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HUEMUL HERESIES: BELIEFS IN SEARCH OF SUPPORTING DATA 1. HISTORICAL AND ZOOARCHEOLOGICAL CONSIDERATIONS

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ABSTRACT

Patagonian huemul (*Hippocamelus bisulcus*) were eliminated from many former ranges before arrival of early explorers who already acknowledged their rareness. Considering ungulates in mountains back home analogous, huemul was called a mountain deer, which is repeatedly cited without validation and remains the orthodox interpretation. Yet species considered analogous also use lowlands, flatlands, deserts and grasslands, and *H. antisensis* uses habitat with high affinity to Patagonian grasslands. Recent comparative analyses of postcranial morphologies show that huemul cannot be associated with rock climbing species, but fall within ranges of other cervids. Analyses of past human utilization rely on one study of economic anatomy and bone remains, frequently concluding that huemul were unimportant to hunter-gatherers. However, considering only bone fat and omitting easy removable fat is erroneous. Total energy of deer in autumn/winter partitions into 53% as fat and hunter-gatherers elsewhere focused on deer during the peak fat cycle, using all easy removable fat (>1200% more energy than bones) and consuming fat/marrow while butchering. Natives likely influenced huemul distribution and density in winter ranges due to high incentives (fat) and easiness to kill. Sparse evidence likely stems from surveys in Patagonia being biased toward 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 northeastern Brazil. *Hippocamelus* would only reach and cross Andes after deglaciations. As mixed feeder, huemul utilized 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 agricultural lifestyle. Introductions of horses and livestock converted native economies through an equestrian lifestyle and based on millions of introduced animals, which thus affected early writings. Only few records indicate 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. Paleoeology, zoogeography, and land use history in southern South American indicate that mountain huemul are secondary relicts created by impacts of European settlements. We caution against the rigid application of modern huemul habitats in interpreting past habitat use, and simply considering the few extra-Andean accounts as abnormal outliers and thus ignoring them.

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

INTRODUCTION

Huemul (*Hippocamelus bisulcus*) were often compared by early explorers and naturalists to fauna confined to remote mountains back in their home country, namely ibex (*Capra ibex*), chamois (*Rupicapra rupicapra*), mountain goat (*Oreamnos americanus*), and bighorn sheep (*Ovis canadensis*) (Flueck and Smith-Flueck 2011a). These and other observations which appeared in old reports have been mentioned repeatedly throughout the years, but without any rigorous scrutiny of their validity. Interpretations based on such nonmetric traits contain a high degree of inter- and intraobserver subjectivity of qualitative descriptions and thus proneness to false dichotomies. As securing reliable data is difficult on species highly reduced in numbers and remaining mainly in remote refuge areas, the continuing lack of well-substantiated information on the biology and ecology of huemul results in the reliance on old sources and hearsay. Due to their 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 last three decades. Similar impediments were reported for panther

(*Puma concolor coryi*) where unreliable inferences have appeared in prominent, 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 utilized dogmatically, even in scientific publications, but that do not appear to hold up under scrutiny. This analysis is presented in three separate papers and aims at improving our understanding of huemul and its conservation. While the second part reevaluates antlers, group size and density, predation, diet, diseases and competition, and the third part covers reproduction, resource defense, genetic isolation and sexual segregation, in this first part we reevaluate analogies made to other ungulates, body shape, human utilization of huemul, and their natural distribution.

ANALOGY TO OTHER UNGULATES OCCURRING IN MOUNTAINS

Early descriptions come largely from initial naturalists exploring interior Patagonia, with only rare accounts from Pacific and Atlantic coastal areas. Even before the arrival of early explorers, huemul had been eliminated from much of the former range (Diaz 1993; Diaz and Smith-Flueck 2000). Thus early encounters with huemul were often in remote and barely accessible Andean mountains, and initial writings already acknowledged the prevailing rareness, process of disappearing, or even referred to the endangerment of huemul (Flueck and Smith-Flueck 2011a). Since explorers were mainly finding huemul in mountain refuge areas, they compared them with ungulates found in mountains back home: these, however, were just subjective statements. Yet this interpretation that huemul were synonymous with *mountain deer* persists even today (MacNamara 1982; Eisenberg 1987; Redford and Eisenberg 1992; Webb 1992; De Nigris 2004; Merino *et al.* 2005; Iriarte 2008; Guérin and Faure 2009; Muñoz-Pederos and Valenzuela 2009; Cruz *et al.* 2010; Vila *et al.* 2010).

Species claimed analogous to ‘mountain huemul’ do of course utilize mountain habitats. Bighorn sheep, however, are well known to also inhabit low, flat, deserts and grasslands (Geist 1985; Fairbanks *et al.* 1987). Chamois as an ‘Alpine’ species is an artefact of past human-induced displacements (Senn and Suter 2003): currently they are re-occupying forest-covered rolling hills, and referred to as ‘forest chamois’ (Molinari-Jobin *et al.* 2002; Baumann *et al.* 2005). Lastly, even Alpine ibex is a misnomer: extirpation was much easier and much earlier at low and medium altitude, resulting in a prejudice in early conservation efforts whereby reintroductions were made to high elevations because that’s where the last remaining groups had been seen (Choisy 1994). These reintroductions actually created an artificial model of an animal of high altitude, living there all year above the tree line (Choisy 1994; Phoca-Cosmetatou 2004; Lyman 2006). Yet many remains have been found down to sea level, sometimes as dominant prey species in archeological sites. Thus altitude clearly was not a factor in ibex ecology (Phoca-Cosmetatou 2004). Accordingly, recent reintroductions to very low elevation areas were successful. There are even cases of natural recolonization, from high elevation populations to low elevation areas (Choisy 2001). Historical comparisons of huemul to ibex and chamois were therefore done under the misbelief that both latter species were specialists for high altitudes and extreme rocky areas: instead, the only link between these three species appears to be historical anthropic displacement from favorable habitats. Moreover, the only sister species, taruca (*H. antisensis*) - considered by several authors osteologically indistinguishable and thus possibly a mere subspecies (Philippi 1857; Dabbene 1911; Krieg 1925; Diaz 1995) - currently also utilizes treeless grassland habitat with high affinity to Patagonian grasslands (Fernández and Busso 1997), and coexists with several camelid and other cervid species (Jungius 1974; Hershkovitz 1982; Miller and Burger 1995; González *et al.* 2006; Nunez 2006; Barrio and Ferreyra 2008). However, taruca as well has been displaced very early by human pressures (Dabbene 1911; Horkheimer 1960). They used to also occupy Prosopis forests down to the Pacific coast based on several different lines of evidence (Horkheimer 1960; Sinclair 2009). Although now mainly found above tree line, some populations are still found, even exclusively, in Polylepsis and yungas forests, also due to continued hunting pressure (Aldenderfer 1998; Tarifa and Yensen 2001), or in foothill areas (Siefeld and Guzmán 2011). Also historically, populations occurred to just west of the Mato Grosso with one area disconnected from the Andes, the Sierra Pampeana, still containing remnant taruca populations (Diaz 1995). Lastly, taruca were bred successfully in the Berlin zoo at sea level for over a decade, and several zoos since 1890 reported that taruca was one of the easier species to maintain, including regarding forage (Vidal *et al.* 2011).

BODY SHAPE

Huemul has foremost been considered a mountain deer based on subjective qualitative descriptions of its physiognomy and historic distribution. The external appearance of *Hippocamelus*, like stockiness and short legs, was compared to ibex by Heck already in 1897 (Frädrich 1978), and to ibex and

chamois by Kurten (1979), who referred to them as *mountain deer*. Kurten's conclusion unfortunately was based on an erroneous construct of a new fossil 'mountain deer' which was later declared a *nomen nudum* (Morejohn and Dailey 2004), and without having any type of data on *Hippocamelus* (Kurten 1975). Similarly, without providing data, huemul were claimed to have body proportions reminiscent of bighorn sheep (Eisenberg 1987). There is no lack of further references to stocky and massive huemul resembling mountain goats, chamois, bighorn sheep and ibex right up to today (Krieg 1925; Heck 1969; Kolliker Frers 1969; Kurten 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, a recent study, analyzing for the first time the postcranial morphology of huemul and comparing it to ungulates claimed to be analogous to huemul in the use of rugged mountains, found no supporting evidence (Flueck and Smith-Flueck 2011a). Comparing leg morphometrics of huemul and 12 other ungulates revealed that huemul cannot be associated with rock climbing species, and the morphology does not overlap with species previously considered analogous, but falls within the range of other cervids (Fig. 1). Rather, the alert 'horseshoe' stance and long-haired coat may have influenced early description (Flueck and Smith-Flueck 2011a).

NATURAL DISTRIBUTION

The pre-Columbian distribution of huemul has its roots in founding stock, likely of the *Odocoileus* line (Morejohn and Dailey 2004), which dispersed through the Panama land bridge during the Great American Interchange. Species had to pass this equatorial filter, presumably a continuous savanna habitat, and the ones succeeding were generalists and predominantly savanna-adapted (Webb 1978). *Hippocamelus* were established by the Pleistocene, and considering the paleoclimatic conditions, dispersed south on the eastern side of the Andes through continuous savanna habitat (Hoffstetter 1963; Hershkovitz 1969; Frailey *et al.* 1980; Markgraf and Kenny 1997). Several periods of glaciation kept ancestral *Hippocamelus* repeatedly away from the Andes, and fossil *Hippocamelus* are even known as far north as 8°S, 36°22'W in the most eastern tip of Brazil, and from the plains of Argentina, Uruguay and southeastern Brasil (Castellanos 1944; Magalhaes *et al.* 1992; Eisenberg 2000; da Silva *et al.* 2006; Guérin and Faure 2009).

During glacial periods, the Andes were covered with ice even at northern latitudes to near the equator (Clapperton 1993; Coltorti *et al.* 2007), and a continuous sheet covered the mountains from about 33 to 56°S during the last glacial maximum. Glaciers south of about 42°S dipped into the Pacific, and were overlaying the Andes about 1600–1800 m thick, which intensified this orographic wind barrier. Glaciers reached hundreds of kilometers into eastern Patagonian plains where only treeless habitat existed (Fig. 2), with Patagonia-like grasslands reaching way into Brazil, and much of South America covered by savannah and grasslands (Marshall 1988; Clapperton 1993; Rasmussen 1994; Markgraf and Kenny 1997; Tatura 2002; Rabassa and Coronato 2009). Moreover, the sea level was about 120 m lower and the Atlantic coastline located 300 km or more to the east of the present coastline in some latitudes, which greatly extending the flat paleosteppe region eastwards (Fig. 2).

During the last glaciation, Fireland was connected to continental Patagonia when guanaco (*Lama guanicoe*) reached this southernmost area (González *et al.* 2006): huemul likely arrived simultaneously. Fireland had been separated from the continent only around 8000–10000 years BP, though the Beagle channel, as narrow as 2 km, would not constitute a barrier to good swimmers like huemul. Although extinct today, past presence of huemul on Fireland is indicated by Waterhouse reporting in 1834 on Darwin's collections and Ramón Lista mentioning in 1881 the occurrence of huemul on Fireland (Diaz and Smith-Flueck 2000), by Lacroix's (1841) account of its zoology, and corroborated by remains found in a zooarchaeological site (Mansur and Piqué 2009). Pressure from hunter-gatherers could have led to its local extirpation (see next section).

During glaciations, *Hippocamelus* thus persisted in eastern treeless lowlands, with fossils from the plains of Uruguay, northern Argentina and southern Brazil (Eisenberg 2000). As mixed feeders, huemul are known to be able to incorporate notable amounts of grass in the diet (Smith-Flueck 2003; Prothero and Foss 2007). Furthermore, besides graminiae, Patagonian steppe contains a large component of shrubs, maintains important green grass production throughout winter (Fernandez *et al.* 1991; Adler *et al.* 2005), and deer are known to make much use of seed heads (Takatsuki 2009), which further corroborates past and even historic distributions of huemul in non-forested habitat.

Once eastern regions became glacier-free, huemul were able to reach Andean habitat and when

deglaciation allowed for it, eventually cross the Andes (Hershkovitz 1969; Moreno *et al.* 1994). Faunal exchanges from the east were foremost across low Andean passes and explain the occurrence of late Pleistocene huemul in Chile as far northwest as 30°S by the Pacific coast (Moreno *et al.* 1994; Simonetti 2000; Frassinetti and Alberdi 2001). With the last glacial retreat, forests spread from the few western refuges, and eventually covered the southern Andes again, reaching their current extent only 2-3000 ya (Armesto *et al.* 2010; Markgraf and Kenny 1997; Rabassa and Coronato 2009).

Humans arrived with the last interglacial period, about 10-12'000 ya in the southern Andes. Having been nomadic hunter-gatherers (Latorre *et al.* 2007), they would have had some influence on local distribution of *Hippocamelus* (Dabbene 1911; Horkheimer 1960; Sincaire 2009). However, in northern and central Chile, humans adopted sessile and agricultural lifestyles long before arrival of the Spanish. They reached very high densities, completely changed the habitat through slash and burn, and regionally extirpated several species including huemul (Miller 1980; Simonetti 2000; Armesto *et al.* 2010). The same pattern was also confirmed for pudu deer (*Pudu puda*) (Saavedra and Simonetti 1991). Further south, humans became established mainly along the Pacific coast and focused on marine resources. Consequently, early explorers still found coastal areas abundant with huemul: it quickly became an established fact that such areas indicated low passes across the Andes from which to reach the eastern slopes via expeditions. The logical interpretation was that coastal huemul stemmed from source populations on the eastern side of the continental divide (Moreno 1899; Steffen 1904). East of the Andes, huemul also existed in zones between the Andean foothills and the Patagonian mesas (Finn 1909; Lydekker 1925). Onelli (1905) described huemul regularly occurring in flat grasslands about 120 km east of the Andes (44°55'S, 70°7'W), and as still, although already rarely, occurring up to another 140 km further east. It coincides with Prichard (1902) still collecting huemul at 200 km from the Andes and other historic records of this species at 270 km east of the Andes (Flueck and Smith-Flueck 2011c). However, this species also reached the Atlantic coast (Lydekker 1915). Reports from the 16th, 18th and 19th centuries mention huemul near Port San Joseph and Port Desire (de la Piedra n/d; MacDouall 1833; Moreno 1899; Diaz 1993; Diaz and Smith-Flueck 2000), old shed antlers were still found in steppes by Serret (1990), and Cruz *et al.* (2010) recently found a prehistoric human-modified antler near the Atlantic, although it cannot be ascertained that it stemmed from that locality.

The Spanish arrival resulted in highly significant changes brought about by the introduction of horses, which created an equestrian lifestyle for native people and profoundly changed their economies. Horses first arrived in Buenos Aires in 1537 and became feral, but by 1580 they already reached the Strait of Magellan (Darwin 1839). Introduced livestock immediately became feral and soon roamed by the millions (Darwin 1839; Behm 1880; Ljungner 1959; Torrejon 2001). Native tribes prevented colonization of Patagonia and dominated the region for some 300 years until displaced by wars. Only some intrusion by settlers from Chile was possible. Accordingly, the major industry in these forests was livestock raiding by nomadic intruders and eastern tribes, with 47% of these forest areas having been burnt rather recently or shortly before studies by Willis (1914). Darwin (1839) found that native people knew to use knives, forks, spoons and relished sugar, and having had so much contact with sealers and whalers, that most of the men spoke some English and Spanish. He further noted that these natives traveled up to 750 km inland during summer to hunt in the foothills, each man having 6-7 horses. After overpowering the tribes, fencing and ranching occurred rapidly throughout Patagonia (von Siemiradzki 1893; Torrejon 2001) which further affected the remaining huemul distribution.

As a result of the above mentioned history, the first early writings were posterior to significant anthropogenic changes in the distribution of huemul, with explorers therefore largely unaware of previous history. Their descriptions of huemul often were from remnant populations living in remote and inaccessible places. Subsequent naturalists found an even more reduced distribution, but as locations coincided with the few early accounts, it led to dogmatic descriptions. Thus, decades have gone by further ingraining the notion that huemul are exclusively of Andean forests and not part of lowland central Chile (Osgood 1943; Povilitis 1978; Thornback and Jenkins 1982; Redford and Eisenberg 1992; Corti *et al.* 2010; Vila *et al.* 2010); specially adapted to precipitous rocky terrain, and forest habitats of the Andes (Thornback and Jenkins 1982; Belardi and Otero 1998; Nowak and Walker 1999; Dolman and Wäber 2008; Fernandez 2008); a mountain deer living above tree line (National Research Council 1991; Prothero and Schoch 2002; Guérin and Faure 2009); living between 1300-1700 masl or high elevation mountains (Nowak and Walker 1999; Merino *et al.* 2005); or as preferring steep, rocky, north-facing slopes (Thornback and Jenkins 1982; Redford and Eisenberg 1992; Lord 2007). Preference to the high Andes, principally near the international border along the continental divide, was considered to be due to the conditions in that area being the most favorable to huemul, as

explicitly stated by e.g. Osgood (1943). The problem of basing ecological interpretations on current distribution is illustrated by the suggestion that huemul habitat use moves down about 107 m in elevation for every 11° latitude further south (Gill *et al.* 2008). The conclusion was based on regressing the median elevation of upper and lower elevations of signs registered for some populations with latitude. The upper elevation of habitat use simply coincides with the tree line which progressively diminished at increasing latitude, a trivial observation. The relationship between lower elevation and latitude however is an artefact by leaving out historic and zooarcheologic data. Thus, whereas it is correct to conclude that the upper elevation of huemul habitat use diminishes with lower latitude (parallel to the diminishing tree line), it is fallacious to conclude the same for the lower boundary of current habitat occupation. The lower limits are determined by the altitude of adequate interior winter ranges and sea level on both sides of the continent (Flueck and Smith-Flueck 2011b), and absence of huemul is due to having been displaced. These generalized descriptions of the species, implying preferences, exclusiveness, or most favorable conditions are strong terms with specific ecological meaning, yet such casual statements are not enough to make these inferences. More recently another explanation was offered, namely that “huemul has been reported in all habitats associated with steep, irregular and rough slopes, with rocky terraces or around cliff edges” (Vila *et al.* 2010). While the statement is correct, the authors completely omitted mentioning other types of habitats used by huemul in historic times and even today. Miller *et al.* (1973) already cautioned that characterization the optimal habitat of huemul is difficult due to most huemul having only survived in dense cover. Being well documented (Diaz 1993; Diaz and Smith-Flueck 2000; Smith-Flueck 2003; Flueck and Smith-Flueck 2011a), ignoring these facts distorts the interpretation of basic ecological traits of huemul (Fig. 3).

HUMAN USE OF HUEMUL

Based on a low quantity of zooarcheological remains and the only study on economic anatomy, Belardi and Otero (1998) concluded that huemul were not important to hunter-gatherers. Their interpretations relied on an analysis of two fresh carcasses from late autumn that had no fat in the meat, and bone marrow was considered as the only source of fat. Unfortunately, these authors neglected the fact that their samples were particularly incomplete regarding fat reserves because these animals had been skinned and eviscerated before being sent for analysis, and thus the most important portions were not available. Other studies on huemul also focused on bones, emphasizing the low utility of meat due to lack of fat during the annual cycle, while omitting the issue of dissectable fat (e.g. De Nigris 2004). However, these recent interpretations about huemul utility are in stark contrast to fat reserves in other cervids collected during the same season: McCullough and Ullrey (1983) found that *total energy content* of deer was partitioned in up to 47% as dissectable fat, 1% as marrow, 5% within bone, and 32% in muscle. Fats have the highest energy density and were partitioned on average (by weight) into 65% dissectable fat (up to 76%, most occurring with visceral organs), 8% in high-density fatty visceral tissue, 4% in bone tissue, and 2% in marrow. As dissectable fat averages 12% (up to 16%) of total body weight, but represents up to 47% of the deer energy content, it explains observations on hunter-gatherers elsewhere who focused on deer during the autumn/winter peak of fat. Cracking long bones takes little effort compared to energy return, and boiling bones for further fat extraction also does not take much effort (Church and Lyman 2003), although it requires fuel. Marrow and bone grease extraction is well documented for many hunter-gatherers, including in Patagonia (Bourlot 2006). Although this practice may render maximally 6% of total fats, it is erroneous to ignore that professional hunter-gatherers would certainly have taken advantage of easy accessible high-density fatty visceral tissue and dissectable fat which present >1200% more energy content than that obtained from bones. Price (1939) noted that northern Natives emphasized eating fatty visceral tissue, used marrow for various preparations and as milk substitute for children, but gave much of the muscle to their dogs. Moreover, human foragers generally ignored poor or starved animals for their lack of fat (Lipo 2007; Morin 2007), as documented from narratives by Natives regarding huemul hunting: "in stormy days, when herds of huemul came down from the Andes, we chose the fattest one to eat" (Diaz and Smith-Flueck 2000).

In autumn, 20-30% or more of body weights of cervids may consist of fat (McCullough and Ullrey 1983; Cook *et al.* 2007), and therefore north American hunter-gatherers preferentially killed deer in autumn/winter for being the easiest period and because cervid fat accumulation was maximal (Thomas and Toweill 1982; Lipo 2007). More importantly, while butchering they consumed dissectable fat, fatty visceral tissue and marrow, and then transported remaining bones for marrow and tallow extraction at camp (Price 1939; Thomas and Toweill 1982; Morin 2007; Speth 2010). The same traditions existed with Patagonian hunter-gatherers utilizing guanaco, where accessible fat including marrow was the favored part, and together with organs were consumed raw at butchering (Steward 1946; Tavener 1955;

Bourlot 2006). Guanaco also have annual fat cycles peaking in autumn/winter (Raedeke 1979), which is likely more pronounced in migratory populations.

Models of reconstructed hunter-gatherer diets have frequently assumed that muscle tissue was the sole animal tissue consumed; however, many ethnographic reports of various hunter-gatherer societies show that nearly all of the edible carcass was consumed. Moreover, analyzing 229 hunter-gatherer societies showed that virtually all potential fat contained in animal carcasses would generally be consumed (Cordain *et al.* 2000). Similarly with guanaco, no selective transportation operated in the past, instead all body parts were utilized and no anatomical units were abandoned unused (De Nigris and Mengoni Gonalons 2005), indicating that kills could be done near the shelter. This was suggested for huemul and guanaco based on bone assemblies also in other sites, where bone processing was fat-oriented (Fernandez 2008).

Hunter-gatherers commonly moved according to seasonal movements of prey, and such seasonal logistic mobility has been documented in several instances. Distances up to 150 km for hunting, particularly in autumn and early winter, best explained logistic mobility in low-density hunter-gatherers in northern environments (Lovis *et al.* 2005). From hunting camps, groups of young men would make roundtrips of >100 km in about three days. Moreover, these hunters have been able to portray detailed maps covering 240,000 km² and animal movements within (Lovis *et al.* 2005). Deer being preferred, a temporary camp would remain if there were individuals within 50 km (Lovis *et al.* 2005; Lipo 2007). Considering historic reports of winter concentrations of huemul, foraging conditions in the pre-Colombian era were likely even superior in terms of hunter-gatherers.

Bones of guanaco and huemul regularly coexist in archeological sites in Andean foothills between ca. 2500-6500 years BP, based on four stratigraphic layers (De Nigris 2007). The domination of guanaco in excavations has been explained by the supposed range-wide rarity of huemul and by hunter-gatherers being able to exploit ungulates most effectively where they are territorial, which is the case for guanaco (Muñoz and Mondini 2008). Alternative explanations include: (a) the well-documented ease to kill huemul which could easily result in local overhunting and produce rareness through exploitation depression (see Lipo 2007), (b) being non-territorial (Flueck and Smith-Flueck 2011*d*), huemul will temporarily evade hunting parties by moving to other sites, resulting in more mobile hunting which leaves little or no signs, and (c) given more mobile hunting, bones may be left behind as bone grease would only present about 4% additional fat compared to easily recoverable fat (Price 1939).

If tactics to hunt huemul differed from hunting guanaco, which is almost certainly the case, then most of the kill and butchering sites of huemul may remain undescribed. Similarly, Fiedel and Haynes (2004) found no descriptions of kill sites east of the Plains where large mammal like elk, deer, bear, or woodland bison were utilized by paleoindians during the past 12,500 years. If archaeologists in eastern North America have not yet stumbled upon the remains of any such butchered carcasses – 12,500 years with no discoveries - what is the likelihood of finding a butchered huemul? Empirical evidence, from analogous modern cases, show that even overkill would leave few fossil remains behind to identify the very processes involved in the resulting extinctions (Fiedel and Haynes 2004). Although there is no doubt that 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 hunting behaviors by men towards huemul and the associated impacts on huemul distribution. Borrero (2008) acknowledges that so far there had been a bias in surveys in Patagonia which focused on caves that represent more permanent sites. Transient hunting camps and movements are thus under-represented and difficult to document anyway.

GENERAL DISCUSSION

Horses and livestock brought by the Spanish soon became feral and roamed by the millions, which transformed lifestyles and economies of native tribes and allowed them to resist the Spanish for >300 years. Highly mobile, the Native's impact on the vegetation augmented as they increasingly hunted wildlife and feral livestock to trade with the colonies. As early writings by explorers were posterior to these significant anthropogenic changes, they described remnant huemul populations in remote and inaccessible places. References of huemul being analogous to other ungulates using mountainous terrain was intuitive in such historic settings and for apprehensible reasons: mainly because huemul had already been eliminated from much of their former range, were rare and mainly found in mountain refuge areas. Understandably, they were labeled as *mountain deer*. Yet to be known was the fact that

these other ungulates were stereotyped mountain dweller that too had experienced anthropogenic displacements. Now it is shown that these once existed -and currently exist again- in non-mountainous habitats.

Historic remarks used huemul body shape as circular reasoning for labeling it a mountain deer. These nonquantitative assertions were dismissed by a recent analysis of postcranial morphology showing that huemul are not analogous to rock climbing species, but fall within the range of other cervids (Flueck and Smith-Flueck 2011a). Using mountains is not a unique trait of huemul among cervids. For instance, Allen (1900), of the famous Allen's rule, observed that Mountain caribou used the same range occupied by the rock specialist Stone sheep (*Ovis dalli stonei*) and had habits much like those of sympatric Stone sheep. Strikingly, the literature abounds with casually labeled mountain ungulates: 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 like Plains reindeer, Forest reindeer, Woodland caribou, Plains mule deer, Forest chamois, Field roe deer, Steppe red deer, etc. None of these labels constitute a scientific concept and merely refer to local adaptations. Most extant huemul then may be considered as satellite subpopulations that utilize mountains and have assumed some "mountain mannerisms" as an expression of intraspecific variation (reviewed in Putman and Flueck 2011). Still, modern circular reasoning continues to invoke remnant huemul as having primarily survived in remote areas like upper drainages in inaccessible mountains due to: a) being prime habitat, b) being specialized and selecting to live in steep and broken terrain, and c) having short legs and stocky build as evidence for specialization. By necessity this construct only holds up by marginalizing historic evidence and insights from zooarcheology, paleontology and paleoclimate.

Understanding past utilization of huemul by humans has implications for interpreting the prehistoric distribution. Although it is frequently claimed that pre- and post-Columbian Natives did not hunt huemul much, presumably due to their leanness, this contrasts comparative data from other cervids. Deer in seasonal environments accumulate fat by autumn/winter such that >50% of total energy is in fat, mostly in highly accessible deposits and often consumed at butchering, as also practiced by Patagonians. Accordingly, and due to substantial hunter mobility, camps were maintained if deer were within 50 km. Natives in upland Peru used 53% camelids and 31% cervids like the congeneric taruca, before domesticating camelids (Miller and Burger 1995). In contrast to common belief, due to extreme ease to kill huemul particularly in autumn/winter, their large winter concentrations in the past, and strong incentives due to their high energy density, Natives likely influenced huemul distributions and density in winter ranges, particularly once Natives had access to horses for mobility. Given the productivity of ecotones and adjacent steppes based on current biomass of exotic herbivores, densities of other *Odocoileus* in similar habitat elsewhere, and the few indicative records about huemul density in those areas before extirpation, we posit that huemul abundance was substantial. As Cabrera and Yepes observed in 1940: in the past huemul was one of the most frequently hunted by Patagonians who traded their skins to Carmen and even Bahia Blanca (Atlantic ports).

A necessary look at evolutionary history provides further leads regarding past distribution. To reach South America, cervids, as generalists, were able to pass through the Panama land bridge filter. Considering paleoclimatic conditions, huemul dispersed south on the eastern side of the Andes, also because glaciations pushed them eastward with fossils encountered in northeastern Brazil. As the ice reached the Pacific, huemul could only enter Andean habitat and cross the Andes when deglaciation allowed for it. As a mixed feeder, huemul could utilize 'Patagonian' steppe with its many shrubs and important green grass production throughout winter, being far removed from isolated small forest refuges in midwestern Chile coasts. During glaciations, Patagonian' steppe reached way into Brazil and down to Fireland. Evidence of huemul presence exists for Fireland and areas near the Atlantic even historically. Regardless, interpretation of a prehistoric human-modified huemul antler recently found near the Atlantic followed orthodox descriptions of huemul: the current huemul distribution was considered more valid than historic accounts, and thus it was concluded that more likely, paleoindians had walked the 250 km to the Andes and received the antler that way (Cruz *et al.* 2010).

Knowledge of historical ranges is important regarding endangered species, because recovered or recovering species have been found to occupy a greater percentage of their historic range than declining species. Instructively, anthropogenically-caused range contraction of ungulates with broad former historic distributions were heavily skewed toward loss of low elevation ranges (Laliberte and

Ripple 2004). Often it is assumed that when a species becomes endangered, its geographical range should contract inwards, with the core populations persisting until the final stages of decline. However, analyzing patterns of range contraction of many cases, Channell and Lomolino (2000) found that most species persist in the marginal periphery of their historical geographical ranges. Populations that persisted the longest were those last affected by the crawling spread of historic extinction forces; that is, those along the edge of the range, on an isolated and undisturbed island, or at high elevations (Channell and Lomolino 2000).

CONCLUSION

Past distribution and morphological studies show that huemul fit comfortably within the ranges for other deer and ungulate species using sub-alpine habitats. Previous use of Patagonia steppe areas far from forests is similar to habitat use by the only congeneric taruca and other *Odocoileus*. The seasonal fat cycle and congregations likely made huemul a prime candidate for hunter-gatherers, who would have therefore influenced their distribution and density. Several other ungulates had mainly lost their low elevation habitats from anthropogenic pressures and range contraction allowed them to persist only in marginal peripheral habitat, concentrated at high elevations or otherwise inaccessible sites. Historical ranges are thus an important consideration for conservation strategies of endangered species like huemul. Paleocology, zoogeography, and history of land use in the southern cone of Latin American indicate that mountain huemul are secondary relicts created by post-Columbian anthropogenic impacts. We caution against the rigid application of modern huemul habitats in interpreting past habitat use and against simply considering the few extra-Andean accounts as abnormal outliers that one can thus ignore. 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 indicate that conservation programs could benefit from broadening strategies accordingly.

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Figure 1. Examples of male and female huemul showing body proportions while in summer coat.



Figure 2. Continuous ice sheet covering the Andes down to 56°S. Glaciers south of about 42°S dipped into the Pacific, and reached at times hundreds of kilometers into the Patagonian plains east of the Andes such that only treeless habitat existed east of the Andes. The coast line also was shifted eastwards by hundreds of kilometers (from Auk 111:143, 1994).

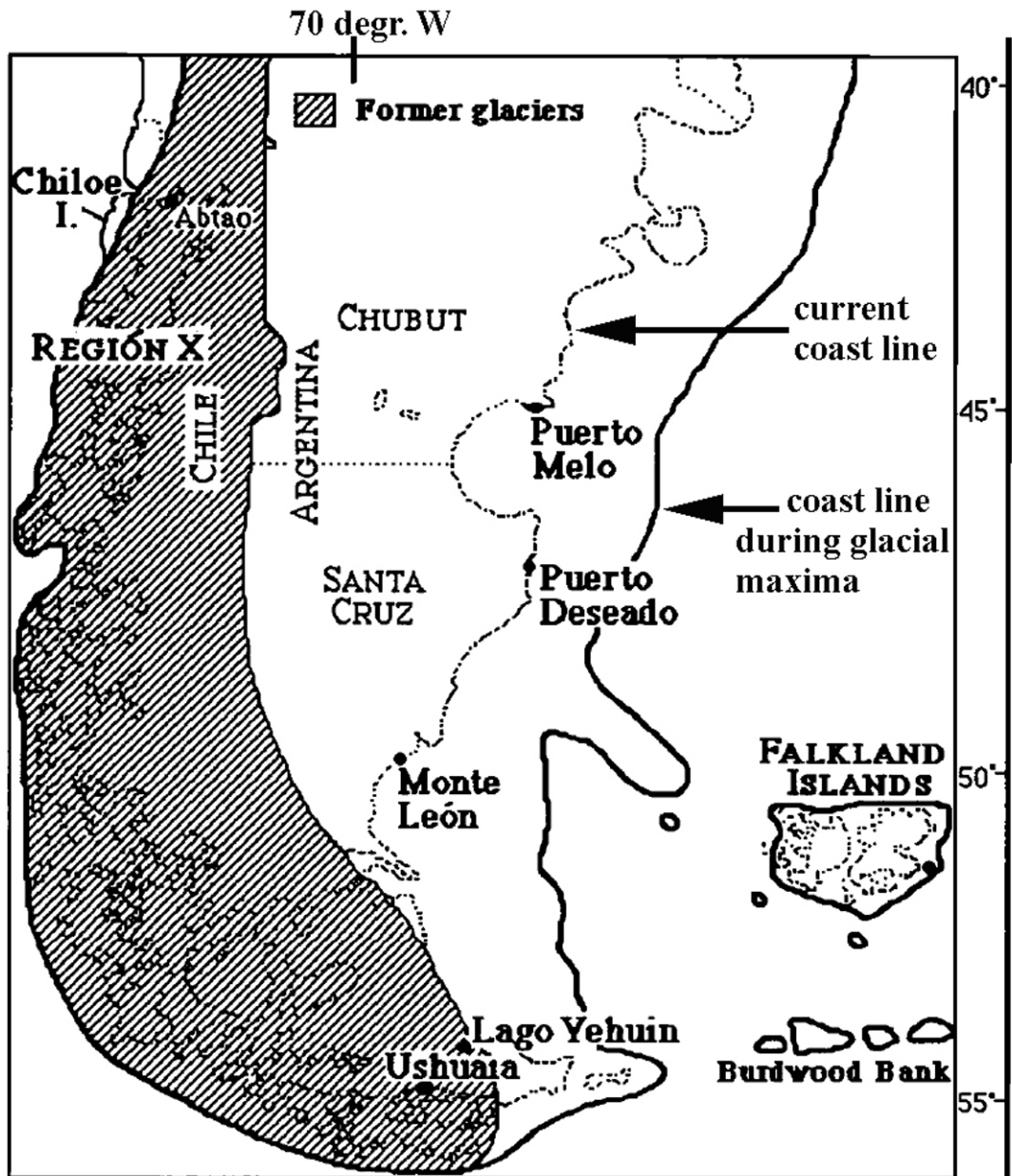


Figure 3. Past and current use of open and flat habitat by huemul, far from forests and cover. Note that use of such habitat occurs during full daylight hours.

