas (Buenos Aires) 7(300):58.

Bahre CJ. 1979. Destruction of the Natural Vegetation of North-Central Chile. University of California Publications in Geography, Vol 23, Berkeley, USA. 117 pp.

Behm, E. 1880. Reise im südwestlichen Patagonien von J.T. Rogers und E. Ibar, 1877, nebst den Tagebüchern von A. de Viedma 1782 und J.H. Gardiner 1867. Petermanns Geographischen Mitteilungen 26(2):47-64.

Burmeister, C.V. 1893. Nuevos datos sobre el territorio Patagonico de Santa Cruz. Revista del Museo de la Plata 4:227-256 and 338-352.

Burmeister, C.V. 1901. Memoria sobre el territorio de Santa Cruz. Imprenta La Nación, Ministerio de Agricultura de la Republica Argentina.

Carballo Marina, F., Manzi, L.M., Campan, P.A., Belardi, J.B., Tiberi, P., Manero, A., Saenz, J.L. 2008. Distribución del registro arqueológico en la cuenca del rio Gallegos (Santa Cruz): línea de base y aporte a la preservación del patrimonio. Pages 175-225 In: (Eds. Borrero LA and Franco N) Arqueología del Extremo sur del Continente Americano. Editorial Dunken, Buenos Aires.

Cardich, A., Miotti, L. 1983. Recursos Faunísticos en la Economia de los Cazadores-Recolectores de Los Toldos (Provincia de Santa Cruz). Relaciones de la Sociedad Argentina de Antropologia 16:145-157.

Diaz, N.I. 1993. Changes in the range distribution of Hippocamelus bisulcus in Patagonia. Z. Säugetierkunde 58:344-351.

Diaz, N.I. 2000. The huemul (Hippocamelus bisulcus Molina, 1782): a historical perspective. Pages 1-31 In: (Eds. Diaz, N.I. and J. Smith-Flueck) The Patagonian huemul, a mysterious deer on the brink of extinction. L.O.L.A., Buenos Aires.
Díaz, N.I., Prieto, A., Bahamonde, G. 2007. Guanacos timidos, huemules confiados: el limite occidental de los cazadores terrestres australes. Magallania, (Chile) 35(1):133-138.

Eastman, C.R. 1915. Beginnings of American natural history. The America Museum Journal 15(7):349-355.

Goni, R.A. 1988. Arqueologia de momentos tardios en el Parque Nacional Perito Moreno (Santa Cruz, Argentina). Pages 140-151 In: Precirculados del IX Congreso Nacional de Arqueologia Argentina. Universidad de Buenos Aires, Buenos Aires.

Goni, R.A., Belardi, J.B., Re, A., Nuevo Delaunay, A., Molinari, R.L., Ferraro, L. 2007. Los grabados de la meseta del lago Strobel (Patagonia argentina) desde una perspectiva regional. Pages 427-438 In: Actas del Primer Simposio Nacional de Arte Rupestre (Cusco, noviembre de 2004). Institut Francais d’Etudes Andines, Peru.

Hatcher, J.B. 1903. Reports of the Princeton University expeditions to Patagonia, 1896-1899. Vol. I: Narrative of the Expeditions. Geography of Southern Patagonia. E. Schweizerbart'sche Verlagshandlung, Stuttgart. 314 pp.

Johnson, L. 1976. Informe sobre una prospección arqueológica en magallanes. Ans. Inst. Pat., Punta Arenas (Chile) 7:87-94.

Lacroix, F. 1841. Historia de la Patagonia, Tierra de Fuego, e Islas Malvinas. Imprenta del Liberal Barcelones, Barcelona, Spain

Laming-Emperaire, A., Lavallée, D., Humbert, R. 1972. Le site de Marazzi en Terre de Feu. Objets et Mondes 12(2):225-244.

Lista, R. 1881. La Tierra del Fuego y sus habitantes. Boletin del Instituto Geografico Argentino 2:109-114.

MacDouall, J. 1833. Narratives of a voyage to Patagonia and Terra del Fuego. Renshaw and Rush, London. 320 pp.

Mansur, M.E., Piqué, R. 2009. Between the Forest and the Sea: Hunter-Gatherer Occupations in the Subantarctic Forests in Tierra del Fuego, Argentina. Arctic Anthropology 46:144-157.

Massone, M. 1984. Los paraderos tehuelches y proto-tehuelches en la costa del Estrecho de Magallanes. Anales del Instituto de la Patagonia 15:27-42.

Moreno, F.P. 1898. Apuntes preliminares sobre una excursion a los territorios del Neuquen, Rio Negro, Chubut y Santa Cruz. Rev. Museo de La Plata 8(1): 200-459.

Moreno PI, Villagran C, Marquet PA, and Marshall LG. 1994. Quaternary paleobiogeography of northern and central Chile. Revista Chilena de Historia Natural 67:487-502.
Onelli, C. 1905. El huemul. Su patria: su vida. Revista del Jardin Zoológico de Buenos Aires Epoca II. Vol. 1(4): 370-374.

Paillan, J.T., Tello, G.E. 2012. Los recursos naturales y culturales, 28 de Noviembre, Guer Aaike. Santa Cruz: su importancia turistica y patrimonial. ICT-UNPA-35-2012. Pg. 1-15.

Paula Couto, C. 1953. Paleontologia Brasileira (Mamíferos). Instituto Nacional do Livro. Rio de Janeiro, Brasil. Pg. 1-516.

Paula Couto, C. 1979. Tratado de paleomastozoologia. Academia Brasileira de Ciencias, Rio de Janeiro, Brasil. Pg. 1-590.

Prichard, H.H. 1902. Through the heart of Patagonia. D. Appleton and Co., New York. 346 pp.

Prichard, H.H. 1902. Field notes upon some of the larger mammals of Patagonia made between September 1900 and June 1901. Proc. Zool. Soc. London 1, 272-277.

Re, A., Delaunay, A.N., Ferraro, L. 2005. Grabados en la meseta del lago Strobel (provincia de Santa Cruz, Argentina), el sitio laguna del Faldeo Verde. Relaciones de la Sociedad Argentina de Antropologia XXX. 30:245-256.

Reichlen, H. 1959. Huemul in Fell's Cave, Chile: Specimen MNHN-2M-MO-1988-211. Museum National d'Histoire Naturelle, Paris (France) http://coldb.mnhn.fr/catalognumber/mnhnizm/mo-1988-211

Rosas, Y.M., Peri, P.L., Herrera, A.H., Pastore, H., Pastur, G.M. 2017. Modeling of potential habitat suitability of Hippocamelus bisulcus: efectiveness of a protected areas network in Southern Patagonia. Ecological Processes 6(28):DOI 10.1186/s13717-017-0096-2.

Rusconi, C. 1967. Animales Extinguidos de Mendoza y de la Argentina. Mendoza: Imprenta Oficial, Argentina. Pg. 1-489.

Saavedra B., and Simonetti J.A. 1991. Archaeological evidence of Pudu pudu (Cervidae) in central Chile. Zeits. Saeugetierkunde 56:252-253.

Serret, A. 1990. Observaciones preliminares de huemul, Hippocamelus bisulcus, en el lago Nansen del Parque Nacional Perito Moreno, Provincia Santa Cruz. Fundacion Vida Silvestre Argentina:23.

Siewert, C. 1896. Un viaje a Patagonia. Boletin del Instituto Geografico Argentino 17(7,8,9):363-391.

Silveira, M.J. 1979. Analisis e Interpretacion de los Restos Faunisticos de la Cueva Grande del Arroyo Feo. Relaciones de la Sociedad Argentina de Antropologia 13:229-253.

Skottsberg, C. 1911. The wilds of Patagonia. Edward Arnold, London. Pg. 1-336.
Steffen, H. 1900. Reisen in den Patagonischen Anden. Verhandlungen der Gesellschaft für Erdkunde zu Berlin 27(4): 194-220.

Teta, P., Rodríguez, D. 2020. Mammalogy National Collection (MACNMa). Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’ (MACN): Occurrence dataset doi.org/10.15468/ukdxqp

Waterhouse, G.R. 1839. Mammalia. In: the Zoology of the Voyage of H.M.S. Beagle, Under the Command of Captain Fitzroy, During the years 1832-1836. Smith, Elder and Co., London.

Weber, A. 1903. Chiloe: su estado actual, su colonizacion, su porvenir. Imprenta Mejia, Santiago, Chile. 194 pp.
General References used for Supplementary File S1

Aldenderfer MS. 1998. *Montane Foragers: Asana and the South-Central Andean Archaic*. University of Iowa Press: Iowa.

Ale, A. 2014. A social economic formation of hunter-gatherers in the semiarid northern Chile: a revaluation of San Pedro Viejo of Pichasca site. *La Zaranda de Ideas* 11:67-88.

Anonymous. 1904. Excursión del gobernador del Chubut. Caras y Caretas (Buenos Aires) 7(300):58.

Anonymous. 2021. Descubren los restos fósiles de seis ciervos prehistóricos. Agencia CTyS-UNLaM/DICYT, www.dicyt.com, 7 Oct.

Armesto JJ, Manuschevich D, Mora A, Smith-Ramirez C, Rozzi R, Abarzuja AM, and Marquet PA. 2010. From the Holocene to the Anthropocene: A historical framework for land cover change in southwestern South America in the past 15,000 years. *Land Use Policy* 27: 148-160.

Aschero CA. 2010. Las escenas de caza en Cueva de las Manos: Una perspectiva regional (Santa Cruz, Argentina) In: *IFRAO Congress – Symposium: Pleistocene art of the Americas (Pre-Acts)*

Avital E, Jablonka E. 2000. *Animal traditions*. Cambridge Univ. Press, Cambridge, UK. 446 pp.

Bahre CJ. 1979. *Destruction of the Natural Vegetation of North-Central Chile*. University of California Publications in Geography, Vol 23, Berkeley, USA. 117 pp.

Behm E. 1880. Reise im südwestlichen Patagonien von J.T. Rogers und E. Ibar, 1877, nebst den Tagebüchern von A. de Viedma 1782 und J.H. Gardiner 1867. *Petermanns Geographischen Mitteilungen* 26(2):47-64.

Bürger O. 1924. *Aus der Wildnis des Huemuls. Erlebnisse und Abenteuer unter den Kolonisten und Indianern Chiles*. Verlag Deutsche Buchwerkstätten, Dresden. 191 pp.

Burmeister H. 1873. The huemul. *Nature* 9(214): 82.

Cabrera A, and Yepes J. 1940. *Mamiferos sudamericanos*. (1st). Compañia Argentina de Editores, Buenos Aires. 370 pp.

Carballo Marina F, Manzi LM, Campan PA, Belardi JB, Tiberi P, Manero A, Saenz JL. 2008. Distribución del registro arqueológico en la cuenca del rio Gallegos (Santa Cruz): linea de base y aporte a la preservación del patrimonio. Pages 175-225 In: (Eds. Borrero LA and Franco N) *Arqueologia del Extremo sur del Continente Americano*. Editorial Dunken, Buenos Aires.

Cardich A, and Miotti L. 1983. Recursos Faunisticos en la Economia de los Cazadores-Recolectores de Los Toldos (Provincia de Santa Cruz). *Relaciones de la Sociedad Argentina de Antropologia* 16:269–273.
Castellanos A. 1944. Paleontología estratigráfica de los sedimentos neógenos de la Provincia de Córdoba. *Publicaciones del Instituto de Fisiografía y Geología* 23: 1-47.

Church GE. 1903. A traveller in Patagonia. *Nature* 67, 321–322.

Clapperton CM. 1993. Nature of environmental changes in South America at the Last Glacial Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 101: 189-208.

Claraz MG. 1864. Sur l’Equus bisulcus, de Molina. *Revue et Magasin de Zoologie Pure et Apliquee* 241-248.

Coltorti M, Abbazzi L, Ferretti MP, Jacumin P, Paredes Rios F, Pellegrini M, Pieruccini P, Rustioni M, Tito G, and Rook L. 2007. Last Glacial mammals in South America: a new scenario from the Tarija Basin (Bolivia). *Naturwissenschaften* 94: 288-299.

Conway W. 2005. *Act III in Patagonia: people and wildlife*. Island Press, Washington DC, USA. 344 pp.

Cox GE. 1863. *Viaje a las regiones septentrionales de la Patagonia. 1862-1863*. Imprenta Nacional, Santiago, Chile. Pg. 1-266.

Cruz I, Munoz AS, and Caracotche M. 2010. A huemul (*Hippocamelus bisulcus*) antler artefact in archaeological deposits of the Atlantic coast. Implications for human mobility and species distribution. *Magallania* 38, 287–294.

Dawilov. 1926. *Coihue*. Gmo. van Woerden & Cia, Buenos Aires. Pg. 1-103.

da Silva FM, da Silva Alves R, Franca Barreto AM, Bezerra de Sá F, and Borges Lins e Silva AC. 2006. A megafauna pleistocénica do estado de Pernambuco. *Estudos Geologicos* (Brazil) 16: 55-66.

Dabbene R. 1911. Sobre la existencia del huemul de Bolivia y Perú, Odocoileus (*Hippocamelus*) antisensis (Orb.) y del avestruz petiso, *Rhea darwini* Gould en el N.W. de la República Argentina. *Anales del Museo Nacional Buenos Aires*, Serie 3 14: 293-307.

de Agostini AM. 1941. *Andes Patagónicos: Viajes de exploración a la cordillera Patagónica Austral*. Talleres Gráficos Guillermo Kraft Ltda: Buenos Aires

de Agostini AM. 1945. *Andes Patagónicos: viajes de exploración a la cordillera Patagónica Austral*. (Vol. 1), Buenos Aires. Pg. 1-409.

de la Cruz L. 1836. Descripción de la naturaleza de los terrenos que se comprenden en los Andes, poseídos por los Peguenches; y los demás espacios hasta el rio de Chadileubu. Pages 1-67 In: (Ed. de Angelis P) *Colección de obras y documentos relativos a la historia antigua y moderna de las provincias del Río de la Plata; ilustrados con notas y disertaciones*. Imprenta del Estado, Buenos Aires.

Diaz NI. 1993. Changes in the range distribution of *Hippocamelus bisulcus* in Patagonia. *Z. Säugetierkunde* 58:344-351.
Diaz NI. 1995. Antecedentes sobre la historia natural de la taruca (Hippocamelus antisensis) y su rol en la economía Andina. Chungara 27: 45-55.

Diaz NI, and Smith-Flueck J. 2000. The Patagonian huemul. A mysterious deer on the brink of extinction. Buenos Aires: Literature of Latin America.

Diaz NI, Prieto A, and Bahamonde G. 2007. Guanacos tímidos, huemules confiados: el límite occidental de los cazadores terrestres australes. Magallania, (Chile) 35(1):133-138.

Donoso D, Iriarte A, Segura B, and Tirado M. 2017. Antecedentes de Huemul (Capítulo 1). Pages 13-61 In: (Eds. Iriarte A, Donoso DS, Segura B, and Tirado M) El Huemul de Aysén y otros rincones. Ediciones Secretaría Regional Ministerial de Agricultura de la Región de Aysén y Flora & Fauna Chile Ltd, Aysen, Chile.

Eastman CR 1915. Beginnings of American natural history. The America Museum Journal 15, 349–355.

Eisenberg JF. 2000. The contemporary Cervidae of Central and South America. Pages 189-202 in: Antelopes, deer, and relatives, Vrba ES and Schaller GB (eds). Yale University Press: New York.

Falkner T. 1774. A description of Patagonia and the adjoining parts of South America: containing an account of the soil, produce, the religion, government, and some particulars relating to Falkland Islands. Hereford, London, 1-144.

Fernández OA, and Busso CA. 1997. Arid and semi-arid rangelands: two thirds of Argentina. Pages 41-60 in: Proceedings from an International Workshop in Iceland. Rala Report no. 200, Arnalds O and Archer S (eds). Agricultural Research Institute: Reykjavik.

Fernandez PM, Cruz I, Bautista Belardi J, de Nigris M, and Muñoz S. 2016. La explotación del huemul (Hippocamelus bisulcus, Molina 1782) en la Patagonia a lo largo del holoceno. Magallania 44(1):187-209.

Festa-Bianchet M. 2018. Learning to migrate. Science 361(6406):972-973.

Flint RF, and Fidalgo F. 1969. Glacial Drift in the Eastern Argentine Andes between Latitude 41° 10' S. and Latitude 43° 10' S. Bulletin of the Geological Society of America 80:1043-1052.

Flueck WT. 1989. The effect of selenium on reproduction of black-tailed deer (Odocoileus hemionus columbianus) in Shasta County, California. University of California, Davis, USA.

Flueck WT, and Smith-Flueck JM. 2011. Recent advances in the nutritional ecology of the Patagonian huemul: implications for recovery. Animal Production Science 51(4):311-326.

Flueck WT, and Smith-Flueck JM. 1993. Über das in Argentinien angesiedelte Rotwild (Cervus elaphus L., 1758): Verbreitung und Tendenzen. Zeitschrift für Jagdwissenschaft 39(3):153-160.
Flueck WT, and Smith-Flueck JM. 2012a. Huemul heresies: beliefs in search of supporting data. 1. Historical and zooarchaeological considerations. *Animal Production Science* 52: 685-693.

Flueck WT, and Smith-Flueck JM. 2012b. Huemul heresies: beliefs in search of supporting data. 2. Biological and ecological considerations. *Animal Production Science* 52(8):694-706.

Flueck WT, and Smith-Flueck JM. 2018. Radio marking the first group of endangered Patagonian huemul deer in Argentina. *J Neotrop Mammal* 25(2):461-465.

Frailey D, Campbell KE, and Wolff RG. 1980. Additions to the knowledge of Hippocamelus, Ctenomys, and Myocastor from the middle Pleistocene of the Tarija basin, Bolivia. *Occasional Papers of the Museum of Natural History, University of Kansas* 85: 1-14.

Gay C. 1847. *Historia Fisica y Politica de Chile: Zoologia*. Museo de Historia Natural de Santiago, Santiago, Chile. 495 pp.

Gazzolo C. 2006. Botanical composition of taruka (*Hippocamelus antisensis*) diet during rainy season in Huascaran national park, Peru. In: *Advances in deer biology*, Bartos L, Dusek A, Kotrba R, and Bartosova J (eds). Research Institute of Animal Production: Praha; 216.

Giai AG. 1936. Huemul, inofensivo venado de las soledades cordilleranas de la Patagonia. *La Chacra* (Arg.) 6(70):99-101.

Gigoux EE. 1929. El huemul. *Revista Chilena de Historia Natural* 23: 573–82.

Goni RA. 1988. Arqueologia de momentos tardios en el Parque Nacional Perito Moreno (Santa Cruz, Argentina). Pages 140-151 In: *Precirculados del IX Congreso Nacional de Arqueologia Argentina*. Universidad de Buenos Aires, Buenos Aires.

Goss RJ. 1983. *Deer Antlers: Regeneration, Function and Evolution*. Academic Press, New York, USA.

Grosse A. 1949. El huemul - ciervo de los Andes y emblema del escudo Chileno. *Condor (Revista Chileno Alemana)* 12(22):10-12.

Guérin C, and Faure M. 2009. The Cervidae (Mammalia, Artiodactyla) of the Upper Pleistocene/Lower Holocene deposits of the Serra da Capivara National Park Region (Piauí, Brazil). *Geobios* 42: 169-195.

Guineo O, Guineo Garay R, and Garay G. 2008. *Conociendo al huemul de Torres del Paine*. La Prensa Austral, Punta Arenas, Chile. 94 pp.

Günther A. 1875. Comments about Sclater and *Cervus chilensis*. Pages 44-46 In: *Proceedings of the Scientific Meetings of the Zoological Society of London*. Messrs. Longmans, Green, Reader, and Dyer, London.

Haller H. 2002. Der Rothirsch im Schweizerischen Nationalpark und dessen Umgebung. Eine alpine Population von *Cervus elaphus* zeitlich und räumlich dokumentiert. *Nationalpark-Forschung Schweiz* 91:1-144.
Hatcher JB. 1903. *Reports of the Princeton University expeditions to Patagonia, 1896–1899. Vol. I: Narrative of the Expeditions. Geography of Southern Patagonia*. Stuttgart, Germany: E. Schweizerbart’sche Verlagshandlung.

Hauman L. 1926. *Étude phytogéographique de la Patagonie*. *Bulletin de la Société Royale de Botanique de Belgique* 58(2):105-179.

Hershkovitz P. 1969. The recent mammals of the Neotropical region: A zoogeographic and ecological review. *The Quarterly Review of Biology* 44: 1-70.

Hershkovitz P. 1972. The recent mammals of the neotropical region: a zoogeographic and ecological review. Pages 311-431 in: *Evolution, mammals, and southern continents*, Keast A, Erk FC, and Glass B (eds). State Univ. New York Press: Albany, New York.

Hoffstetter R. 1963. *La faune pléistocène de Tarija* (Bolivie). Note preliminaire. *Bulletin Muséum National d’Histoire Naturelle* 35: 194-203.

Horkheimer H. 1960. *Nahrung und Nahrungsgewinnung im vorspanischen Peru*. Colloquium Verlag: Berlin.

Housse PR. 1953. *Animales salvajes de Chile en su clasificación moderna: su vida y sus costumbres*. Ediciones de la Universidad de Chile, Santiago, Chile. 189 pp.

Ibar Bruce J. 1973. *Aisen, hombres y naturaleza*. Imprenta de la Armada, Valparaiso, Chile. Pg. 1-164.

Iglesias RE. 1965. *El huemul*. *La Montaña* (Arg.) (7):26-28.

Jakopak RP, LaSharr TN, Dwinnell SPH, Fralick GL, Monteith KL. 2019. Rapid acquisition of memory in a complex landscape by a mule deer. *Ecology* 100(12):e02854. 10.1002/ecy.2854.

Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Beck JL, Courtemanch AB, Hurley MA, McWhirter DE, Miyasaki HM, Monteith KL, and Kauffman MJ. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* 361(6406):1023-1025.

Johnson L. 1976. Informe sobre una prospección arqueológica en magallanes. *Anales Inst. Patagonico, Punta Arenas* (Chile) 7:87-94.

Kolliker Frers A. 1969. *Das Waidwerk und die autochthonen Cerviden in Argentinien*. Pages 25–31 in: *Parque Diana*. Vogel CA, editor. München, Germany: Stefan Schwarz Verlag.

Krieg H. 1940. *Als Zoologe in Steppen und Wäldern Patagoniens*. Bayerischer Landwirtschaftsverlag, Muenchen, Germany. 197 pp.
Krieg H. 1925. Biologische Reisestudien in Südamerika. V. Die chilenischen Hirsche. Zeitschrift für Morphologie und Ökologie der Tiere 4: 585-597.

Laming-Emperaire A, Lavallée D, and Humbert R. 1972. Le site de Marazzi en Terre de Feu. Objets et Mondes 12(2):225-244.

Latcham RE. 1935. Expedicion cientifica Macqueen al Aysen. Boletín del Museo Nacional (Chile) 14: 7-31.

Liebermann J. 1962. Sobre la historia natural del huemul. Anales de la Academia Argentina de Geografía 6:157-168.

Lingle S and Wilson WF. 2001. Detection and avoidance of predators in white-tailed deer (Odocoileus virginianus) and mule deer (O. hemionus). Ethology 107:125-147.

Lydekker R. 1898. The deer of all lands : a history of the family Cervidae, living and extinct. R. Ward, London. Pg. 1-329.

MacDouall J. 1833. Narratives of a voyage to Patagonia and Terra del Fuego. Renshaw and Rush, London. 320 pp.

Magalhaes, RM, MG Mello, and Bergqvist LP. 1992. Os cervidas pleistocenicos da regiao nordeste Brasileira. Anais da Academia Brasileira de Ciencias 64: 149-154.

Magne de la Croix P. 1937. El huemul. Caras y Caretas (Buenos Aires) 40, 117.

Markgraf V, and Kenny R. 1997. Character of rapid vegetation and climate change during the late-Glacial in southernmost South America. Pages 81-90 in: Past and Future Rapid Environmental Changes: Spatial and Evolutionary Responses to terrestrial Biota, Huntley B (ed). Springer-Verlag: Berlin.

Marshall LG. 1988. Land Mammals and the Great American Interchange. American Scientist 76: 380-388.

Massone M. 1984. Los paraderos tehuelches y proto-tehuelches en la costa del Estrecho de Magallanes. Anales del Instituto de la Patagonia 15:27-42.

Machon JF, and Juarez FN. 2013. Patagonia 1892 : diario del explorador suizo Dr. Francisco Machón. Editorial Dunken, Buenos Aires.

McClure MF, Bissonette JA, and Conover MR. 2005. Migratory strategies, fawn recruitment, and winter habitat use by urban and rural mule deer (Odocoileus hemionus). Eur J Wildl Res 51:170-177.

Miller S, Rottman J, and Taber RD. 1973. Dwindling and endangered ungulates of Chile: vicugna, lama, Hippocamelus, and Pudu. Transactions of North American Wildlife and Natural Resource Conference 38:55–67.

Molina JI. 1809. The geographical, natural, and civil history of Chili. Vol. 1. Longman, Hurst,
Rees, and Orme: London.

Moreira-Arce D, PefiaAranda DA, Lopéz R, Stipicic GJ, Hidalgo-Hermoso E, and Simonetti JA. 2021. Observations of a coastal population of huemul, Hippocamelus bisulcus (Artiodactyla: Cervidae) in Riesco Island, Magallanes Region, Chile: a conservation opportunity. *Mammalia* 85(4):291-295.

Morejohn GV, and Dailey DC. 2004. The identity and postcranial osteology of Odocoileus lucasi (Hay) 1927. *Sierra College Natural History Museum Bulletin* 1: 1-54.

Moreno FP. 1898. Apuntes preliminares sobre una excursion a los territorios del Neuquen, Rio Negro, Chubut y Santa Cruz. *Revista del Museo de La Plata* 8(1):200-459.

Moreno FP. 1899. Explorations in Patagonia. *Geogr J* 14: 241–69.

Moreno PI, Villagran C, Marquet PA, and Marshall LG. 1994. Quaternary paleobiogeography of northern and central Chile. *Revista Chilena de Historia Natural* 67:487-502.

Moser CA. 1962. *The bighorn sheep of Colorado: a review of Colorado’s bighorn sheep studies*. Technical Publication No. 10. The Colorado Game and Fish Department, Denver, Colorado, USA. Pg. 1-49.

Musters RN. 1871. A year in Patagonia. *J Royal Geogr Soc London* 41:59-77.

Mysterud A, Loe LE, Zimmermann B, Bischof R, Veiberg V, and Meisingset E. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? *Oikos* 120:1817-1825.

Neveu-Lemaire M, and Grandidier G. 1911. *Notes sur les mammifères des hauts plateaux de l’Amérique du Sud*. Imprimerie nationale, Paris. Pg. 1-127.

Onelli C. 1904. *Trepando los Andes*. Compania Sud-Americana de Billetes de Banco, Buenos Aires. 297 pp.

Onelli C. 1905. El huemul. Su patria: su vida. *Revista del Jardin Zoológico de Buenos Aires* Epoca II. Vol. I.(4):370-374.

Osgood WH. 1923: in Patterson BD. 1983. *The journal of Wilfred Osgood: The Marshall Field Chilean Expedition of 1922-23*. *Field Museum of Natural History Bulletin* 54(2): 8-11; 28-33.

Paillan JT, and Tello GE. 2012. Los recursos naturales y culturales, 28 de Noviembre, Guer Aaike. Santa Cruz: su importancia turistica y patrimonial. ICT-UNPA-35-2012. Pg. 1-15.

Pefaur J, Hermosilla W, DiCastri F, Gonzalez R, and Salinas F. 1968. Estudio preliminar de mamíferos silvestres chilenos: su distribución, valor económico e importancia zoonótica. *Revista de la Sociedad de Medicina Veterinaria* (Chile) 18: 3-15.
Pennant T. 1793. History of quadrupeds. (3rd). B & J White, London.

Perez AE, and Batres DA. 2008. Los otros cazadores. Explotación de cérvidos en la Localidad Arqueológica Meliquina, Parque Nacional Lanín, República Argentina. Pages 89-107 in: Zooarqueología hoy. Encuentros Hispano-Argentinos, Diez JC (ed). Universidad de Burgos: Burgos.

Philippi RA. 1857. Über den Guemul von Molina. Archiv für Naturgeschichte 23:135-136.

Philippi RA. 1873. Zoología: Sinonimia del huemul. Anales de la Universidad de Chile 717-722.

Philippi RA. 1892. El guemul de Chile. Anal. Museo Nac. Chile, Primera Seccion Zoologica 2:1-9.

Prichard HH. 1902a. Through the heart of Patagonia. New York: D. Appleton and Co.; 346 pp.

Prichard HH. 1902b. Field notes upon some of the larger mammals of Patagonia made between September 1900 and June 1901. Proceedings of the Zoological Society of London 1, 272-277.

Prichard HH. 1910. Hunting camps in wood and wilderness. London: William Heinemann; 274 pp.

Prothero DR, and Foss SE. 2007. The Evolution of Artiodactyls. JHU Press: Baltimore.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am. Naturalist 132:652-661.

Putman R, and Flueck WT. 2011. Intraspecific variation in biology and ecology of deer: magnitude and causation. Animal Production Science 51(4):277-291.

Rabassa J, and Coronato A. 2009. Glaciations in Patagonia and Tierra del Fuego during the Ensenadan Stage/Age (Early Pleistocene–earliest Middle Pleistocene). Quaternary International 210: 18-36.

Rabassa J, Coronato A, and Martinez O. 2011. Late Cenozoic glaciations in Patagonia and Tierra del Fuego: an updated review. Biological Journal of the Linnean Society 103: 316-335.

Ramirez Morales F. 1991. Apuntes para una historia ecológica de Chile. Cuadernos de Historia 11:149-196.

Rasmussen, PC. 1994. Geographic variation in morphology and allozymes of south american imperial shags. The Auk 111(1):143-161.

Re A, Delaunay AN, and Ferraro L. 2005. Grabados en la meseta del lago Strobel (provincia de Santa Cruz, Argentina), el sitio laguna del Faldeo Verde. Relaciones de la Sociedad Argentina de Antropología XXX. 30:245-256.

Reichlen H. 1959. Huemul in Fell’s Cave, Chile: Specimen MNHN-2M-MO-1988-211. Museum National d’Histoire Naturelle, Paris (France) http://coldb.mnhn.fr/catalognumber/mnhnizm/mo-1988-211
Ringuelet RA. 1946. Serie Técnica y Didáctica Nr. 2: Temas de Ciencia Naturales. ProBiotA (2003). División Zoología Vertebrados, Museo de La Plata: Argentina.

Roulin M. 1835. Mémoire pour servir a l’histoire du tapir: et description d’une espece nouvelle (le tapir pinchaque) appartenant aux hautes régions de la Cordillere des Andes. Mémoires des Savans étrangers 6:5-112.

Saavedra B., and Simonetti J.A. 1991. Archaeological evidence of Pudu pudu (Cervidae) in central Chile. Z. Saeugetierkunde 56:252-253.

Santos Gollan J. 1946. Contribución al conocimiento de los mamíferos del Parque Nacional de Nahuel Huapi. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina. Pg. 1-66.

Sclater PL. 1873. Remarks on Cervus chilensis and Cervus antiensis. Journal of Natural History Series 4 11(63):213-214.

Sclater PL. 1875. On Cervus chilensis. Proc. Zool. Soc., Lond. Feb. 2:44-47.

Serret A. 1990. Observaciones preliminares de huemul, Hippocamelus bisulcus, en el lago Nansen del Parque Nacional Perito Moreno, Provincia Santa Cruz. Fundacion Vida Silvestre Argentina, Buenos Aires, 23 pp.

Sierralta D. 2003. La microhistología de fecas para el estudio de dieta del huemul. In: Huemul Ecology Research for Conservation Planning. Darwin Initiative (ed). Cochrane: Chile; CD ROM.

Silveira MJ. 1979. Analisis e Interpretacion de los Restos Faunisticos de la Cueva Grande del Arroyo Feo. Relaciones de la Sociedad Argentina de Antropologia 13:229-253.

Simmonds PL. 1883. A dictionary of useful animals and their products. E. & F.N. Spon, London. 136 pp.

Sinclaire C. 2009. Daily life among the fishermen of the fog. Page 41-48 in: Fishermen of the fog: The Changos and their ancestors. Museo Chileno de Arte Precolombino, Santiago, Chile.

Smith-Flueck JM. 2003. The ecology of huemul (Hippocamelus bisulcus) in Andean Patagonia of Argentina and considerations about its conservation. Doctoral Dissertation, Universidad Nacional Comahue: Argentina.

Stankowich T. 2008. Tail-Flicking, Tail-Flagging, and Tail Position in Ungulates with Special Reference to Black-Tailed Deer. Ethology 114:875-885.

Stankowich T and Coss RG. 2006. Effects of predator behavior and proximity on risk assessment by Columbian black-tailed deer. Behavioral Ecology 17(2):246-254.

Steffen H. 1895. Die Erforschung de Rio Puelo. Petermanns Geographischen Mitteilungen 41(8):190-193.
Steffen H. 1897. Die chilenische Aisen Expedition. Verhandlungen der Gesellschaft für Erdkunde zu Berlin 24:461-474.

Steffen H. 1900. Reisen in den Patagonischen Anden. Verhandlungen der Gesellschaft für Erdkunde zu Berlin 27(4):194-220.

Steffen H. 1910. Viajes de exploracion: estudio en la Patagonia occidental 1892-1902. Anales de la Universidad de Chile 2(50):1-419.

Steward JH. 1946. Handbook of South American Indians. Volume 1. The marginal tribes. (Smithsonian Institution: Washington, D.C.)

Stringham SF and Rogers LL. 2017. Fear of Humans by Bears and Other Animals (Anthropophobia): How Much is Natural? Journal of Behavior 2(2):1009.

Tarifa T, and Yensen E. 2001. Mammals of Bolivian Polylepis woodlands. Revista Boliviana de Ecología y Conservación Ambiental 9: 29-44.

Tatura A, del Valle R, Bianchi M, Outes V, Villarosa G, Niegodisz J, and Debaene G. 2002. Late Pleistocene palaeolakes in the Andean and Extra-Andean Patagonia at mid-latitudes of South America. Quaternary International 89: 135-150.

Teta P, and Rodriguez D. 2020. Mammalogy National Collection (MACNMa). Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' (MACN): Occurrence dataset doi.org/10.15468/ukdxqp

Thirgood SJ. 1995. The effect of sex, season and habitat availability on patterns of habitat use in fallow deer. J. Zool., Lond. 235:645-659.

Tonko J. 2008. Kawesqar travel narratives. Onomazein 18(2):11-47.

Torrejon F. 2001. Variables geohistoricos en la evolucion del sistema economico Pehuenche durante el periodo colonial. Revista Universum (Chile) 16:219-236.

Vidaurre FG. 1782. Des Herrn Abts Vidaure kurzgefasste, geographische, natürliche und bürgerliche Geschichte des Königreichs Chile. Carl Ernst Bohn: Hamburg.

von Colditz R. 1925. Im Reiche des Kondor. Paul Parey, Berlin, Germany. 415 pp.

Wagner JU. 1855. Die Säugthiere in Abbildungen nach der Natur. L.D. Weigel, Leipzig, Germany.
Webb SD. 1978. A history of savanna vertebrates in the New World. Part II: South America and the Great Interchange. *Annual Review of Ecology, Evolution, and Systematics* 9: 393-426.

Wolffsohn JW. 1910. Notas sobre el huemul. *Revista Chilena de Historia Natural* 14:227-34.
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 (Hones 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 fulfill 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 macroand micronutrients, rather than protein and energy supplies. As Liebermann (1962) al-
already 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 re-colonizing 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). Odocoilines 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 Odocoilines 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 (Honess 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).

References

Adams AW. 1982. Migration. Pages 301-321 In: (Eds. Thomas, J. W. and D. E. Toweill) Elk of North America. Ecology and Management. Stackpole Books, Harrisburg, PA.

Andersen R. 1991. Habitat deterioration and the migratory behavior of moose (Alces alces L.) in Norway. J Appl Ecol 28: 102–8. doi:10.2307/2404117

Avital, E., Jablonka, E. 2000. Animal traditions. Cambridge Univ. Press, Cambridge, UK. 446 pp.

Bar-Ilan J, Halevi G. 2021. Retracted articles – the scientific version of fake news. Pages 47-70 In: (Eds. Greifeneder R, Jaffé ME, Newman EJ, and Schwarz N) The Psychology of Fake News: Accepting, Sharing, and Correcting Misinformation. Taylor & Francis Group, New York.

Battin J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. Cons. Biol. 18(6):1482-1491.0

Baumann M, Babota C, Schibler J. 2005. Native or naturalized? Validating alpine chamois habitat models with archaeological data. Ecological Applications 15(3):1096-1110.

Berger J, Steven L, Cain SL, Berger KM. 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. Biology Letters 2(4):528-531.

Berger J, Wangchuk T, Briceno C, Vila A, Lambert JE. 2020. Disassembled Food Webs and Messy Projections: Modern Ungulate Communities in the Face of Unabating Human Population Growth. Frontiers in Ecology and Evolution 8(128):doi: 10.3389/fevo.2020.00128.

Brandborg SM. 1955. Life history and management of the mountain goat in Idaho. Wildlife Bulletin No. 2. Department of Fish and Game, State of Idaho, Boise, Idaho. 142 pp.

Bubenik GA, Bubenik AB. 1990. Horns, pronghorns, and antlers. Springer-Verlag: New York.

Cromsigt JPGM, Kerley GIH, Kowalczyk R. 2012. The difficulty of using species distribution modelling for the conservation of refugee species – the example of European bison. Diversity and Distributions 18:1253-1257.

Faurby S, Araujo MB. 2018. Anthropogenic range contractions bias species climate change forecasts. Nature Climate Change 8:252–256.
Festa-Bianchet M. 2018. Learning to migrate. Science 361:972-973.

Fielder PC. 1986. Implications of selenium levels in Washington mountain goats, mule deer, and Rocky Mountain elk. Northwest Sci 60:15-20.

Flueck, W.T. 1989. The effect of selenium on reproduction of black-tailed deer (Odocoileus hemionus columbianus) in Shasta County, California. University of California, Davis, USA.

Flueck WT. 2005. Spatio-temporal movements among red deer males, Cervus elaphus, introduced to Patagonia. Pages 330-332 In: (Ed. Pohlmeyer, K), XXVIIth Congress of the International Union of Game Biologists, Hannover. DSV-Verlag, Hamburg (GE).

Flueck WT. 2010. Exotic deer in southern Latin America: what do we know about impacts on native deer and on ecosystems? Biological Invasions 12:1909-1922.

Flueck WT. 2015. Osteopathology and selenium deficiency co-occurring in a population of endangered Patagonian huemul (Hippocamelus bisulcus). BMC Res Notes 8:330.

Flueck WT. 2018. Elusive cranial lesions severely afflicting young endangered Patagonian huemul deer. BMC Research Notes 11:638.

Flueck WT. 2020. Nutrition as an etiological factor causing diseases in endangered huemul deer. BMC Research Notes 13(276):1-12.

Flueck WT, Smith-Flueck JM. 2006. Predicaments of endangered huemul deer, Hippocamelus bisulcus, in Argentina: a review. Europ. J. Wildl. Res. 52(1):69-80.

Flueck WT, Smith-Flueck JM. 2008. Age-independent osteopathology in skeletons of a south American cervid, the Patagonian huemul (Hippocamelus bisulcus). Journal of Wildlife Diseases 44(3):636-648.

Flueck WT, Smith-Flueck JM. 2011. Recent advances in the nutritional ecology of the Patagonian huemul: implications for recovery. Animal Production Science 51(4):311-326.

Flueck WT, Smith-Flueck JM. 2017. Troubling disease syndrome in endangered live Patagonian huemul deer (Hippocamelus bisulcus) from the Protected Park Shoonem: unusually high prevalence of osteopathology. BioMed Central Research Notes 10:739.

Flueck WT, Smith-Flueck JM, Mincher BJ, Winkel LHE. 2014. Soil selenium levels corroborate direct evidence of selenium deficiency in endangered Patagonian huemul deer (Hippocamelus bisulcus). Pages 52-53 In: (Eds. Ma J, Zhang M, Halbrook R, Liu B, and Zhang W) Proceedings of the 8th International Deer Biology Congress. Northeast Forestry University, Harbin, China.

Geist V. 1998. Deer of the world. Stackpole Books, Pennsylvania, USA. 421 pp.

Gogan PJP, Klaver RW, and Olexa EM. 2019. Northern Yellowstone Mule Deer Seasonal Movement, Habitat Selection, and Survival Patterns. Western North Amererican Naturalist, 79:403-427.

Gonzalez V, Tapia V. 2017. Manual bovino de carne. Boletín INIA (Chile), 4:1-173.
Grotta-Neto, F, Duarte, JMB. 2019. Movements of Neotropical Forest Deer: What Do We Know? Pages 95-109 In: (Eds. Reyna-Hurtado R, and Chapman C) Movement Ecology of Neotropical Forest Mammals Focus on Social Animals. Springer Nature, Switzerland.

Guineo, O, Guineo Garay, R, Garay, G. 2008. Conociendo al huemul de Torres del Paine. La Prensa Austral, Punta Arenas, Chile. 94 pp.

Haller, H. 2002. Der Rothirsch im Schweizerischen Nationalpark und dessen Umgebung. Eine alpine Population von *Cervus elaphus* zeitlich und räumlich dokumentiert. Nationalpark-Forschung Schweiz 91:1-144.

Honess RF, Frost NM. 1942. A Wyoming bighorn sheep study. Wyoming Game and Fish Department Bulletin 1:1-127.

Howard WE. 1960. Innate and environmental dispersal of individual vertebrates. Amer. Midl. Naturalist 63(1):152-161.

Jakopak RP, LaSharr TN, Dwinnell SPH, Fralick GL, Monteith KL. 2019. Rapid acquisition of memory in a complex landscape by a mule deer. Ecology 100(12):e02854. 10.1002/ecy.2854.

Jesmer BR, Merkle JA, Goheen JR, Aikens EO, Beck JL, Courtemanch AB, Hurley MA, McWhirter DE, Miyasaki HM, Monteith KL, Kauffman MJ. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 361(6406):1023-1025.

Kauffman MJ, Copeland HE, Berg J, Bergen S, Cole E, Cuzzocreo M, Dewey S, Fattebert J, Gagnon Gelzer E, Geremia C, Graves T, Hersey K, Hurley M, Kaiser J, Meacham J, Merkle J, Middleton A, Nuñez T, Oates B, Olson D, Olson L, Sawyer H, Schroeder C, Sprague S, Steingisser A, Thonhoff M. 2020. Ungulate migrations of the western United States. Volume 1. U.S. Geological Survey Scientific Investigations Report 2020–5101. 119 pp.

Kerley GIH, Kowalczky R, Cromsigt JPM. 2012. Conservation implications of the refugee species concept and the European bison: king of the forest or refugee in a marginal habitat? Ecography 35:519-529.

Koprowski JL, Krausman PR. 2019. International wildlife management: conservation challenges in a changing world. Johns Hopkins University Press, Baltimore, USA. 248 pp.

Krieg H. 1940. Als Zoologe in Steppen und Waeldern Patagoniens. Bayerischer Landwirtschaftsverlag, Muenchen, Germany. 197 pp.

Ladio AH, Lozada M. 2004. Summer cattle transhumance and wild edible plant gathering in a Mapuche community of northwestern Patagonia. Human Ecology 32:225-240.

Laliberte AS, Ripple WJ. 2004. Range contractions of North American carnivores and ungulates. BioScience 54(2):123-138.

Lea JMD, Kerley GIH, Hrabar H, Barry TJ, Shultz S. 2016. Recognition and management of ecological refugees: A case study of the Cape mountain zebra. Biological Conservation 203:207-215.

Leopold AS, Cain SA, Cottam C, Gabrielson IN, Kimball TL. 1963. Wildlife Management in the National Parks. American Forests 4:32-35, 61-63.

Liebermann J. 1962. Sobre la historia natural del huemul. Anales de la Academia Argentina de Geografia 6:157-168.

Lyman RL. 2006. Paleozoology in the service of conservation biology. Evol Anthropol 15:11-9. doi:10.1002/evan.20083
Lyras GA, Giannakopoulou A, Lillis T, van der Geer AAE. 2019. Paradise lost: Evidence for a devastating metabolic bone disease in an insular Pleistocene deer. International Journal of Paleopathology 24:213-226.

Massara Paletto V, Buono G. 2020. Métodos de evaluación de pastizales en Patagonia Sur. Buenos Aires: Ediciones INTA, Centro Regional Patagonia. 288 pp.

McClure MF, Bissonette JA, Conover MR. 2005. Migratory strategies, fawn recruitment, and winter habitat use by urban and rural mule deer *(Odocoileus hemionus)*. Eur J Wildl Res 51:170-177.

Mincher, BJ, J Mionczynski, PA Hnilicka, RD Ball, TX Houghton. 2008. Some aspects of geophagia in Wyoming bighorn sheep *(Ovis canadensis)*. E J Wildl Res 54(2):192-198.

Morrison TA, Merkle JA, Hopcraft JGC, et al. 2021. Drivers of site fidelity in ungulates. J Anim Ecol 90:955-966.

Moser CA. 1962. The bighorn sheep of Colorado: a review of Colorado’s bighorn sheep studies. Technical Publication No. 10. The Colorado Game and Fish Department, Denver, Colorado, USA. Pg. 1-49.

Nelson ME, Mech LD. 1999. Twenty-year home-range dynamics of a white-tailed deer matriline. Canadian Journal of Zoology 77:1128-1135.

Nüchel J, Bocher PK, Xiao W, Zhu AX, Svenning JC. 2018. Snub-nosed monkeys (Rhinopithecus): potential distribution and its implication for conservation. Biodiversity Conservation 27:1517-1538.

Packard FM. 1946. An ecological study of the Bighorn sheep in Rocky Mountain National Park, Colorado. Journal of Mammalogy 27(1):3-28.

Peters W, Hebbelwhite M, Mysterud A, Spitz D, Focardi S, Urbano F, et al. 2017. Migration in geographic and ecological space by a large herbivore. Ecological Monographus 87:297-320.

Phoca-Cosmetatou N. 2004. Site function and the ‘ibex-site phenomenon’: myth or reality? Oxford Journal of Archaeology 23(3):217-242.

Putman R, Flueck WT. 2011. Intraspecific variation in biology and ecology of deer: magnitude and causation. Animal Production Science 51(4):277-291.

Rau, JA. 2003. Crecimiento poblacional de huemules del sur nativos y reintroducidos en la zona austral de Chile. In: Acosta-Jamett G, editor. 4ta Reunión Chileno-Argentina sobre Estrategias de Conservación del Huemul: CONAF and CODEFF, Las Trancas, Chile: pp. 43-45.

Ren JZ, Zhou ZY, Pan B, Chen W. 1987. Selenium distribution in four grassland classes of China. In: Comb GF, Spallholz JE, Levander OA, Oldfield JE, editors. Selenium in biology and medicine. New York: AVI Books: pp. 769–774.

Riquelme C, Estay SA, López R, Pastore H, Soto-Gamboa M, Corti P. 2018. Protected areas’ effectiveness under climate change: a latitudinal distribution projection of an endangered mountain ungulate along the Andes Range. PeerJ 6:e5222; DOI 10.7717/peerj.5222

Rissenhoover KL, Bailey JA, Wakelyn LA. 1988. Assessing the Rocky Mountain Bighorn Sheep Management Problem. Wildlife Society Bulletin 16(3):346-352.

Ryan SJ. 2006. The role of culture in conservation planning for small or endangered populations. Conserv Biol 20: 1321–4. doi:10.1111/j.1523-1739.2006.00347.x
Sawyer H, Middleton AD, Hayes MM, Kaufman MJ, and Monteith KL. 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. Ecosphere 7(10):e01534. 10.1002/ecs2.1534.

Sawyer H, Merkle JA, Middleton AD, Dwinnell SPH, Monteith KL. 2019. Migratory plasticity is not ubiquitous among large herbivores. Journal of Animal Ecology 88:450-460.

Soga M, Gaston KJ. 2018. Shifting baseline syndrome: causes, consequences and implications. Frontiers in Ecology and the Environment 16(4):222-230.

Spitz DB, Hebblewhite M, Stephenson TR, German DW. 2018. How plastic is migratory behavior? Quantifying elevational movement in a partially migratory alpine ungulate, the Sierra Nevada bighorn sheep (Ovis canadensis sierrae). Can J Zool 96:1385-1394.

Teitelbaum CS, Fagan WF, Fleming CH, Dressler G, Calabrese JM, Leimgruber P, Mueller T. 2015. Ecological Letters. Ecological Letters 18(6):545-552.

Thirgood SJ. 1995. The effect of sex, season and habitat availability on patterns of habitat use in fallow deer. J. Zool., Lond. 235:645-659.

van de Kerk M, Larsen RT, Olson DD, Hersey KR, and McMillan BR. 2021. Variation in movement patterns of mule deer: have we oversimplified migration? Movement Ecol. 9, 44.

Van Soest PJ. 1982. Nutritional Ecology of the Ruminant. O & B Books, Inc., Corvallis, Oregon, USA. 373 pp.

Via S, Gomulkiewicz R, DeJong G, Scheiner CD, Schlichting SM, Van Tienderen PH. 1995. Adaptive phenotypic plasticity: consensus and controversy. TREE 10(5):212-217.

von Colditz R. 1925. Im Reiche des Kondor. Paul Parey, Berlin, Germany. 415 pp.

von Thüngen J, Lanari MR. 2010. Profitability of sheep farming and wildlife management in Patagonia. Pastoralism 1(2):274-290.

Wells KW, Stangl FB. 2003. Superior size and antler development in populations of white-tailed deer (Odocoileus virginianus) from the North Texas rolling plains. Texas Journal of Science 55(4):337-346.

Xu W, Barker K, Shawler A, Van Scoyoc A, Smith JA, Mueller T, Sawyer H, Andreozzi C, Bidder OR, Karandikar H, Mumme S, Templin E, Middleton AD. 2021. The plasticity of ungulate migration in a changing world. Ecology, in press, doi:10.1002/ECY.3293

Yockney IJ, Hickling GJ. 2000. Distribution and diet of chamois (Rupicapra rupicapra) in Westland forests, South Island, New Zealand. New Zealand Journal of Ecology 24(1):31-38.