Recent advances in the nutritional ecology of the Patagonian huemul: implications for recovery

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Abstract. Huemul (*Hippocamelus bisulcus*) numbers had already declined drastically by the 1800s. Only ~500 animals remain along 1800 km of the Argentine Andes between 34 and 54°S, without cases of recolonisation or numerical responses. In Chile, at least two populations have increased; the remaining populations have either decreased or are assumed to be stable. During a Chilean–Argentine meeting in 1992 several factors were hypothesised to be important for huemul recovery (cattle, exotic trees, irrational forestry, exotic animals, illegal hunting, diseases, dogs, reduced numbers), but these can be rejected as key explanations for the general lack of recovery. Each factor may play an additive role – alone or in combination – in certain populations, but none of them are likely a primary cause. Our objective is to evaluate alternative factors and several indications warrant us to postulate that nutritional ecology instead plays a central role in the general absence of recovery. A wide range of antler quality is encountered among huemul today, with well developed specimens known primarily from historic times. If antler expression in huemul is homologous to other cervids, it follows that most extant populations are under suboptimal conditions. Another important clue is a high prevalence of age-independent osteopathy among adults. We hypothesised that such generalised secondary chronic alveolar osteomyelitis, osteoarthritis and periodontitis were hypothesised to relate to nutritional ecology. Meagre antler development with frequent asymmetry, high prevalence of osteopathy, and low recruitment rates could all be related to common and limiting nutritional factors known to cause the described phenomena. Initial investigations point to several lines of evidence that support the hypothesis that deficiency in iodine and selenium (Se) might be involved. Among other things, such deficiencies impair bone growth, reproduction, neonatal development, the immune and nervous systems, and cause periodontitis in ruminants. Se deficiency directly affects iodine metabolism. Only decades ago, overt iodine deficiency in humans living in these areas was very common. For free-ranging livestock, overt Se deficiency has been described in Chile: supported by geology, pedology, topography, and climatic patterns. It is well known that valley bottoms, flood plains, and habitats downwind from glacial areas provide higher provision of iodine and Se. The nexus to the nutritional ecology of huemul likely is the inaccessibility of most traditional winter ranges, elimination of migratory traditions, and concomitant elimination of source populations. Se and iodine provisions diminish with altitude, which at the same time increases physiological needs due to hypoxia, and intensified radiations and exercise. Most extant huemul populations occur in remote high-altitude refuges, or inaccessible Pacific coastal areas. Migration, an acquired behaviour, has been eliminated through past overhunting of this population segment; huemul being very vulnerable to human predation were killed by the thousands to feed people, dogs, chicken and pigs, and their skins were used for shelters. Huemul currently dispersing from refuges are generally being killed when entering former source areas now occupied by settlers and their dogs. Other ungulates driven into mountain refuges have been shown to be deficient in these trace minerals and responded well to mitigation of the deficiency. Thus, prevention of reaching traditional winter ranges or valley bottoms might result in inadequate mineral supply to huemul.

Additional keywords: behaviour, *Hippocamelus bisulcus*, migration, iodine, overhunting, selenium, trace minerals.

Introduction

Huemul (*Hippocamelus bisulcus*) occur in the southern cone of Chile and Argentina, where, by the 19th century, they had declined drastically. While Chile implemented total protection in 1929, it was not until 1983 that huemul were recognised as vulnerable in Argentina, not gaining endangered status until 1996. There are only ~1000 huemul left in Chile and ∼500 in Argentina, between ~34 and 54°S.[1] The first Chilean-Argentine meeting, organised in 1992 to evaluate the conservation predicament of huemul, resulted in a preliminary list of factors considered potentially important for recovery of ~100 remaining small huemul populations. Subsequent meetings (1995, 1998, 2002, 2006), the national recovery plan (2001) and government of Argentina dogmatically list the same factors as causes of declines and failures of recovery.[2] Meanwhile, some mitigation has been initiated based on this belief system, but without monitoring, the importance of these factors as threats cannot be substantiated nor ranked. Concurrently, there are no signs suggesting recuperation of those populations that have been confirmed during the last three decades. With no direct studies ever conducted on huemul in Argentina or on most populations in Chile, the actual role played by each assumed negative factor on population dynamics still remains unidentified. For instance, extensive livestock production is claimed to be a threat, yet huemul have coexisted with feral cattle for centuries.[3] Some populations have declined, are declining or became extinct without apparent contact with livestock,[4] casting doubt on the importance of cattle as a general detrimental cause. There are no studies supporting suppositions that replacement of native forest with exotic trees, or 'irrational management' of native forests have affected extant huemul. On the contrary, the only two expanding populations are in areas previously logged and burnt and huemul there have responded positively, similar to other cervids. Moreover, two populations are currently recolonising treeless areas, which agrees with huemul presence hundreds of kilometres from forests even historically.[3,5] Then, there are no studies supporting the conjecture that exotic animals impact or displace huemul. Exotic herbivores may eat the same plant species or have similar preferences as huemul,[6] however, this becomes only relevant if it reduces the population growth rate lambda of huemul to <1.[4] Considering known huemul diet behaviour, they can likely shift diets without necessarily driving lambda to <1, as known for other cervids.[7] Furthermore, with respect to several exotics including red deer (*Cervus elaphus*), huemul populations have also declined or became extinct in their absence.[4] Considering the impressive densities of exotic domestic and wild herbivores in former huemul habitat,[8] it was considered unlikely that such areas are limiting to huemul in terms of energy and major plant nutrients.[4,9] Moreover, mammalian herbivore communities commonly are multi-species assemblages, and the presence *per se* of other herbivore species is unlikely to be problematic for huemul, as evidenced by documented coexistence with livestock, pudu (*Pudu puda*) and guanaco (*Lama guanicoe*). There are no studies supporting claims that illegal hunting or dogs prevent recovery, solely occasional kills have been documented.[4] No study supports the supposition that diseases transmitted from domestic and wild exotic herbivores caused declines or prevent recovery of huemul,[4,10] and practically all of the described parasites are generally considered nonthreatening, are common in livestock and thus occur in most areas with livestock.[10]

Taking a holistic approach we posited that major underlying problems possibly explaining the general lack of recovery of huemul have not yet been considered.[11] Here we describe a working hypothesis in which we propose a new ecological explanation using an epidemiological approach. We suggest that huemul are likely subjected to deficiencies of trace minerals that are important for adequate recruitment as deduced from: (i) huemul currently existing principally in areas that were subjected to glaciation and are dominated by igneous bedrock with low provision of trace minerals; (ii) prevalent volcanic ash layers (with a high degree of trace mineral binding) that are thicker with increasing altitude and precipitation where most huemul remain; (iii) distance downwind from the Pacific regarding aerial trace mineral deposition; (iv) lack of access by huemul to valley bottoms and former winter ranges where trace mineral concentrations should be higher; (v) anthropogenic impacts known to reduce trace mineral availability (fires, biomass extraction); (vi) iodine and selenium (Se) deficiency occurring in local human and livestock populations; and (vii) a high incidence of age-independent osteopathology in skeletons of huemul.[12] Se and iodine are intricately interacting, with deficiencies of Se causing secondary iodine deficiency, and due to their basic biochemical functions, their effects span many aspects of biology and ecology. Endangered ungulates suffering from deficiencies of these two trace minerals in other montane regions of the world have exhibited reduced reproductive rates, reduced growth rates of juveniles, higher predation rates on juveniles, and increased susceptibilities to diseases. We suspect similar underlying causes to be responsible for the current predicament of the huemul.

We ask, what might account for a generalised absence of numeric responses and recolonisations of huemul? Only two Chilean populations have increased, and no such cases are known from Argentina. The frequently claimed factors, though perhaps of relevance on local scales, do not account for the overall trend of decline throughout the huemul's entire distributional range and thus can be excluded as causes for the general lack of recovery. Given that population dynamics reflect the interplay of reproduction and mortality rates, we evaluate the potential role of nutritional factors that are known to affect reproduction and survival.

Selenium

Geology, pedology and climate

Areas providing marginal or low Se in forage elsewhere are characterised by volcanic and basaltic rocks, granite, argillites and quartzites, andesitic and puroclastic rocks, glacial deposits, and cold-humid soils.[13–15] An additional major source is vapour-phase Se from the ocean, resulting in a uniform aerial concentration.[16] In Norway, the deposition is highest by the coast and decreases further inland (Fig. 1*a*).[14,17,18] This effect stems from prevailing wind patterns resulting in decreasing dry and wet depositions going inland, with wet deposition contributing as much as 82% of intake to grazing animals.[19] Washout is further potentiated due to orographic precipitation which is extremely pronounced in the southern cone of Patagonia (Fig. 2): current huemul refuges are concentrated in southern wet Pacific coastal areas (3–6 m precipitation), and inland along the continental divide (2–6 m precipitation). Moreover, the topography modulates soil Se concentrations as leaching occurs on ridge land and results in a decrease of soil Se, while adjacent valley soils maintain or increase Se levels.[20] Extensive areas thus exhibit lower plant concentrations at high rather than low altitude,[13,21,22] as reflected in mountain goats living at higher altitudes having lower Se than elk and deer from lower areas,[23] or resident rodents along a forested altitudinal gradient (Fig. 3).[24] Agostoni *et al*.[25] also found that people from the high

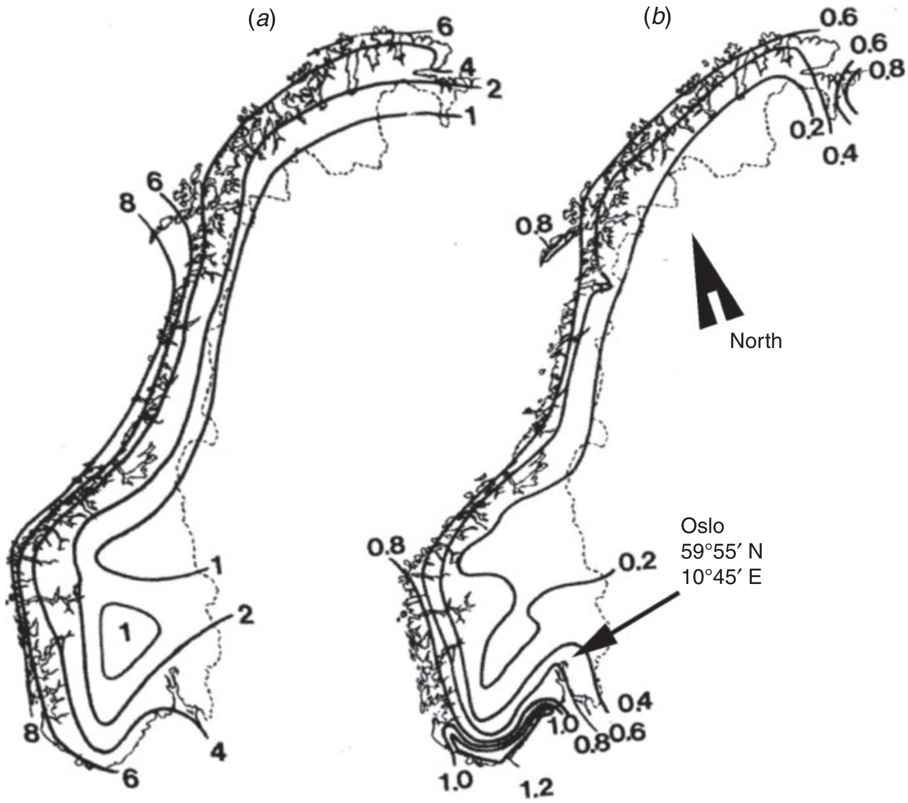

Fig. 1. (*a*) Selenium gradient measured in moss (ppm) due to aerial deposition from westerlies. (*b*) Iodine gradient measured in moss (ppm) due to aerial deposition from westerlies (courtesy of E. Steinnes). The dotted line is the border with Sweden.

Andes had significantly reduced glutathione peroxidase (GPx) activity from low Se serum levels, as compared with lowland people.

There are no known biochemical functions for Se in plants, which mainly provide an index to bioavailable Se as they take it up according to soil solubility. Bioavailability of Se is reduced in more acidic soils by transforming Se into forms unavailable for plant uptake.[26,27] In addition, export of plant biomass, directly or indirectly as through herbivores, removes important proportions of bioavailable Se and results in further soil acidification.[28,29] Ruminants deposit Se in feces and urine in forms principally unavailable to plants.[30–33] Therefore, artificially high densities of ruminants impact immobilisation rates of Se. Also of importance are fires as they remove Se from the system by volatilisation, which may be substantial in areas with marginal or low Se concentrations because much of the Se available to plants occurs in standing biomass.[34,35]

Biochemical functions

Selenium metabolism probably evolved early along with air respiration, as many mammalian selenoproteins can be traced back to ancestral unicellular eukaryotes.[36] Only recently discovered, the genetic code had to be expanded with Se now forming part of the 21st naturally occurring amino acid, selenocysteine, essential in all mammals.[37] Se is the active part of several enzyme systems involved in oxygen metabolism (e.g. GPx) functioning at very basic biochemical levels,[38] and deficiency is thus expressed in myriad ways. In all animal species studied, Se deficiency impairs reproductive performance of both males and females. It affects litter size, conception rate, embryonic mortality, age of first breeding, neonatal mortality, and also causes retention of placentas.[39] In ruminant neonates, White Muscle Disease (WMD) is a common expression of deficiency. For Se-deficient males, spermatogenesis may continue, but with abnormalities, leading to a reduction in sperm tail stability. Consequently, sperm count and fertility are sharply reduced even though some sperm motility may persist.[39] Furthermore, Se is involved in bone disease,[40,41] is fundamental for proper immune function and infectious disease resistance, myocardial disease, cancer prevention, aging processes and iodine metabolism.[37,39,42] Several selenoproteins are residents of the endoplasmic reticulum (ER), revealing the emerging important role of Se in ER function, with four selenoproteins nearly exclusive to vertebrates.[36]

Interaction with iodine metabolism

Selenium plays an essential role in thyroid hormone metabolism and thus plays a major role in secondary iodine deficiency. First, all three deiodinases contain Se and they regulate synthesis and degradation of the biologically active thyroid hormone T3, required for normal growth and development, and for energy

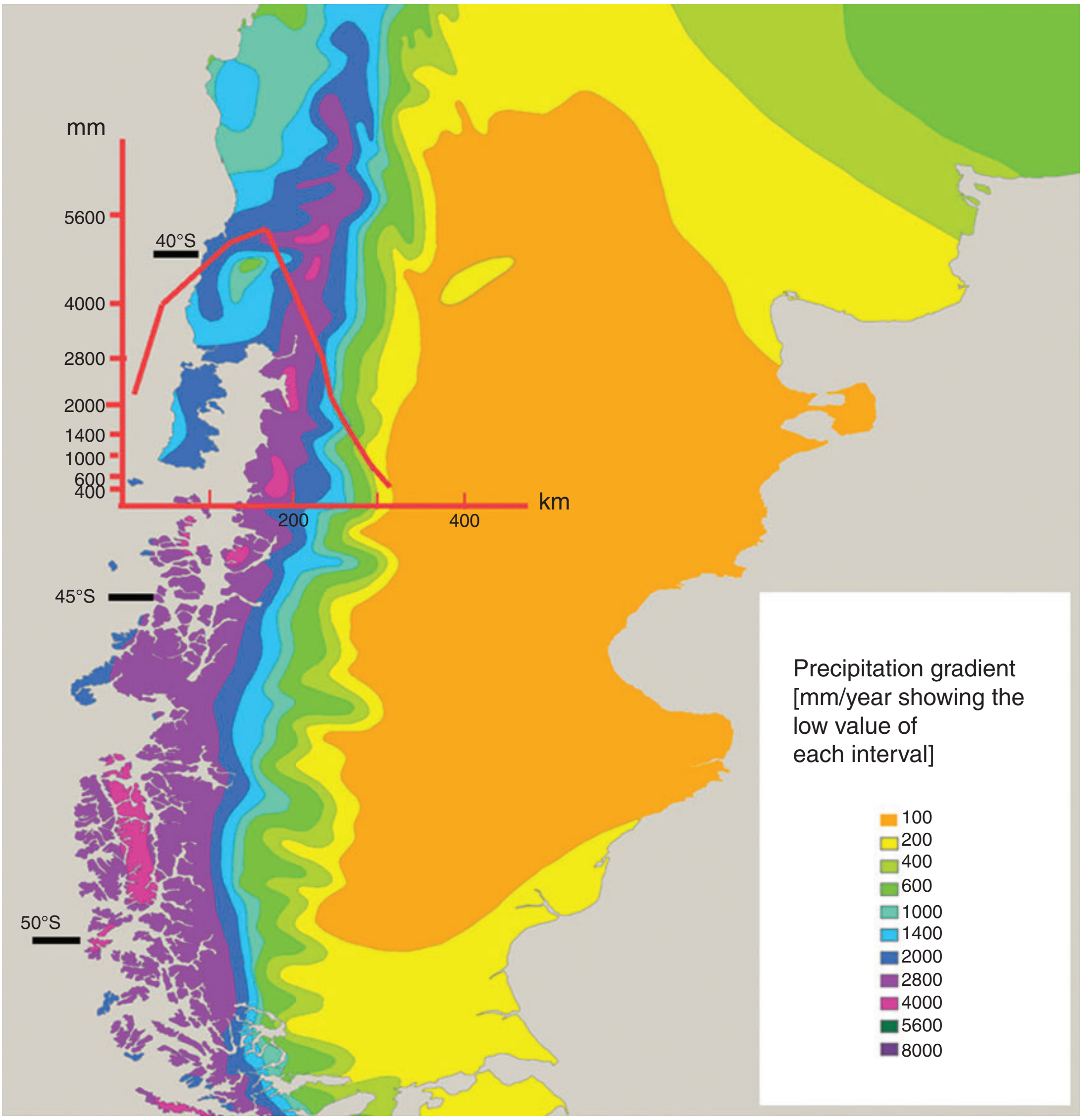

Fig. 2. Precipitation pattern in the southern cone of Patagonia dominated by the Andean orography. The graph represents an east–west transect at 45°S.

production and O_2 consumption in cells. Second, selenoperoxidases and possibly thioredoxin reductase protect the thyroid gland from H_2O_2 produced during the synthesis of thyroid hormones.[42,43] Supplementation in Se-deficient cattle resulted in higher T3 activity and higher immunoglobulin concentrations in colostrum.[44,45] Also, physiological demands for Se and iodine under high-altitude conditions (hypoxia, temperature, radiation, exercise) are higher.[46]

Iodine

Geology, pedology and climate

Natural iodine minerals are rare and form a negligible amount of the earth's available total iodine, occurring mainly as very insoluble iodides of silver and copper.[47] Intrusive and extrusive igneous rock have similar mean concentrations of 0.24 mg/kg, sedimentary rocks contain around 2 mg/kg, and the median in metamorphic rock is ~0.37 mg/kg. Soils tend to have a higher concentration of total iodine, but only a low percentage is soluble. Soils rich in organic matter and humus are also rich in iodine. More acidic soils reduce the iodine uptake by plants which, on the other hand, enrich the iodine content of terrestrial ecosystems by trapping iodine from dry and wet precipitation. This enrichment occurs, providing the vegetation is not cropped and removed. Cropping can remove up to 0.6 mg/m^2 and deplete the soils of iodine, if input is less.[47] Burning also results in losses into the atmosphere. Reith[48] showed that Dutch soils used for agriculture lost iodine over time. Glaciation is also an important factor in producing iodine-poor soils, as the time for subsequent soil formation is very short.[47,49]

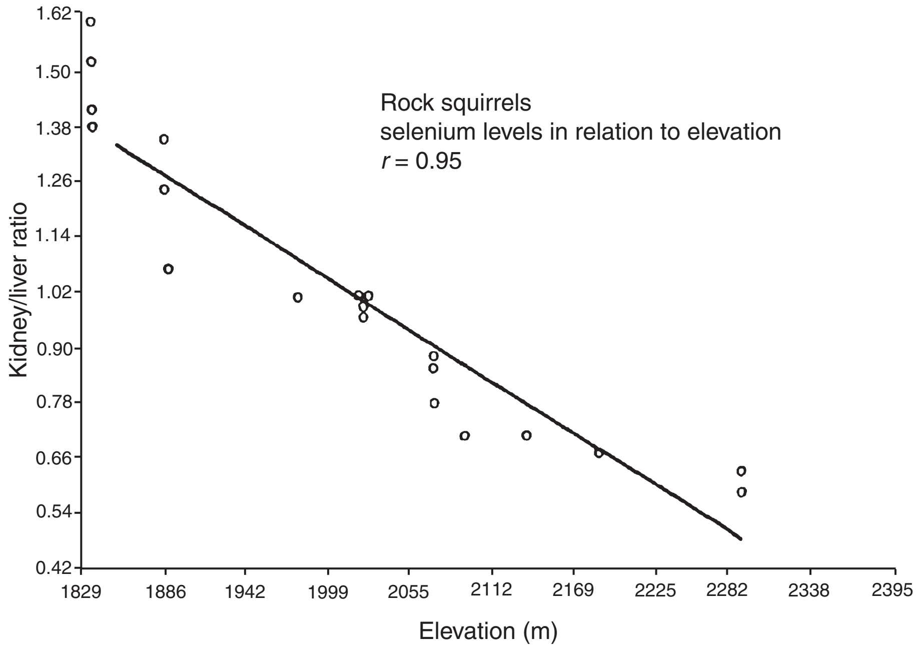

Fig. 3. Selenium levels in resident rodents along a forested altitudinal gradient. Kidney : liver ratios of >l were taken to indicate that selenium intake was adequate (from [24]).

Soils, however, are a poor index of environmental iodine status as the geochemical cycle of iodine is dominated by volatilisation from the soil–plant interface to the atmosphere.[50] Iodine is very mobile in the lithosphere, hydrosphere and atmosphere. In the biosphere, however, it is immobilised through assimilation and accumulation in decaying organic matter. Consequently, iodine soil concentrations diminish abruptly with increasing distance from the ocean as atmospheric deposition is by far the most important input for iodine (Fig. 1*b*).[17,18,49] Iodine in the atmosphere also decreases with increased altitude,[22] dropping to 40% at 1000 m a.s.l. from concentrations at sea level,[18,33] and thus creating an altitudinal gradient in plant concentrations as noted for Se. Furthermore, the loss in soil from leaching is proportional to the amount of precipitation,[22] which is significant in the southern cone of Patagonia due to Andean orography (Fig. 2). Only a small proportion of the naturally occurring iodine in soils of humid temperate regions is soluble in water.[51]

Biochemical functions

Thyroids are present in all vertebrates and are unique among endocrine glands in storing their secretory products (thyroid hormones) extracellularly. These hormones play an indispensable role in numerous biochemical reactions in peripheral tissues such as skeletal and heart muscle, liver and kidney which collectively control the basal metabolic activity of the organism. Iodine is also essential for late-gestational development, particularly of the central nervous system.[36,52,53] Iodine deficiency during pregnancy has negative and irreversible effects on the developing fetus, and postnatal deficiency is associated with further cognitive deficits.[54,55] Although many physiological processes in ruminants require normal activity of the thyroid, mainly its role regarding reproductive physiology has generally been emphasised. Due to iodine involvement in many metabolic processes, deficiency has many different expressions. In ruminants, common problems include abortions, young born dead, weak neonates, increased neonatal mortality, prolonged gestation and infertility. In addition, juvenile growth is deficient, neurological development is aberrant, plus various other less specific symptoms.[56,57] Humans and other mammals of similar size have ‘lost’ the ability to reabsorb iodide efficiently, and are especially susceptible to iodine deficiency,[58] which is exacerbated by Se deficiency.

Animal migration as a means to fulfil nutritional requirements

Colonisations or invasions of cold-temperate habitats occur by dispersal from source areas which normally consist of productive habitats. Seasonal migration is a facultative trait which originates from sedentary populations, as part of the process of colonising new areas during summer (i.e. summer ranges).[7,59] As occupied ranges expand, migration distances may increase over several generations with individuals returning annually to ancestral winter (source) ranges. Animals then may cross several mountain ranges to get to traditional winter–summer areas,[60] and migratory tradition can override habitat quality and predation risks. Migration is not a species-specific trait. Even in highly migratory species like *Rangifer*, there are usually always sedentary members in a population.[61] Migratory or sedentary traditions are transmitted vertically as cultural traits, being perpetuated within family units, or even copied by others, and thus, cervid populations commonly have simultaneously sedentary as well as migratory individuals.[7]

Additionally, a small proportion of subadults, which disperse independently, can start new traditions. This pattern has been described for red deer recolonising the Swiss National Park: initial populations established as sedentary animals in the most productive areas, and only when densities increased, did satellite areas become populated in a migratory manner.[59] This phenomena also occurred with red deer introduced onto former huemul winter ranges in Nahuel Huapi park (Argentina) (W. T. Flueck and J. M. Smith-Flueck, unpubl. data).

Carter *et al*.[13] found that forage produced on most upper elevational summer ranges in north-western USA were low in Se concentration, and livestock losses from WMD and other Se-responsive diseases would occur on these rangelands if it were not for intermittent grazing on adequate winter range allowing a build-up of Se reserve. Livestock have been shown to be Se deficient at high, but not at low elevation in the Columbian Andes, with GPx differing by 41%.[62] Thus livestock grazing on the upper summer ranges often do not obtain adequate diet Se for that part of the year. Low Se diets may not represent a WMD hazard if animals can build or replenish protective reserves, because a few months of Se reserve protects animals (including offspring) from WMD for a full year.[13] Thus, prevention of reaching traditional winter ranges or valley bottoms might result in inadequate mineral supply to the animal.

Use of mineral licks is an important adaptive behaviour in areas with mineral deficiencies: mineral licks are actually used by all North American species of ungulates and are considered critical to population health.[63] Kalkus[64] observed that wild deer were free of disease in regions where goitre was common in domestic livestock, attributing this difference to deer frequenting licks with soil having 21 times more iodine than found in forage. Similarly, mountain goats (*Oreamnos americanus*) will travel 25 km during spring and summer to get to natural and artificial licks on winter ranges, crossing large stretches of habitat considered unsuitable for mountain goats. Some licks were high in phosphorus, but goats preferred sodium iodide over nine other types of salts.[63,65] Increased iodine intake from mineral licks has been noted in other ungulates as well.[66,67] Although enriched sodium frequently appears to be the attractant, animals often prefer certain mineral licks over salt licks.[68] Several other ungulates including cervids are known to have made long-distance migrations at least in the past and to thereby access low-elevation licks.[60,69] Thus, not only are mineral licks commonly found at low elevations, especially on winter ranges, but animals may briefly leave their summer range (1–2 days), and make large excursions to winter ranges solely to use mineral licks for a few hours to a few days, even at increased risk from predation.[63,66,70–72] This activity increases intake of several elements, including iodine and Se.[67,72,73] Topographical location of licks suggested that they frequently present accumulation sites for runoff from higher elevations, or they are next to water ways.[66,70,74] Thus, traditional migratory behaviour is often in concert with traditional use of mineral licks, but the latter are used independent of climate or season.[60,63,65,69,72]

Nexus between nutritional ecology of huemul and lack of recovery

Geology, pedology and climate in Patagonia

The central Andes are characterised by acidic rocks such as andesites, diorites, or granites, with the landscape strongly modified by several past glaciations. Soils are generally acidic and strongly influenced by volcanic deposition.[75,76] Volcanic andosol deposits up to 6 m deep, with pumice layers, overlay glacial deposits and occur as a nearly continuous formation between 36 and 47°S, on both sides of the Andes, and underlay most of the southern beech and cypress forests.[77] The deposits near the continental divide are extensive, also because high rates of precipitation fixed the ashes in local soils which are principally allophanes that often cover glacial subsoils. The influence of volcanic ash diminishes eastwards, as drier climate causes ashes to be blown away.[78–80] These soil characteristics result in low bioavailability of Se and iodine[81] and are therefore characteristic of areas currently containing remnant huemul.

Patagonia receives minimal aerial Se and iodine input. Due to Pacific westerlies, deposition of these nutrients is highest by the coast and decreases further inland.[16,18] This decreasing trend of depositions towards the east is exacerbated due to the orography of the Andes.[18,47] Consequently, Se and iodine provision in Argentina east of the Andes is expected to be lower than in Chile. Moreover, south Pacific aerial iodine concentrations are several fold lower than those in the northern Pacific: measurements by Hawaii showed gaseous iodine to be 3–4 times higher and particulate iodine 3–5 times higher than in the southern Pacific,[82] where iodine deficiency would thus be more exaggerated.

Selenium and iodine status in Patagonia

Selenium concentrations in most forages in southern Chile are deficient.[83] Cattle showed depressed GPx and T3 (iodine) activities that improved upon supplementation with Se,[84] and notably, overt cases of WMD have also been diagnosed.[85] Another important aspect of Se relates to ruminants affecting soil Se concentrations. As stocking rates are increased, so do the proportion of Se unavailable to the biological cycle, as ruminants return Se to soils mainly in unsoluble forms.[33] Moreover, livestock products that leave the system, take with them Se and other nutrients.[28]

Iodine levels in the soil-plant-animal system in Patagonia are dominated by persistent westerlies, low absolute aerial concentrations, with levels expected to drop quickly along the precipitation and altitudinal gradients, and high soils absorption. Indeed, most aerial iodine becomes washed out and is deposited in coastal areas where the highest precipitation occurs (3–8 m/year). Moreover, the landscape raises quickly eastwards reducing iodine air concentrations even further.[47] Accordingly, Quintana *et al*.[86] found that iodine concentrations in cow milk near the coast were 6 times higher than found inland at higher altitude where it resulted in clinical symptoms. With precipitation at the continental divide still quite high at 2–5 m/year, iodine concentration in air would be expected to be very low when air masses finally reach the eastern side of the Andes. In addition, soils, which are very young due to recent glaciation events and of a sandy nature, provide little organic matter for trapping deposited iodine and add it to the local cycle.[49] Moreover, the prevalent influence from volcanism is reflected in widespread allophanes and andosols, which results in a high degree of iodine and Se sequestration through absorption, leaving even less to enter the biological cycle.[87]

The average iodine concentration in forage samples between 38 and 44°S of Chile was 0.20 ± 0.08 ppm, at some 50–150 km from the coast, with all forage lacking adequate concentrations for cattle.[88] Muzzo *et al*.[89] showed that iodised salt supplementation was necessary to reduce endemic iodine deficiency in Chilean inhabitants living in areas of current huemul distribution. These results suggest iodine deficient forage in southern Chile, which may be associated with reported low blood concentrations of T4 in grazing cattle[57] and a moderate prevalence of goitre in livestock east of the Andes.[90]

In accordance, historic presence of endemic goitre on both sides of the Andes is well documented. In northern Chile, cretins and dwarfs have been described, and the goitre rate varied from 10 to nearly 40% in some districts. Farther south, cases were found along many valleys down to O'Higgins Province.[91] While in interior Chile deficiency was generally moderate, it was more severe on the eastern slopes in Argentina, particularly in the foothills of the provinces Mendoza, Rio Negro, Chubut, Santa Cruz and Tierra del Fuego. In this great 2000-km strip of territory, goitre has been known since the Spanish conquest; there are still focal areas with endemic goitre in this region of Patagonia.[92]

Skeletal disease in huemul as an indication of nutritional deficiencies

Iodine and Se play major roles in bone disease. Antler bone provides an excellent tool to interpret myriad biological and ecological relationships, due to being a luxury appendage regrown annually. Huemul antlers with four tines were once common and even five tines were documented in the past; yet erroneously, such multi-tine antlers are considered abnormal, which is clearly incompatible with modern understanding of antler biology.[4] Frequent subnormal antlers in extant huemul likely stem from nutritional deficiencies (Fig. 4*a*) as no cases of

Fig. 4. *Top 2 rows*: subnormal antler development in huemul. *Bottom row*: Normal antler development in red deer using the full spectrum of former huemul habitat. For examples of three- and four-point huemul antlers, see [4].

other potential factors like parasites, infectious disease, or injuries have been reported.[4,93] Corroborating the involvement of Se and iodine deficiency in exceedingly small and malformed antlers is the clear relationship between such deficiencies and reduced antler growth in other wild cervids.[94,95] Moreover, exotic red deer using the full spectrum of former huemul habitat show normal antler development (Fig. 4*b*). Protein or energy deficiencies as alternative explanations have not been reported for any of the current low-density small groups of huemul and appear improbable considering that equivalent habitats support 3000–5000 kg/km^2 of exotic ruminant biomass (huemul do not occur sympatrically with exotics at high density),[8] which is supported by very high marrow fat contents measured in huemul.[96] This supports our claim that shed antlers and racks of huemul from historic times and places present the standard norm.

Another important clue stems from one of the larger populations in Argentina, where we found a conservative prevalence of osteopathy of 52% among adults.[12] Of affected huemul, 63% showed mandibular, 100% maxillary, and 78% appendicular lesions. We also have observed similar lesions in populations in southern Chile. Lesions were age-independent; also discarded as primary etiologic factors were gender, fulminating infections, congenital anomalies, disorders of the metabolic, endocrine, genetic, or neurologic systems, parasitism or marasmus, and fluorosis. Instead, the generalised secondary chronic alveolar osteomyelitis and osteoarthritis were hypothesised to relate to the nutritional ecology of huemul.

Fig. 5. Wild huemul kept on a ranch in southern Argentina, 1911 (courtesy J. Taylor).

Huemul migrations as a clue to the current predicament?

Sedentary populations

Traditional winter ranges and valley bottoms were the likely source areas for huemul populations and migratory behaviour. This is corroborated by reports (1864–1953) of all-year resident huemul in quiet valley bottoms[3,9,97–101] or far from the Andes[102], and was compared with 'forest chamois' (*Rupicapra rupicapra*), which remain in low areas as opposed to chamois moving to high elevation Alps during the summer.[9]

Cases of migration

Huemul regularly moved between the high Andes and eastern low lands as late as 1850, whereas on the western side they moved down to coastal areas by the Pacific.[3,103,104] As recently as 1940, huemul were abundant in winter in some valley bottoms in Argentina, whereas most people living there now have never seen a huemul.[93] According to old inhabitants of Santa Cruz province in the 1930s (corroborated by old shed antlers), huemul used to migrate in groups of 50 from the high Andes to treeless steppe at 50 km, currently used for livestock.[105,106] Wintering groups of 100 or more huemul before 1902 were reported in treeless grasslands 80–100 km from mountain forests,[3] and Gigoux remarked that ranchers who did not hunt near their houses were able to hand-feed huemul when they came to these grasslands in large groups during winter[107] (Fig. 5). Based on telemetry in Chile, huemul will spend the evening and night in valley bottoms and move to higher elevations in the morning. However, this is only in valleys that are not settled or used by humans (C. Saucedo, pers. comm.; also see [108]). Such behaviour is in agreement with migratory behaviour of other Odocoilines that move from forested high mountains down to relatively flat grasslands and steppes.[109,110] Moreover, Philippi, a well recognised Chilean naturalist,[111] reported in 1892 that huemul feeding with cattle on summer ranges were commonly among groups of cattle being herded together to lower elevations for the winter (see also [93,98,99,107]).

Presence of huemul far from forested Andes

Like Odocoilines utilising the Rocky Mountain foothills and eastern prairies, huemul east of the Andes likely were a mixture of residents and migrators (see above). According to Moreno, huemul east of the Andes principally existed in the intermediary zone between the Patagonian tablelands and the foothills,[112] but also reached areas near the Atlantic coast (see also [93,113]). Sedentary behaviour would be possible based on current all-year presence of other ungulates (guanaco, livestock) in such areas.

Early explorers commonly found huemul occurring in great numbers together with guanaco in the bare hills and undulating areas of the 'so-called Patagonian pampa' to 270 km from the Andes.[3,5,100,114–116] Indigenous people in Argentina knew the animal well and hunted it regularly for skins and meat,[93] and tamed young deer as with guanaco.[114] Where feasible, they hunted huemul preferentially and hides were traded on the

Atlantic coast[104] and also in Punta Arenas in Chile.[117] Crews of early expeditions travelling through landscapes of steppe and open forest patches still found numerous groups of huemul such that, during a 3-week traverse of the area, one large crew was plenished with fresh meat every day.[100,115,118] Other explorers were 'not greatly surprised' to encounter huemul at 200 km from the Andes in treeless grasslands. Based on shooting many huemul, they 'could have very easily shot 10 huemul in a day' in the open habitat far from forests through which they were travelling. Local indigenous people affirmed to them that these deer were at one time even more numerous in that same region.[3,5]

Process of eliminating migratory huemul

Osgood described open landscapes with remnant huemul that 'looked like Wyoming and parts of eastern Colorado at the foot of the Rockies'[115], where one company was holding 150 000 sheep and 'everyone carries a gun here, usually in his belt on his belly in front'.

Sedentary huemul were likely the first to be extirpated as human pressure increased in favourable valleys; huemul's curious nature and apparent lack of fear would have made them an easy target. Eventually, this process of overhunting would have extended to migratory huemul as well.[3,5,101,107,115,119] In terms of fearlessness, Osgood[115] was able to throw rocks at individuals 10 m away; indigenous people even killed them with just rocks.[93] Equestrian pre-colonial Natives 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.[3,103] Once the use of feral and controlled livestock became common, huemul, when driven down by snow to lower forests, valley bottom and further out to open flats, were then much persecuted by the gauchos and their dogs.[119,120] As colonisation advanced and with it the rarity of huemul, hunters in one region were honoured with a feather in their hats if able to kill a huemul.[3]

The current absence of migratory huemul is thus related to having been killed by the thousands each year at rates up to 1–2 animals/km^2.[103,106,121] Huemul not only provided for human subsistence, but also were fed to dogs, chicken and pigs, and their skins served as shelters for people and domestic animals.[9,106,107,121] During the colonisation, loggers additionally hunted many huemul.[122] Eventually, only the most inaccessible areas provided refuges for the remaining huemul[99], and by 1952 it was acknowledged that the formerly abundant huemul only escaped total extinction from human encroachments by having survived in remote refuges of national parks.[123] Without a doubt, huemul were much easier to hunt than guanaco or feral cattle and thus, when present, were selected.[3,5,93,115] In 1897 Onelli related that during his many expeditions to the Andes, huemul numbers were already few due to the constant and heavy hunting pressure.[107] Early on, all areas useful as winter ranges for livestock were settled and forests were partially cleared by fire.[124–126] Instructively, during severe winters, livestock were lost by the thousands due to overstocking, which likely affected the few huemul that still had remained migratory to that point.

Although migratory huemul populations no longer exist, some seasonal altitudinal shifts, depending on the harshness of Winter, do occur and are more pronounced east of the Andes. A recent study, however, found that huemul did not use lower elevations and suggested it was due to prevalent livestock grazing and other human activities.[127] Nowadays, any huemul that make it to lower elevations in areas containing people are either killed (Nahuel Huapi National Park , Glaciares National Park in 2011), taken as pets (Lago Puelo National Park, one died; Futaleufu Reserve, confiscation), or killed by vehicles (Torres del Paine) (W. T. Flueck, unpubl. data). There are no reports of any huemul living in suburban or rural areas populated with people as known with other cervids, except for Torres del Paine Park where huemul remain near houses because neither hunting nor dogs are tolerated.

Consequences

By eliminating sedentary populations and selectively removing migratory huemul, the remaining animals become tied year round to refuges on summer ranges (Fig. 6). Beneficial behavioural traditions essential to survival are then lost, such as migratory routes to winter ranges and traditional mineral licks. Furthermore, loss of both migratory and low-altitude sedentary populations substantially reduces gene flow since systems involving both combined sedentary and migratory animals greatly enhance genetic mixing.[7]

Huemul potentially dispersing from such remnant populations would tend to follow prime habitat like valley bottoms and be at high risk of being eliminated by people or dogs. Alternatively, they could end up in vacant areas unable to form new population nuclei. For many, if not most, remaining huemul populations in Argentina, there are severe barriers preventing migrations to former valley bottoms and winter ranges. Harsh winters might induce individuals to move to more favourable lower areas, as they used to in the past, but they would be exposed to high risks. In contrast, two small populations in good Chilean areas have been recovering after reducing impact from hunting and ranching. No such cases are known from Argentina, likely because current populations do not live in source areas. It appears recruitment in all Argentine populations and in many Chilean ones is too low to allow for recolonisation or numeric increases.

In great contrast to low-density huemul populations condemned to refuge areas are the impressive historic and current densities of exotic herbivores, both domestic and wild, occupying former huemul habitat, particularly winter habitat.[8] The most parsimonious explanation for this discrepancy is the fact that exotic herbivores are able to use the full range of this grazing system, extending from the upper summer to the lower winter ranges and valley bottoms. Already in 1940, Krieg observed that the huge quantity (mass) of livestock and red deer, of excellent physical development, refutes the argument of limiting forage to explain the then already absence of huemul.[9] Most remaining huemul refuges occur near the continental divide at high elevations, which is thus frequently inferred to represent optimal habitat (Fig. 7). However, receiving high precipitation, distant from the Pacific, and with plant communities growing on soils strongly

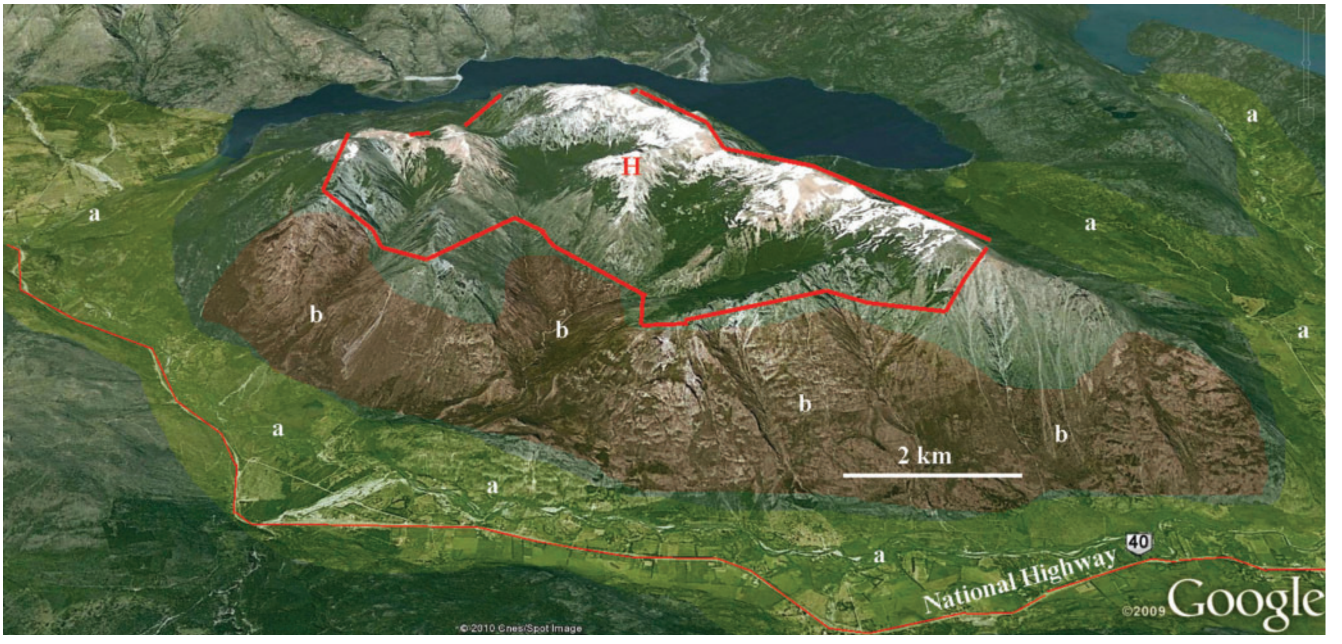

Fig. 6. Typical remnant huemul population (S42°9′, W71°28′): the area marked with 'a' is under intense agricultural use along a highway (i.e. inaccessible winter range); the area marked with 'b' is burnt forest and used heavily with free-ranging cattle; the circled high-elevation area marked with 'H' contains a few huemul as an island population, with some seasonal cattle presence.[6]

influenced by igneous rocks, glaciation and volcanism, we posit that these areas likely provide suboptimal trace mineral concentration to huemul. Deficiencies in trace minerals affect their reproduction and survival because they no longer have the ability to compensate for these nutritional imbalances by migrating to more favourable nutrient hot-spots like valley bottoms, historical winter ranges and mineral licks. The currently occupied refuges may thus be marginal or even sink areas, based on the consistent feature of absent numeric responses and recolonisations of huge areas of similar, yet unoccupied habitats.

Land use affecting trace mineral cycles

Additional concerns relate to potential impacts from land use that might affect areas currently inhabited by huemul. During colonisation, intentional fires had burnt 47% of forests in these areas by the 1900s[125] to open pasture for livestock.[3,100,126,128] During combustion, much iodine and Se would have been removed by volatilisation.[129,130] Further mineral depletion would have occurred from continuous extraction of wood, livestock and wildlife products.[128] For marginally available microelements like Se, bioavailability can be reduced within a few decades.[28,130,131] Most refuges currently inhabited by huemul contain potentially low trace mineral levels due to the geophysical history and past extensive land use practices.[132–134] Current extractive land use in areas of some remnant huemul populations will continue to deplete nutrients even further.

Discussion

Currently favoured factors implied in the failure of huemul recovery do not explain several observations. If these factors were working in concert, they might result in declines. But this is not the case. In fact, there are populations that might not be exposed to any of these factors and yet they still do not recover. Certainly, the loss of any individual in a highly reduced population (<20) can be problematic and even lead to local extinction.[135] However, in ample populations of cervids, even when at low density, losses from predation by puma, foxes and feral dogs,[136,137] casual illegal hunting and accidents would not present problems. One huemul population in Chile has increased in the presence of occasional predation by dogs and predators (puma, foxes) and poaching.[138] Healthy native cervids elsewhere are generally not affected by coexisting domestic and exotic wild herbivores, as most plant–herbivore systems are multi-species in nature.[8] Exotic herbivores as disease agents also do not generally affect ample populations of native cervids (in contrast to wild ovids), although risks from introducing epidemiologically important new diseases cannot be ignored. Given that huemul have coexisted with feral livestock for hundreds of years – in one ranch having been sympatric for the last 112 years[1] – livestock cannot therefore explain the decline of the entire species. Individual huemul or isolated groups could be affected by any one or more of these proposed factors and current conservation efforts thus aim at reducing or eliminating some of these. Being unsubstantiated conjectures, it is unknown if these factors do in fact explain the population dynamics, or if the applied conservation actions have made any improvements on a landscape scale.[139–141] Given the fact that populations appear not to recover, even in the absence of one or several supposedly detrimental factors, a more generalised explanation has been wanting.

A striking feature is the geology, pedology and climate underlaying the ecosystem with respect to the ranges currently occupied by huemul (Fig. 7). Other areas affected by glacial events, vulcanism or similar precipitation patterns are characterised by suboptimal bioavailability of trace minerals important for mammalian herbivores and people at high altitudes, such areas being prone to Se and iodine deficiencies.[22,49] Historical use of winter ranges and valley bottoms by huemul would likely have served to compensate for nutritional deficiencies on upper summer ranges. However,

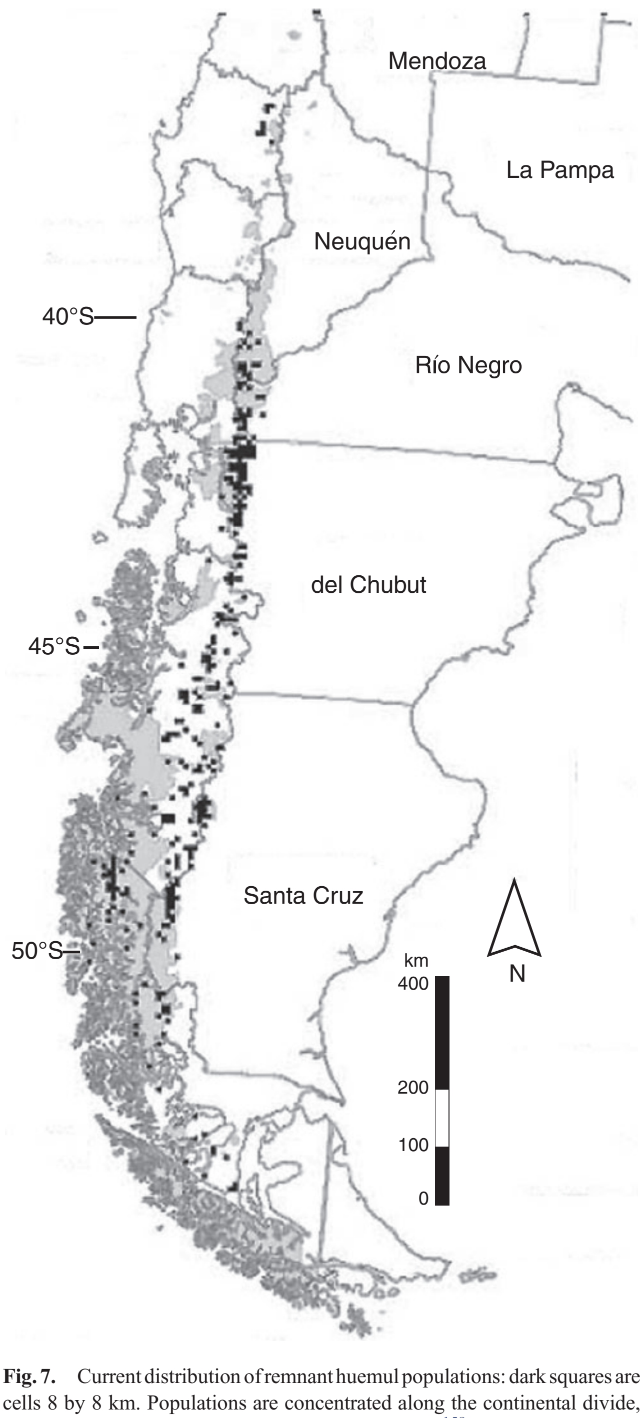

Fig. 7. Current distribution of remnant huemul populations: dark squares are cells 8 by 8 km. Populations are concentrated along the continental divide, except around 48°S where some coastal herds exist.[159]

traditional migratory behaviour was eliminated by overhunting, and new dispersers or migrators today will inevitably end up dead.[120] The importance of differential quality of seasonal ranges has been recognised previously for other species, with proposals to create corridors such that animals can move from summer to winter ranges, or even to transport animals from one site to the other.[142]

Availability of iodine is increasingly reduced from the Pacific Ocean to the east side of the Andes, and concurrent low bioavailability of Se would further depress iodine metabolism. This is substantiated by historic presence of endemic goitre on both sides of the Andes, being more severe on eastern slopes in Argentina. Therefore, huemul living in high-altitude refuges, and particularly east of the continental divide would be expected to be exposed to very low levels of iodine. Lack of access to valley bottoms, former winter ranges and mineral licks would exacerbate low iodine intake. Due to iodine's effect on central nervous system development, behavioural responses of huemul might be affected by deficiencies, including antipredator behaviour. Bioavailability of Se east of the continental divide is also expected to be low. Records of overt Se deficiency in livestock from the Chilean side further support that hypothesis. In addition, besides lower Se concentrations in forage at high altitude, Se enzyme activities are much lower at high altitude.[62,143] Therefore, huemul living in high-altitude refuges near the continental divide are expected to be exposed to compromised Se metabolism, and lack of access to habitats formerly used would exacerbate low Se intake. Overall, the anthropogenically induced distribution of current remnant huemul populations (Fig. 7) largely coincides with areas having the worst possible provision of key nutrients within the biophysics of this region (Figs 1–3) due to the biogeochemical properties of iodine and Se. As numerous remnant populations occur in rather limited spaces of few square kilometres, they are likely exposed to concomitant nutritional stress (Fig. 6).

Access to only marginal or low dietary iodine and Se levels results in a plethora of changes. Absence of clinical signs has long been considered inappropriate as evidence for adequate mineral nutrition,[70] and subclinical deficiencies are widespread and more important.[72,131,144,145] Although iodine and Se deficiencies are biochemical phenomena, these are expressed in reduced immune functions,[146,147] reduced systemic growth and reproductive potential, and behavioural changes. Thus, the proximate diagnosis for ungulates restricted to upper portions of mountains might be death due to some disease, but the ultimate factor might be lack of microelements.[148,149] Similarly, predation rates might be taken as the cause of the problem, whereas the ultimate factor might be behavioural or musculoskeletal changes due to nutritional deficiency of iodine and/or Se, causing animals to be weak, uncoordinated and behaviourally impacted, i.e. physically and cognitively handicapped.[148,149] Many huemul populations are beyond subclinical stages: poor antler development and osteopathology clearly show that extant huemul live under acute geochemical stress.[12]

Micronutrients like iodine and Se have been proposed to influence ecosystems such as by shaping communities in Australia or New Zealand[129,150] due to their cascading effect via modifying the population dynamics of large herbivores. The influence exerted by large herbivores over plant communities is well documented and depends on their population dynamics. It has been shown experimentally that increasing Se to otherwise deficient wild deer increased the recruitment rate by 260%.[131] More recently, Mincher *et al*.[72] reported drastic responses of bighorn sheep (*Ovis canadensis*) with access to Se licks, including diminished predation losses. Sheep left summer ranges to make short bimonthly round-trip migrations (linear 26 km covering 2000 m elevation) to visit mineral licks situated on their winter range. In comparison, huemul had also been observed in Chile to make summer movements to valley bottoms. The difference is those individuals would only survive if areas are free from disturbance by people and dogs. The absence of such behaviour in Argentine populations likely stems from the continuous elimination of huemul reaching lower areas populated with people where hunting and dog predation currently prevent the reestablishment of traditional migratory behaviour and recolonisations. Cultural traits in ungulates such as migrating and using mineral licks can go back 5000–6000 years.[151,152] Preserving such cultural traits is important, especially for endangered species.[153]

Interestingly, in 1975 Murillo and Ramb[154] published a novel – *The Battle of Huemul*, based on 'realistic and detailed field observations'. They recognised that huemul used to inhabit open grasslands and steppes forming large groups even at low altitudes and were sympatric with guanaco. They told how increasing human pressure made them 'retreat' further into the mountains where food was not as rich, where snow heavily covered the forage, making it difficult to move, and where snow storms forced them to go back down to the deepest available parts of the canyons. Although huemul found refuge in high mountains, they were in poor condition, and Murillo and Ramb then asked: was this poor looking lot the same herd that had once roamed freely through low forests and flat lush grasslands down to the shores of the lakes? Without being able to track the source of their information, we have come to the same conclusion based on nutritional ecology. Bighorn sheep populations had a similar history of overhunting in flat open lowlands, elimination of their migrations, artificial extant settings and problems of recovery.[155]

Still, first and foremost is the need for scientific studies on subpopulations, directly on huemul such as with telemetry and tissue sampling. Given the circumstances of remaining subpopulations, efforts to document scientifically valid population responses by indirect methods like pellet surveys would be cost-prohibitive.[139] In the worst case, decisions will be made on unreliable data, thereby compromising the future of the species. Furthermore, telemetry may be the only tool to determine factors affecting vital rates, population dynamics, metapopulation dynamics, dispersal, and migratory behaviour, which is some of the more critical information required to guarantee recovery of huemul.[156] Such information would allow us to rank the threats and design effective conservation actions. The aim of this contribution is to assist the decision makers in evaluating future research proposals on huemul. Specifically, future field studies should contemplate testing our working hypothesis. As argued elsewhere,[139,157,158] these and a plethora of other important questions could be addressed efficiently with huemul in a controlled situation, accompanied by future reintroductions located on former winter ranges, as part of an adaptive management strategy.

Future efforts should be directed beyond the current paradigm, which rests upon a belief system of causes supposedly explaining the lack of recovery of most populations. It has already lead to conclusions like 'Little known and practically condemned to disappear, huemul are hiding in Patagonian forests trying to avoid becoming a legend' (http://www.welcomeargentina.com/parques/, verified 9 February 2011). However, for huemul the three Ds are from dogma to doubt to data. Making a leap in the conceptualisation of the ultimate causes could release huemul from its current imperilment. The lack of science-based monitoring prevents us from drawing any conclusions about cause and effect, allowing us perhaps solely to document the extinction of huemul.

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