

# Huemul heresies: beliefs in search of supporting data.

## 1. Historical and zooarcheological considerations

Werner T. Flueck<sup>A,B,C,D,E</sup> and Jo Anne M. Smith-Flueck<sup>D</sup>

<sup>A</sup>National Council of Scientific and Technological Research (CONICET), Rivadavia 1917, 1033 Buenos Aires, Argentina.

<sup>B</sup>Swiss Tropical and Public Health Institute, University of Basel, Socinstrasse 57, 4051 Basel, Switzerland.

<sup>D</sup>Institute of Natural Resources Analysis (IARN) – Patagonia, Universidad Atlántida Argentina, C.C. 592, 8400 Bariloche, Argentina.

<sup>E</sup>Corresponding author. Email: [wtf@deerlab.org](mailto:wtf@deerlab.org)

**Abstract.** Patagonian huemul (*Hippocamelus bisulcus*) was eliminated from many former ranges before arrival of early explorers who already acknowledged its rareness. Considering huemul analogous to ungulates in mountains back home, huemul was called mountain deer, which is repeatedly cited without validation and remains the orthodox interpretation. Yet other species considered analogous also use lowlands, flatlands, deserts and grasslands, and the only congeneric, *H. antisensis*, uses habitat with high affinity to Patagonian grasslands. Recent comparative analyses of the post-cranial morphology show that huemul cannot be associated with rock-climbing species, but falls within ranges of other cervids. Interpretations of past human utilisation rely on one study of economic anatomy and bone remains, frequently concluding that huemul was unimportant to hunter-gatherers. However, considering only bone fat and omitting easily removable fat is erroneous. Total energy of deer in autumn–winter partitions into 53% as fat and hunter-gatherers elsewhere focussed on deer during the peak fat cycle, using all easily removable fat (>1200% more energy than in bones) and consuming fat and marrow while butchering. Natives are likely to have influenced huemul distribution and density in winter ranges due to high incentives (fat) and easiness to kill. Sparse evidence is likely the result of surveys in Patagonia having been biased towards caves, leaving out transient movements and camps. Generalist cervids passed the Panama land-bridge filter to reach South America. Considering paleoclimate, *Hippocamelus* dispersed east of the Andes, pushed by glaciations even to north-eastern Brazil. *Hippocamelus* would reach and cross Andes only after deglaciations. As a mixed feeder, huemul utilised Patagonian steppe. Hunter-gatherers arrived after the last glaciation and influenced the local distribution of *Hippocamelus*, especially in northern and central Chile, after early adoption of an agricultural lifestyle. Introduction of horses converted native economies through adoption of an equestrian lifestyle and arrival of millions of introduced livestock, which thus affected early writings. Only few records indicate the presence of large groups of huemul far from forests, and substantial killings. Human-caused range contractions of northern ungulates affected mainly losses at low elevations and most species persisted in the marginal periphery, including high-elevation refuges. Paleocology, zoogeography and land-use history in southern South America indicate that mountain huemul is a secondary relict created by impacts of post-Columbian colonisation. We caution against the rigid application of modern huemul habitats in interpreting past habitat use and huemul ecology, and simply considering the few extra-Andean accounts as abnormal outliers.

**Additional keywords:** biogeography, *Hippocamelus bisulcus*, *H. antisensis*, historical condition, human influence, morphology, range contractions.

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### Introduction

Initial descriptions of Patagonian huemul (*Hippocamelus bisulcus*) stemmed from early explorers who often compared it to fauna confined to remote mountains in their countries (Flueck and Smith-Flueck 2011a). These and other remarks that appeared in old reports have been repeated throughout the years, but without rigorous scrutiny of their validity. Interpretations based on such non-metric traits contain a high degree of inter-

and intra-observer subjectivity of qualitative descriptions and thus are prone to false dichotomies. Because securing reliable data is difficult on species highly reduced in numbers and remaining in remote refuge areas, the continuing lack of well substantiated information on the biology and ecology of huemul has resulted in relying on old sources of hearsay. Due to uncritical application, this belief system presents important obstacles in current conservation efforts, and in part might explain the absence of

successful recovery of huemul during the past three decades. Similar impediments have occurred for panther (*Puma concolor coryi*) where unreliable inferences have appeared in peer-refereed scientific journals and have been repeatedly cited and miscited, thus compromising panther conservation (Conroy *et al.* 2006). Here, we review historical and zooarcheological information in relation to some aspects of the biology and ecology of huemul being utilised dogmatically, even in scientific publications, but that do not appear to stand up under critical scrutiny. We re-evaluate analogies made to other ungulates, human utilisation of huemul, and the past natural distribution, with the aim at improving our understanding of huemul and its conservation. Additional details and a completed list of cited sources are in Flueck and Smith-Flueck (2011b).

## Materials and methods

We review literature on huemul and other related deer species and use a comparative approach to analyse and interpret questionable information that originates in historic sources and that continues to be used to describe huemul. A comprehensive search was conducted using cross-search of ISI Web-of-Knowledge and 17 external databases, three books and four dissertations on huemul, and historical and grey literature available in a collection containing 547 entries on huemul.

## Results

### *Analogy to other ungulates occurring in mountains*

Early descriptions of huemul come from initial naturalists exploring interior Patagonia, with only rare accounts from Pacific coastal areas, although before their arrival, huemul had been eliminated from much of the former range. Thus, early encounters with huemul were often in remote and inaccessible Andes, and initial writings already acknowledged the huemul's rareness, disappearance or endangerment (Flueck and Smith-Flueck 2011a, 2011b). Explorers found huemul mainly in mountain refuges, comparing them with ungulates in mountains back home; these, however, were just subjective statements. Yet this interpretation that huemul is synonymous with *mountain deer* persists (MacNamara 1982; Eisenberg 1987; Redford and Eisenberg 1992; Webb 1992; De Nigris 2004; Merino *et al.* 2005; Iriarte 2008; Guérin and Faure 2009; Muñoz-Pedrerros and Valenzuela 2009; Cruz *et al.* 2010; Vila *et al.* 2010).

Species claimed analogous to 'mountain huemul' do of course utilise mountain habitats. Bighorn sheep (*Ovis canadensis*), however, also inhabits lowlands, flatlands, desert and grasslands, and chamois as an 'Alpine' species (*Rupicapra rupicapra*) is an artefact of past human-induced displacements; currently, it is re-occupying forest-covered rolling hills, and is referred to as 'forest chamois'. Furthermore, even Alpine ibex (*Capra ibex*) is a misnomer; extirpation was much earlier and easier at a low altitude (Michahelles 1831), resulting in early prejudiced reintroductions to high elevations because that is where the last ibex had been found. These reintroductions reinforced the artificial model of an animal living all year at a high altitude above the tree line. Yet, ibex remains occur down to sea level, sometimes as a dominant prey species at archeological sites. Accordingly, recent reintroductions to very low elevations

have been successful, as well as natural recolonisations from high-elevation populations to low elevations. Historical comparisons of huemul to ibex and chamois were therefore made under the misbelief that the latter two were high-altitude specialists in extreme rocky areas; instead, the only link among all these species appears to be the historical anthropic displacement from nutritionally favourable habitats (Michahelles 1831). Moreover, the only congeneric, taruca (*H. antisensis*), currently utilises treeless grasslands, with high affinity to Patagonia, coexisting with several camelid and cervid species. However, taruca also has been displaced very early because of human pressures, e.g. from *Prosopis* forests by the Pacific coast. Although now mainly found above the tree line, some populations are still found, even exclusively, in *Polylepis* and yungas forests and, historically, populations also occurred to just west of the Mato Grosso, with remnant taruca in the Sierra Pampeana, but disconnected from the Andes.

### *Body shape*

Huemul is foremost considered a mountain deer on the basis of subjective descriptions of physiognomy and recent distribution. The appearance of *Hippocamelus*, e.g. stockiness and short legs, was compared with ibex in 1897 by Heck (Frädrieh 1978), and to ibex and chamois by Kurtén (1979). Kurtén's conclusion unfortunately was based on erroneously constructing a new fossil 'mountain deer', recently declared a *nomen nudum* (Morejohn and Dailey 2004), and without data on *Hippocamelus* (Kurtén 1975). Similarly without data, body proportions of huemul were claimed to coincide with those of bighorn sheep (Eisenberg 1987). There is no lack of further references to huemul resembling mountain goats (*Oreamnos americanus*), chamois, bighorn sheep and ibex right up to present day (Krieg 1925; Heck 1969; Kolliker Frers 1969; Kurtén 1979; MacNamara 1982; Redford and Eisenberg 1992; Frid 1999; Nowak and Walker 1999; De Nigris 2004; Lord 2007; Cruz *et al.* 2010; Vila *et al.* 2010).

In contrast, recent analyses of postcranial morphologies of huemul, and ungulates claimed analogous to huemul, found no supporting evidence (Flueck and Smith-Flueck 2011a). Leg morphometry of huemul and 12 other ungulates revealed that huemul cannot be associated with rock-climbing species, and does not overlap with species previously considered analogous, but falls within the range of other cervids (Fig. 1). Instead, the alert 'horseshoe' stance and long-haired (8–9 cm) coat may have influenced early descriptions.

### *Natural distribution*

The pre-Columbian distribution of huemul resulted from founders, likely of the *Odocoileus* line (Morejohn and Dailey 2004), which dispersed through the Panama isthmus. Species successfully passing this equatorial filter were generalists and predominantly savanna-adapted. *Hippocamelus* was established by the Pleistocene, and, considering paleoclimatic conditions, dispersed south through continuous savanna habitat east of Andes. Glaciations kept *Hippocamelus* repeatedly away from Andes, with fossils known from north-eastern Brazil (8°9'S, 36°22'W), and from the plains of Argentina, Uruguay and south-eastern Brazil.

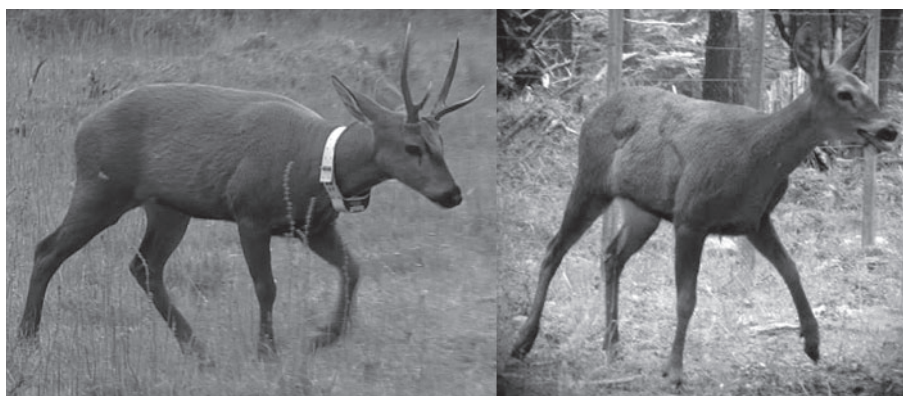


Fig. 1. Male and female huemul do not always resemble mountain goats, ibex, chamois or bighorn sheep.

During the last glacial maximum, continuous ice 1600–1800 m thick covered the Andes from 33°S to 56°S, and glaciers south of 42°S dipped into the Pacific; they reached hundreds of kilometres into eastern Patagonia where only treeless habitat existed, with Patagonia-like grasslands reaching way into Brazil, and much of South America was covered by savanna and grasslands. Moreover, the sea level was 120–150 m lower than at present and the Atlantic coastline located >300 km east of the present coastline (Fig. 2), which almost doubled the eastern flat paleosteppe area (Rabassa *et al.* 2011).

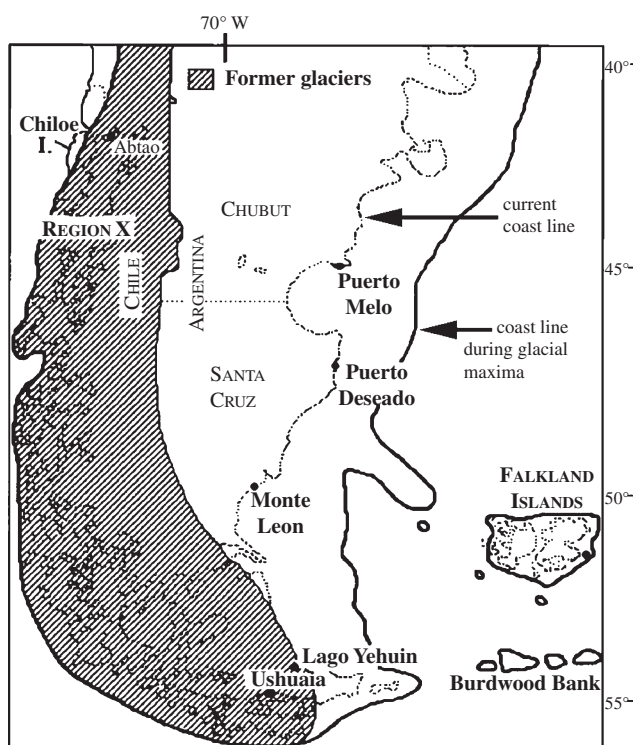


Fig. 2. Continuous ice sheet, covering the Andes down to 56°S. Glaciers south of 42°S dipped into the Pacific, reaching hundreds of kilometres into eastern Patagonian plains, with only treeless habitat east of the Andes. The coast line was shifted eastward by hundreds of kilometres (from Rasmussen 1994).

During the last glaciation, Fireland was connected to continental Patagonia when guanaco (*Lama guanicoe*) arrived; huemul is likely to have arrived simultaneously. Fireland had been separated only 8000–10 000 years ago, although the Beagle channel, as narrow as 2 km, would not constitute a barrier to excellent swimmers such as huemul (Prichard 1902b; Wensing 2005). Analysing narrow-water passages and island distributions of guanaco, Furlong (1912) also concluded that guanaco could easily exchange with continental populations. Presence of huemul on Fireland was reported by Waterhouse in 1834 on the basis of Darwin's collections (Díaz and Smith-Flueck 2000), by Lacroix's (1841) account of its zoology and by Lista (1887); its presence was corroborated by zooarchaeological remains (Mansur and Piqué 2009). Pressure from hunting could have led to its local extirpation.

During glaciations, *Hippocamelus* thus persisted in eastern treeless lowlands, and as a mixed feeder, huemul is known to consume notable amounts of grass (Smith-Flueck 2003; Prothero and Foss 2007). Furthermore, besides graminiae, Patagonian steppes contain many shrubs and maintain important green-grass production throughout winter, and deer are known to heavily use seed heads, further corroborating past and historic distributions of huemul in non-forested habitat. Once eastern regions became glacier free, huemul was able to reach Andean habitat and, when deglaciation allowed, eventually cross the Andes. 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 coast. With the last glacial retreat, forests spread from few western refuges, and eventually covered the southern Andes again, reaching their current extent only 2000–3000 years ago.

Nomadic hunter-gatherers arrived 10–12 000 years ago in the southern Andes and would have influenced local huemul distributions. However, early on, sessile and agricultural people in northern and central Chile reached very high population densities, completely changed habitats through slash and burn, and regionally extirpated several species including huemul and pudu (*Pudu puda*), long before Spanish arrival (Bahre 1979). Further south, humans established mainly along the coast, focusing on marine resources. Consequently, early explorers still found huemul regularly in the coastal areas; it was an established fact that such areas indicated low passes across the

Andes from which to reach the eastern slopes via expeditions. East of the Andes, huemul existed between Andean foothills and the Patagonian mesas, but also reached the Atlantic (Church 1903). Reports from the 16–19th centuries mentioned huemul near ports of San Joseph and Desire (e.g. Pigafetta 1521 and van Noort 1598, both cited in Eastman 1915; MacDouall 1833); old shed antlers are still being found in steppes, with a prehistoric human-modified antler recently found near the Atlantic.

The Spanish introduced horses, which created an equestrian lifestyle for native people and profoundly changed their economies. Introduced livestock immediately became feral and soon roamed by the millions. The mobile native tribes prevented colonisation of Patagonia, dominating for 300 years until finally being displaced by wars (in the 1880s). Only some intrusion by settlers from Chile was possible. Accordingly, the major industry was livestock raiding by nomadic intruders and eastern tribes, with 47% of the forests having been burnt before 1911 (Willis 1914). After the tribes were overpowered, fencing and ranching occurred rapidly throughout Patagonia, further affecting the remaining huemul individuals.

Given this history, early writings occurred after significant anthropogenic changes in huemul distribution, with explorers unaware of these changes in distribution. Descriptions came from remnant populations living in remote and inaccessible places. Subsequent naturalists found an even more reduced distribution, but because locations coincided with earlier accounts, it led to dogmatic descriptions. Thus, decades have gone by, further ingraining the notion that huemul occurs exclusively in Andean forests and not in lowland central Chile (Osgood 1943; Povilitis 1978; Redford and Eisenberg 1992; Corti *et al.* 2010; Vila *et al.* 2010), is specially adapted to precipitous rocky terrain, and Andean forests (Belardi and Otero 1998; Nowak and Walker 1999; Dolman and Wäber 2008; Fernández 2008), is a mountain deer living above the tree line (National Research Council 1991; Prothero and Schoch 2002; Guérin and Faure 2009), is living between 1300 and 1700 m asl or high elevations (Nowak and Walker 1999; Merino *et al.* 2005), or prefers steep, rocky, north-facing slopes (Redford and Eisenberg 1992; Lord 2007). Preference to high Andes along the continental divide was considered to be due to conditions being most favourable there (e.g. Osgood 1943). The problem of basing ecological interpretations on current distribution is illustrated by the

suggestion that habitat use moves down 107 m per 1° latitude southward (Gill *et al.* 2008), using extant signs in upper and lower elevations. The upper elevation of utilisation simply coincides with the tree line, which progressively diminishes with an increasing latitude – a trivial observation. The correlation of latitude with lower elevation of utilisation, however, is artefactual due to omitting historic and zooarcheologic data; it is fallacious to imply latitude as a cause for the lower elevation of utilisation. Lower limits are determined by altitudes of adequate interior winter ranges and sea level on both sides of the continent, and the absence of huemul at low elevations and grasslands is due to displacement and elimination of migratory traditions (Conway 2005; Flueck and Smith-Flueck 2011c). These generalised descriptions of huemul, implying preferences, exclusiveness, or most favourable conditions are strong terms with specific ecological meaning, yet such casual statements are not enough to make these inferences. Omitting habitats used historically distorts interpretations of basic ecological traits of huemul (Fig. 3).

#### *Human use of huemul*

The current absence of huemul from low-elevation portions of mountains is claimed to be natural and related to huemul being a mountain-top species. Anthropogenic displacement from low-elevation habitat has been pre-empted by claims that huemul was not an interesting game species to humans because deer occurred only at very low densities and in high-elevation mountains. Whereas these arguments are based on characteristics of extant populations, an additional argument is based on the nutritional value of the huemul. Thus, after analysing anatomy in terms of energy economy for two fresh carcasses, Belardi and Otero (1998) concluded that huemul was not important to hunter-gatherers because of the leanness of the meat, with bone marrow considered to be the only source of fat. Unfortunately, these authors neglected the fact that these samples were particularly incomplete regarding fat because these animals were skinned and eviscerated before analysis, and thus the most relevant portions were discarded. Others also focussed on bones, emphasising low utility of meat lacking fat, but omitting the issue of dissectable fat (e.g. De Nigris 2004). However, these interpretations about the utility of huemul



**Fig. 3.** Past and current use of open and flat habitat by huemul, far from forests and cover. Note that such habitat is used during full daylight hours.

are in stark contrast to those concerning the fat reserves in other cervids; McCullough and Ullrey (1983) found that *total energy content* of deer was partitioned into 47% as dissectable fat, 1% as marrow, 5% within bone, and 32% in muscle. Fats, presenting the highest-density energy, were partitioned into 65% dissectable fat (max. 76%, mostly with visceral organs), 8% in high-density fatty viscera, 4% in bones and 2% in marrow. Dissectable fat averages 12% (max. 16%) of bodyweight, but represents 47% of deer energy content, thus explaining why hunter-gatherers elsewhere focussed on deer during autumn–winter peaks of fat accumulation, by hunting deer preferentially on winter ranges.

Grease extraction from marrow and bone is common among hunter-gatherers, including in Patagonia (Bourlot 2006). Because this practice renders maximally 6% of total fat, it would be erroneous to assume that professional hunter-gatherers would ignore taking advantage of easily accessible high-density visceral tissue fat and dissectable fat which have >1200% higher energy content than do bones. Northern Natives preferred eating fatty visceral tissue, used marrow for various preparations and as milk substitute for children, but gave much of the muscle to dogs (Price 1939). Moreover, humans generally ignored starved animals or ones in poor condition due to lack of fat (Lupo 2007; Morin 2007), as documented for Natives historically hunting huemul after arriving on winter ranges, as follows: ‘in stormy days, when herds of huemul came down from the Andes, we chose the fattest one to eat’ (Díaz and Smith-Flueck 2000). However, such traditional migratory behaviour of huemul had been eliminated early on mainly by overhunting (Flueck and Smith-Flueck 2011c).

In autumn, 20–35% of cervid bodyweight may be fat, and therefore, northern hunter-gatherers preferentially killed deer in autumn–winter for easiness and because fat accumulation was maximal. Significantly, while butchering, they consumed dissectable fat, fatty visceral tissue and marrow, and then transported the remaining bones for marrow and tallow extraction, often at temporary camps. Patagonian hunter-gatherers similarly favoured accessible fat, including marrow, which was consumed raw together with organs while butchering guanacos (Furlong 1912; Steward 1946; Tavener 1955; Bourlot 2006), and by implication, while butchering huemul. Models of hunter-gatherer diets have frequently assumed that muscle was the sole tissue consumed; however, ethnography of various hunter-gatherer societies shows that nearly all edible parts were consumed. Moreover, analysing 229 societies showed that virtually all potential fat contained in animal carcasses would generally be consumed (Cordain *et al.* 2000). Similarly for guanaco and huemul, processing was fat-oriented; no selective transportation operated in the past, instead all body parts were utilised and no anatomical units were abandoned unused, indicating that killings could have been conducted near the studied shelters (De Nigris and Mengoni Gonalons 2005; Fernández 2008).

Low-density populations of northern hunter-gatherers moved up to 150 km according to seasonal prey, particularly in autumn–winter (Lovis *et al.* 2005). From hunting camps, groups of men would make roundtrips of >100 km in about 3 days. Moreover, these hunters were able to portray detailed maps covering 240 000 km<sup>2</sup> and animal movements within

(Lovis *et al.* 2005). Deer being the preferred species for hunting, temporary camps would remain if animals were within 50 km (Lovis *et al.* 2005; Lupo 2007). Considering historic reports of the concentrations of huemul in winter (Flueck and Smith-Flueck 2011c), foraging conditions in the pre-Colombian era are likely to have been even superior in terms of hunter-gatherers. Bones of guanaco and huemul regularly coexist at archeological sites in lowland Andean foothills between 2500 and 6500 years old (De Nigris 2007). The preponderance of guanaco remains was explained by the supposed range-wide rarity of huemul and by hunter-gatherers exploiting ungulates most effectively where these were territorial, such as guanaco (Muñoz and Mondini 2008). We posit more likely alternative explanations, including the following: (1) the well documented easiness of killing huemul can readily result in overhunting and produce local rareness through exploitation depression (see Lupo 2007), (2) being non-territorial, huemul will temporarily evade hunting parties by moving to other sites, resulting in more mobile hunting which leaves little or no signs, and (3) given more mobile hunting, bones may be left behind because bone grease would present only ~4% additional fat compared with easily recoverable fat (Price 1939). The effectiveness of Patagonian foot-hunters was described by Cook (1901), when six Onan, with the aid of dogs, cornered a large guanaco group and killed 50 with clubs and knives, and broke a leg on 25 more to facilitate future hunting.

If tactics to hunt huemul differed from those when hunting guanaco, then most kill and butcher sites of huemul may remain undescribed. Similarly, Fiedel and Haynes (2004) found no descriptions of kill sites east of the Plains where elk, deer, bear or woodland bison were utilised by paleoindians during the past 12 500 years. If archaeologists in the eastern USA have not yet stumbled on remains of any such butchering – 12 500 years with no discoveries – what is the likelihood of finding a butchered huemul? Modern evidence shows that even overkill would leave only a few remains behind, to identify the very processes involved in the resulting extinctions (Fiedel and Haynes 2004). Although huemul had been used by hunter-gatherers all along, the sparse evidence from a few caves representing camps and settlements may not allow confident reconstruction of early human hunting of huemul and associated impacts on huemul distribution. Borrero (2008) acknowledged the bias in Patagonia by focusing on caves that represent more permanent sites. Transient hunting camps and movements are thus under-represented and difficult to document (Benedict 2005). Instructively, early descriptions at contact referred to some pedestrian hunter-gatherers as ‘huemules’, due to their clothes being made from huemul skins.

#### *Biological indicators*

Antler development, group sizes and density indicate that conditions were distinct historically. For instance, antlers with five tines were documented (Philippi 1895; Osgood 1923), whereas more recently, antlers beyond forks have been quite rare. Huemul used to form wintering groups of 100 or more, and although lacking density estimates for historic times, we can deduce that densities commonly must have been substantial on the basis of documented hunting success rates and fur trading

(reviewed in Flueck and Smith-Flueck 2012). These data stem from areas where huemul no longer exists, but which currently produce 3000–5000 kg/km<sup>2</sup> of exotic ruminant biomass (Flueck 2010), equivalent to 40–60 huemul/km<sup>2</sup> if they would forage similarly, as expected from mixed feeders. When huemul still occurred at 200 km (Fig. 3; Prichard 1902a) and even 270 km east of the Andes (Anonymous 1904: 42.13°S, 68.75°W), Allen (1905) described huemul as grazing there. Extant huemul ate 16% grass (Sierralta 2003), whereas congeneric taruca had 60% of grass (15 species) in diet (Gazzolo 2006). Also, Patagonian steppes contain a large component of shrubs and forbs, and maintain the important green-grass production throughout winter, which further substantiates huemul persisting in such habitats. In comparison, apart of taruca, other similar-sized *Odocoileus* species also live in broken table grassland (<300 mm precipitation) and deserts (74 mm precipitation).

## Discussion

Millions of feral horses and livestock transformed lifestyles and economies of native tribes and allowed them to resist the Spanish in Argentina for >300 years. The increased mobility of the native tribes led to more fires and more hunting of wildlife and feral livestock to trade with the colonies. Early explorers came after these significant anthropogenic changes and mainly described remnant huemul in remote and inaccessible places. Considering huemul analogous to other ungulates using mountains was intuitive in such historic settings, because huemul had been eliminated from much of their former range. Yet, as with huemul, these other ungulates were also stereotyped mountain dwellers that previously had experienced anthropogenic displacements.

Historic remarks entailed circular reasoning, using the body shape of huemul to label it as a mountain deer; however, morphology shows that huemul is not analogous to rock-climbing species, but falls within the range of other cervids. Using mountains is not a unique trait among cervids. For instance, Allen (1900), of the famous Allen's rule, observed that mountain caribou used the same range as occupied by the rock specialist stone sheep (*Ovis dalli stonoi*), and had habits much like those of the sympatric sheep. Strikingly, the literature abounds with casually labelled mountain ungulates, including Alpine reindeer, mountain caribou, mountain mule deer, mountain roe deer, Alpine roe deer, Alpine red deer, Alpine chamois, mountain bison, mountain guanaco or mountain vicuña. However, whereas huemul is often claimed to be *exclusively* a mountain deer, other ecotypes are accepted unequivocally for other ungulates such as e.g. plains reindeer, forest reindeer, woodland caribou, plains mule deer, forest chamois, field roe deer, steppe red deer. None of these labels constitutes a scientific concept and merely refers to local adaptations. Most extant huemul populations may be considered as satellite subpopulations that utilise mountains and have assumed some 'mountain mannerisms' as an expression of intraspecific variation (Putman and Flueck 2011). By necessity, huemul holds up exclusively as a mountain deer only by marginalising historic evidence and insights from zooarcheology, paleontology and paleoclimate.

Understanding human utilisation of huemul has implications for interpreting the prehistoric distribution. The frequent claim that Natives did not hunt huemul much, due to low density and leanness of huemul, contradicts insights from other northern cervids that accumulate >50% of body energy as fat by autumn–winter. Accordingly, being highly mobile, Natives maintained hunting camps if deer were within 50 km. Natives in upland Peru used 53% camelids and 35% cervids such as the congeneric taruca, before domesticating camelids (Miller and Burger 1995; Goepfert 2010). Contrary to common belief, due to extreme easiness of killing huemul in autumn–winter, their past large winter concentrations, and strong incentives due to fat reserves, Natives are likely to have influenced huemul distribution and density on winter ranges, particularly once possessing horses for mobility. On the basis of current biomass of exotic herbivores on former huemul range and densities of cervids in similar habitat elsewhere, huemul abundance was substantial. As Cabrera and Yepes (1940) observed, 'In the past, huemul was one of the most frequently hunted animal by Patagonians who traded their skins to Atlantic ports' (p. 271, translated from Spanish). Paleobiogeography further supports the notion that huemul used 'Patagonian' steppe through Uruguay into Brazil. Historical and current cases have shown that group size and density can be substantially larger than those in orthodox descriptions of huemul, which are based on remnant populations in marginal habitats. Relying on such biased information results in circular reasoning when interpreting zooarcheological data, paleodiets, prehistoric distribution and the ecology of huemul in general. North American game species were similarly affected when adoption of horse nomadism lead to abandonment of traditional hunting, five or six generations before the first literate explorers arrived, resulting in absent eyewitness accounts or credible oral traditions about the past, particularly regarding densities and the loss of seasonal migration patterns of the animals (Benedict 1999, 2005).

Knowledge of historical ranges is important regarding endangered species, because recovered or recovering species occupy a greater percentage of historic ranges than do declining species. Instructively, anthropogenically caused range contraction of ungulates with broad former historic distributions was heavily skewed towards a loss of low-elevation ranges (Laliberte and Ripple 2004). Analysing range contractions of many cases, Channell and Lomolino (2000) found that most species persist only in marginal peripheries of their historical ranges, and persisted the longest where the crawling spread of historic extinction forces operated last; that is, along the edge of their ranges, on isolated and undisturbed islands, or at high elevations.

## Conclusions

Past distribution and morphology show that huemul fits comfortably within the range of other deer species using subalpine habitats. Previous use of Patagonia steppes far from forests is similar to the use of habitats by congeneric taruca and other *Odocoileus*. Seasonal fat cycle and congregations, and the extreme easiness of hunting are likely to have made huemul a prime candidate for human predation, which would have

influenced local distributions and densities. Several other ungulates had lost low-elevation habitats mainly because of anthropogenic pressures, and range contraction allowed persistence only in marginal peripheral habitat, concentrated at high elevations or otherwise inaccessible sites. For interpreting zooarcheology or past distribution, historical indications on abundance need to be considered. Historical ranges are thus an important consideration for conservation strategies of endangered species such as huemul. Paleocology, zoogeography and history of land use in Patagonia indicate that mountain-dwelling huemul is a secondary relict created by post-Columbian anthropogenic impacts.

Population assessments should be based on confirmed parameters regarding reproduction, predation, diet, competition, duration of coexistence with other herbivores, antler development, diseases, group size and density, habitat use and barriers, because the use of erroneous parameters leads to spurious conclusion and may distract from discovering the factors underlying the lack of recolonisation generally observed in currently reduced huemul populations. We caution against the rigid application of modern huemul habitats in interpreting past habitat use and against considering extra-Andean accounts as abnormal outliers to be ignored. Although adopting a uniform conservation program over a large geographical area is attractive to policy-makers and conservation planners, the large range of past geographical and ecological sites used by huemul and the previous migratory behaviour indicate that conservation programs could benefit from broadening strategies accordingly. Whereas active management should aim to increase recruitment with all possible means for the short term, to prevent extinction of highly reduced remnant subpopulations, sustained recovery may depend on re-establishing source populations on more productive habitats, guided by zooarcheological and historical data.

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