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HUEMUL HERESIES: BELIEFS IN SEARCH OF SUPPORTING DATA 2. BIOLOGICAL AND ECOLOGICAL CONSIDERATIONS

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ABSTRACT

The continuing lack of well-substantiated information about huemul (*Hippocamelus bisulcus*) results in reliance on early sources of interpretations. The repeated citing of such hearsay is scrutinized here for their validity. Huemul antlers provide clues about well-being and past changes as up to 5 tines have been documented historically. Antlers are misinterpreted by erroneously considering >2 tines as abnormal. The question is: "What conditions in the past allowed many tines, and allowed antler expressions to be closer to the species norm?" Significant past changes resulted in only few early records of large groups, abundance and killing many huemul. Current orthodox descriptions of huemul are based on little data from remnant populations in marginal habitats. Relying on such biased information results in circular reasoning when interpreting zooarcheology, paleodiets, prehistoric distribution, and huemul ecology in general. Claims of inadequate antipredator response due to evolutionary absence of cursorial predators is unsupported as several *Canis* species arrived together with cervids, overlapping with dogs having arrived with paleoindians. Huemul reactions toward dogs are similar to other Odocoilines. However, any predation event in severely reduced huemul subpopulations may be important due to dynamics of small populations. There is no evidence that livestock or red deer (*Cervus elaphus*) have caused declines or prevented recovery of huemul. In contrast, huemul have disappeared in numerous areas lacking livestock or red deer, but have persisted elsewhere with livestock for several hundred years. Recent sympatry with red deer affects <2% of huemul populations and in one case livestock outnumber red deer 2100%. Cervids including huemul exhibit great variation in feeding behavior, irrespective of dental and gastrointestinal features, due to flexibility in behavior, physiology and morphology. Although presence of other herbivores will shift spatio-temporal habitat use and affect performance, persistence of multi-species assemblages is the rule, like huemul coexisting with guanaco (*Lama guanicoe*), pudu (*Pudu puda*) and livestock. However, impacts from management of livestock, particularly the presence of people and dogs exert heavy pressure on wildlife and create incompatibilities. Concerning diseases from exotic ungulates, huemul coexisted with livestock for several centuries, but only recently in a few cases with red deer (but outnumbered 21-fold by coexisting livestock). Parasites found so far in huemul were only at very low levels. These are mostly considered nonthreatening, are found in red deer but commonly in livestock and therefore occur in most areas with livestock. Thus, the primary factor regarding contagious diseases is feral and free-ranging livestock, and being regularly researched and inspected at slaughter, these provide a good proxy for diseases afflicting sympatric red deer.

Additional keywords: *Hippocamelus bisulcus*, antler, group size, density, predation, diet, competition, diseases.

INTRODUCTION

In the accompanying paper about historical and zooarcheological considerations (Flueck and Smith-Flueck 2011a), we analyzed information regarding historical conditions and how it has influenced current interpretations of the biology and ecology of huemul (*Hippocamelus bisulcus*). Together with the current paper, the reports aim to improve our understanding of huemul and its conservation. Here we focus on issues related to antlers, group size and density, predation, diet, competition, and diseases to reveal inconsistencies in currently accepted beliefs that do not stand up under closer scrutiny.

Securing reliable data is difficult because huemul populations contain few individuals and, those remaining, are located in remote refuge areas. However, a detailed search was conducted in ISI Web-of-Knowledge and 17 external databases, three books and three dissertations on huemul, historic and

grey literature available in a collection containing 286 entries on huemul, plus publications on other related deer species to allow a comparative approach to analyze and interpret huemul.

ANTLERS

Antlers are deciduous secondary sexual characteristics, and principle factors influencing their phenotypic expression are recognized as age, nutrition, animal condition and social environment. Antlers provide a phenomenal tool for interpreting a myriad of biological and ecological relationships due to being a luxury tissue regrown annually, the only such regenerating appendage found among mammals. The correct interpretation of antlers therefore is not a trivial issue. Yet the literature on huemul is replete with erroneous interpretations which fail to appreciate the informational content of antlers.

Past literature commonly considered huemul antlers to consist only of simple forks (e.g. Frick 1937). Kurten (1975) even claimed that huemul differed from *Navahoceros* by having two, and not three antler tines. More recently, the same claim continued (Redford and Eisenberg 1992; Webb 2000; Lord 2007; Guérin and Faure 2009), or that forks are typical and 20-25 cm long (Povilitis 1985; Nowak and Walker 1999; Vila *et al.* 2010). However, antlers with three tines are still common in some localities, representing 43% of samples we measured in Chile and Argentina ($n = 47$), while antlers with four tines have been found many times with lengths >34 cm (Fig. 1) (Philippi 1892; Prichard 1910; Krieg 1925; Bubenik and Bubenik 1990; Serret and Borghiani 1998; Díaz and Smith-Flueck 2000). Although in the past antlers with five tines were documented (Osgood 1923), antlers beyond forks were, and still are, labeled *abnormal* (Philippi 1892; Rusconi 1936; Cabrera and Yepes 1940; Vila *et al.* 2010). Larger antlers with multiple tines found historically likely resulted from bucks still having been able to fully develop by reaching older ages and having been described from areas used formerly that provided access to good nutrition. In contrast, some extant remnant populations have very young age structures with no individuals encountered older than four years old (Smith-Flueck and Flueck 2001), and are restricted to small fractions of ranges used previously (e.g. Fig. 6 in Flueck and Smith-Flueck 2011b).

GROUP SIZE AND DENSITY

Group sizes and densities of huemul are often stated categorically when in reality these data only represent particular remnant subpopulations studied recently and occurring in a subset of habitats used formerly. The range for group size is commonly stated as solitary, or 1-5, and to 8 during winter (Redford and Eisenberg 1992; De Nigris 2004; Fernandez 2008; Vila *et al.* 2010). In contrast, groups of 10 huemul in summer (Grosse 1949) and 11 in autumn (Díaz and Smith-Flueck 2000) occurred even recently; they used to form wintering groups of 100 or more (Prichard 1902). Larger groups were reported from more open, and particularly treeless landscapes, in concordance to behavior of other cervids (reviewed in Putman and Flueck 2011).

Similarly, the range of density is stated from 0.002-1.2 huemul/km² (Redford and Eisenberg 1992; Belardi and Otero 1998; Fernandez 2008). However, even some extant populations have densities of about 9 huemul/km² (Wensing 2005), and although there are no density estimates for historic times, we can deduce that densities commonly must have been substantial. For instance, Juan Ladrillero first reported huemul from Chile in 1558, as he commented "...and then we went up to the place known as the Deer Point, where in just one hour two of our men shot fifteen of them with the arquebus..." (Díaz and Smith-Flueck 2000); and they were using weaponry which was less accurate than bow and arrow! Early naturalists regularly mentioned that huemul occurred in great numbers together with guanaco (*Lama guanicoe*) in the "Patagonian pampa" (Burmeister 1873; Steffen 1900; Prichard 1902; Hatcher 1903; Osgood 1923). Natives in Argentina knew huemul well and hunted them frequently, and preferentially where feasible, for food and skins, which were traded at the Atlantic coast (Burmeister 1873; Cabrera and Yepes 1940). Based on shooting many huemul, Prichard "could have very easily shot ten huemul in a day": yet Natives assured him that these deer were at one time even more numerous in that region (Prichard 1902; Hatcher 1903). Crews of early expeditions still found numerous groups of huemul such that hunting was easy and provided large crews with fresh meat every day while three weeks traversing the region (Martin 1899; Steffen 1900; Osgood 1923). Grosse (1949) saw groups every day and so many tracks that he concluded that there were huge herds ("riesige Herden"). Later during colonization however, huemul were killed by the thousands/year and at rates of up to 1-2 deer/km² (Anon. 1936; Grosse 1949; Iglesias 1965), which is about the average density where they often occur now (Díaz and Smith-Flueck 2000). Huemul were not only used for people, but also to feed dogs, chicken and pigs, and skins were used to construct shelters for people and domestic animals (Gigoux 1929; Anon. 1936; Krieg 1940; Madsen 1948; Iglesias 1965). At the same time there were

already huge herds of feral livestock using open areas, huge post-fire areas previously forested, forested areas and open areas above tree line (Veblen and Lorenz 1988): unfortunately, there are no data on their densities. Instructively in terms of capacity, good habitat in eastern foothills and grasslands was quickly filled with a large biomass of livestock (Table 1), reaching a maximum during the 1950s (von Thüngen and Lanari 2010). Today, former huemul range in the ecotone produces 3000–5000 kg/km² of exotic ruminant biomass (Flueck 2010), equivalent to about 40-60 huemul/km² if they would forage similarly, as expected from mixed feeders. Differences in extant and historic group sizes and densities foremost relate to the type localities of reported observations and thus provide important insights about huemul and for planning strategies towards potential recovery.

Table 1. Estimates of livestock, from Willis 1914, Fernández and Busso 1997, and von Thüngen and Lanari 2010

Year	Country and Area	Sheep	Cattle	Horses	Mules
1900	Chile	1,340,000	830,000	?	?
	Argentina	120,000,000	28,000,000	?	?
1908	Argentine Patagonia	10,000,000	834,000	490,000	15,000
1912	Argentine Patagonia	22,000,000	1,400,000	?	?
		Stocking rate is 16-60/km ²			
1952	Argentine Patagonia	25,000,000	?	?	?

PREDATORS

Predation events in severely reduced subpopulations, as now found with huemul, are very important due to dynamics of small populations (Caughley 1994). Nonetheless, it is equally important to understand the underlying causes of supposedly *excess* predation on cervids. Overabundant predators and inappropriate antipredator behavior to novel predators have been implied as major general impediments for huemul (see below), but alternative explanations include elevated morbidity, modified habitat structure, other undetected causes of mortality unrelated to predation, and methodological errors regarding differentiating predation from scavenging and carnivores involved. Even puma (*Puma concolor*) scavenge appreciably, treating scavenged carcasses as they would their own kills: between 8-12 puma scavenged 19 of 44 placed deer carcasses during a mean of 5 days even when rotting and maggot-infested (Bauer *et al.* 2005); 64% of monitored puma scavenged at least once and spending up to 50% of feeding time on carrion (Knopff *et al.* 2010); or a healthy female puma feeding exclusively on four carcasses during at least 22 days (Nowak *et al.* 2000). Interestingly enough, this behavior was already documented by puma scavenging a huemul that was killed earlier by Prichard (1910).

Frequently, predation by dogs is implied as a major factor causing declines or preventing recovery (e.g. Lord 2007), yet only occasional kills are reported and the impact on recruitment has not been quantified conclusively in any population. The assumed highly effective predation from dogs has been asserted to stem from huemul having evolved in, and still inhabiting, areas lacking large cursorial predators (Saucedo and Gill 2004; Corti *et al.* 2009, 2010; Vila *et al.* 2010). However, the cervid radiation to South America was accompanied with members of the Canidae, including at least three species of *Canis* (Hershkovitz 1972; Prevosti 2009). Dire wolf for instance co-existed with huemul into the Holocene (Marshall and Sempere 1991; Hunt 1996; Frid 1999), and existed until after man arrived with domestic dogs (Steward 1946; Orquera 1987; Miotti and Salemme 1999; Simonetti *et al.* 1999; Muñoz and Mondini 2008). Identifiable domestic dogs in Eurasia date back to >14,000 years, and paleoindians likely crossed Beringia already with dogs (Fiedel 2005; Napierala and Uerpmann 2010). By providing humans with hunting assistance, transport as well as emergency food, dogs likely arrived in South America together with paleoindians, with records from late Pleistocene (Miotti and Salemme 1999). Pre-Columbian hunter-gatherers clearly hunted huemul with dogs, and one tribe, with dogs but no horses, was called ‘huemules’ due to their clothes being made from huemul skins (Steward 1946; Díaz and Smith-Flueck 2000). The large fox (*Lycalopex culpaeus*) is sympatric with huemul,

considered analogous to *Canis latrans* in appearance and habits (Hershkovitz 1972), and also is a cursorial species pursuing large prey (Novaro *et al.* 2009). Direct observations of dogs and huemul (Jimenez *et al.* 2008) include: a) a persecuted mature huemul buck bounding side to side to navigate logs apparently attempting to out-run the dogs, b) a female with fawn out-running 2 dogs and escaping, not running to water but contouring a hill for about 1.5km and climbing to higher ground, c) a radio-collared female with a bedded fawn interceding several approaching dogs to distract them from the fawn; she then ran away, making a large circle, to return later to nurse and then take the fawn some 500m away. These observed huemul did basically what has been observed with red deer, Sika, and fallow deer when encountering dogs (Jimenez *et al.* 2008). Considering that huemul have had continuous exposure to cursorial predators for millennia, they likely have retained appropriate antipredator behavior. Furthermore, prey-predator interactions do not appear to become specialized due to prevailing multiprey-multipredator systems (Flueck 2000), and reintroductions of large predators has resulted in rapid readjustments of prey behaviors (Breitenmoser and Haller 1993; Molinari-Jobin *et al.* 2002; Flueck 2004).

Other members of the Odocoileine line besides huemul employ the same escape strategies: they hide and freeze, bolt or run off at close encounter, or take to water. Mule deer tend to bound uphill, imposing a heavy cost on predators, whereas white-tailed deer bolt down and along hillsides (Geist 1981). Huemul are known to snort, stomp the ground, run, trot or race away uphill or downhill and also bound like mule deer (Gigoux 1929; Texera 1974). Their tendency to take to water has been used to capture them (Geist 1981; MacNamara 1982).

With regard to puma predation, severely reduced huemul populations might not be able to sustain additional losses, and temporary predator control might allow recovery to sustainable numbers as documented for bighorn sheep (Williams 2010). On the other hand, a huemul population in Torres del Paine increased despite of foxes, feral dogs and a high-density puma population of 6/km² (Flueck 2010). This is possible when habitat is adequate, puma is the sole main predator, and antipredator responses are adequate as evidenced by huemul evading attacks by a puma with offspring (Prichard 1902) or chasing puma into trees (Murillo and Ramb 1975), similar as has been documented for female red deer (*Cervus elaphus*), and notably, this was a species that did not evolve with puma (Flueck 2004).

Ungulates may form larger mixed-species groups due to foraging advantages and predator avoidance (Stensland *et al.* 2003). In open areas for instance, huemul (Prichard 1902; Osgood 1943; Díaz and Smith-Flueck 2000; Guineo *et al.* 2008) or red deer (Flueck 1996) mix with guanaco, and historically huemul commonly ended up in corrals with livestock having been herded down to winter ranges (Flueck and Smith-Flueck 2011b). Recently, a young female huemul in southern Chile, found among a ranch's cattle, was lassoed and kept in a staple until confiscated by authorities a month later (Vidal *et al.* 2011). Moreover, open habitats with shallow slopes offer the additional benefit of diminished risks from puma predation as it provides little hiding cover for puma to hunt (Atwood *et al.* 2007). Thus, open lowlands east of the Andes likely presented source areas of huemul, because puma as the only main predators had limited impact due to prey forming large group sizes in such habitat, including mixed-species groups, and the large biomass of herbivores sustained in such habitat.

DIET

Circular reasoning is used to claim that huemul needs forests and browse by referring to their molars as being brachyodont, because such teeth supposedly indicate a browser (Vila *et al.* 2010). However, most all cervids have brachyodont teeth, yet even small species thrive exclusively in treeless grasslands, like Pampas deer (*Ozotoceros bezoarticus*) or roe deer (*Capreolus capreolus*) (Perez *et al.* 2008). Many cervids, including *Odocoileus*, are extremely versatile in food exploitation and successfully utilize grasslands, steppes and deserts (Putman and Flueck 2011), and quite independently from their cranial and dental features (Ozaki *et al.* 2007; Codron and Clauss 2010). For instance, mule deer will eat forage of unexpected low digestibility, but by compensating with faster gut passage rate: however, variance in diet between individual deer was greater than between elk, sheep and deer (Hobbs *et al.* 1983). Moreover, there is strong support that leaf-grass mixed feeding was the original feeding style of cervids (DeMiguel *et al.* 2008). Yet importantly, deer existing in steppes or grasslands do not solely rely on the fibrous portion of grasses. Besides other available plant species, deer can heavily use seed heads, particularly in winter (Wright and Kelsey 1997). When huemul still occurred at 200 km (Fig. 2, Prichard 1902) and even 270 km east of the Andes (Fig. 3, Díaz pers. comm.), Allen (1905) described huemul as grazing there. Furthermore, besides Gramineae, Patagonian steppes contain a large component of shrubs, forbs, and maintain important green grass production throughout winter

(Fernandez *et al.* 1991; Adler *et al.* 2005). Extant huemul had 16% of grass in diet (Sierralta 2003), whereas the sister species taruca (*H. antisensis*) had about 60% of grass in diet, composed of 15 species, during the rainy season (Gazzolo 2006). In comparison, similar sized *Odocoileus* also live in broken table grassland (<300mm precipitation) and deserts (74mm precipitation) (Fig. 4, Dusek 1975; Marshal *et al.* 2006). Irrespective, based on an unpublished report, huemul are still claimed to avoid grasslands and steppes and thus would not be expected there according to Cruz *et al.* (2010): huemul antler they found near the Atlantic consequently was suggested to have resulted instead from paleoindians walking 250 km to the Andes.

The biogeographic origin of ancestral *Hippocamelus* indicates that they were savanna-adapted in order to pass the Panama bridge filter, and subsequent periods of glaciation kept them repeatedly away from the Andes and forests, with fossils even known from northeastern Brazil as treeless Patagonia-type habitat then reached way into Brazil (Flueck and Smith-Flueck 2011b). According to Codron and Clauss (2010), gut morphophysiology does not impede feeding in alternate niches because a range of different adaptations may serve for utilizing the same dietary niche. Ingestion of other resources is a physical and physiological possibility and only translates into slight differences in chewing efficiency. It is possible, for instance, to maintain a concentrate selector-type ruminant on a purely grass-based diet, or a cattle-type ruminant on a purely browse-based diet - at least for a period of several weeks to months. Within the adaptive capacity of a ruminant, nutrient acquisition might be such that diet choice is largely random, which could explain why ruminants are so often observed to feed, apparently, suboptimally (Codron and Clauss 2010).

COMPETITION

The decline in distribution and abundance, as well as lack of recovery of huemul are frequently attributed to conflicts with exotic herbivores. Especially red deer is claimed as outcompeting and displacing huemul (Thornback and Jenkins 1982; Miller *et al.* 1983; Lever 1985; Schuerholz 1985; Navas 1987; Saizar 1987; Redford and Eisenberg 1992; Nowak and Walker 1999; Jaksic *et al.* 2002; Lord 2007; Dolman and Wäber 2008; Urrutia and Ojeda 2008; Vila *et al.* 2010). However, Diaz and Smith-Flueck (2000) questioned these assumptions, particularly red deer being responsible for declines of huemul, as no examples have ever been documented (also see Jimenez *et al.* 2008; Flueck 2010). In contrast, huemul were found to have disappeared in several areas lacking cattle, sheep, or exotic red deer (Smith-Flueck 2003). Moreover, feral cattle have co-existed with huemul several hundred years, and over 112 years with ranches cattle in one documented case (Jimenez *et al.* 2008). And although exotic red deer in southern forest habitats ate many of the same plants and had similar dietary preferences as huemul (Smith-Flueck 2003), this is relevant only if it reduces the population growth rate of huemul to <1. Also, considering huemul diet behavior from all studies, it is highly likely that huemul can shift diet without necessarily affecting recruitment (Flueck 2003; Codron and Clauss 2010), as is known for other cervids (Putman and Flueck 2011). Then, considering the impressive densities of exotic domestic and wild herbivores on former huemul habitat, it is considered unlikely that such areas were, or still would be, limiting to huemul in terms of energy and major plant nutrients (Krieg 1940; Flueck 2001, 2003). 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. On the other hand, the ecosystem can be affected if overabundance of herbivores occurs, be it through livestock or exotic wild herbivores.

Many remaining huemul populations share habitat with some livestock (exceptionally with red deer), but no studies show conclusively that there is spatial displacement from avoidance. In contrast, huemul used to mingle with livestock and were commonly driven together to winter ranges (reviewed in Flueck and Smith-Flueck 2011b). However, spatial avoidance could also result from activities related to livestock production, such as human harassment and hunting, and from accompanying unleashed dogs. Lastly, one common difference in habitat use is that only livestock have access to lower lands and valley bottoms, as the anthropogenic pressure does not allow huemul to persist there anymore (Flueck and Smith-Flueck 2011b).

DISEASES

There are frequent claims of huemul being highly susceptible to cattle diseases: *Cysticercus tenuicollis*, foot-and-mouth disease (FMD), coccidiosis, 'parasites', or actinomycosis (Povilitis 1978; Thornback and Jenkins 1982; Schuerholz 1985; Redford and Eisenberg 1992; Simonetti 1995; Wemmer 1998; McCallum and Dobson 2002; Uhart and Chang Reisig 2006; Lord 2007). However, such assertions

were based on hearsay, guesses, or misquoting of original sources. For instance, "*C. tenuicollis* when transmitted by livestock is fatal to huemul", yet the original source stated that presence of *C. tenuicollis* was not considered to be the cause of death. McCallum and Dobson (2002) wrote that *C. tenuicollis* is highly pathogenic to huemul, livestock being the reservoir, and increased habitat fragmentation unequivocally bad as it might maintain high infection rates and hence lead to declines or extinction of huemul. In contrast, in other cervids and ungulates the presence of *C. tenuicollis* is considered trivial (Leiby and Dyer 1971), which appears to be the same for huemul judged by several centuries of coexistence with livestock, millennia with guanaco that also harbor this parasite, and absence of direct evidence. Similarly, the only report on coccidiosis (Texera 1974) was subsequently misinterpreted, or FMD claimed to have wiped out huemul when cervids are currently considered unlikely to be an important factor in the maintenance and epidemiology of FMD in livestock outbreaks. Besides, FMD is self-limiting at normal densities of cervids (reviewed in Flueck and Smith-Flueck 2011c). Furthermore, a recent review of FMD in wild populations of susceptible South American wild species found no reports of any previous disease nor outbreaks (Pinto 2004).

Parasites found so far in huemul occurred only at very low levels. These and other parasites found in livestock and red deer are mostly considered nonthreatening, and being common in livestock occur in most areas where these are found (Love and Hutchinson 2003). Although red deer are suggested to present a special disease threat to huemul, they harbor diseases commonly associated with livestock. Having coexisted with livestock for >100 years, both red deer and livestock play roles in the epidemiology of the various diseases they share. While livestock are commonly sympatric with huemul (nearly 100%), spatial overlap with red deer is exceptionally rare, occurs in <2% of known populations, and occurred in recent time. Even in these latter cases, livestock presence is the determining epidemiological factor, since for each huemul there are 1.2 red deer in contrast to 25.2 livestock. Thus, for huemul the primary factor regarding contagious diseases are feral and free-ranging livestock (Flueck and Smith-Flueck 2011c).

DISCUSSION

Huemul antlers provide clues about changes in historic times and actual well-being. As luxury appendages they represent many biological and ecological relationships. Interpretations about huemul antlers are misguided and the informational content of antlers underappreciated. To consider >2 tines as abnormal is erroneous and clearly incompatible with modern understanding of antler biology. The question rather is: what conditions in the past allowed larger antler growth with up to 5 tines, and thus antler expression to be closer to the species' norm? Of plausible historical changes, the strongest effect likely stems from preventing access to nutritionally superior places (Flueck and Smith-Flueck 2011a, 2011b), followed by few males reaching prime age. It is reminiscent of red deer in primeval Europe when Lords forced the farmers to let deer feed in fertile fields and poaching was punished with death: body and antler sizes were much larger than those from deer now forced to live in closed forest tracks and high mountains (Beninde 1937:164).

Historical and current cases show that group sizes and density can be substantially larger than 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. For instance, prehistoric expansion of agriculture in central Chile led to much clearing of forests with the spread of weeds and other indicators of open habitats, with fires peaking 12000-6000 years BP, and causing local extirpation of several species including huemul (Flueck and Smith-Flueck 2011a). The Spanish colonization rapidly reduced indigenous people due to disease and slaughter, which was followed by a transient expansion of forests into abandoned land. Similarly, war and disease reduced the native population east of the Andes and may have allowed some temporary recovery of huemul in eastern lowlands. This may explain why early explorers again could easily hunt many huemul each day, and hundreds of kilometers from Andean forests (Prichard 1902). However, the subsequent colonization extirpated all huemul in most lowlands and open areas. The expansion of livestock ranching and settlements in most favorable lowlands and valley bottoms resulted not only in the inaccessibility to that part of former range for huemul, but also in the loss of their migratory traditions with likely nutritional consequences (Flueck and Smith-Flueck 2011b).

As marginal habitat results in fragmentation and reduced subpopulations, any mortality factor becomes more important, including predation. Determining the cause of death becomes a central concern and challenge, as predation has to be differentiated from scavenging (and even puma scavenge

appreciably), predator/scavenger species have to be differentiated, and lastly the possibility of underlying debilitating factors (physical condition, disease, etc) have to be evaluated, as these might be concealed by predation events. Claiming that huemul lack adequate antipredator behavior towards cursorial predators due to their absence in the evolutionary history is unwarranted. To the contrary, the cervid radiation to South America was accompanied with several cursorial predators including *Canis* lasting into the Holocene. Furthermore, paleoindians likely arrived in South America together with dogs. Earliest records date to late Pleistocene and Pre-Columbian hunter-gatherers clearly hunted huemul with dogs. Direct observations showed that huemul antipredator tactics towards dogs frequently resulted in preventing death of offspring or adults. Furthermore, cervids can rapidly readjust their behavior to reintroductions of large predators. All cervids can suffer losses from dogs, and although such predation is claimed to be causing declines or preventing recovery in huemul, the impact on recruitment from occasional kills is unknown. Most studies on effects of feral dog predation on *healthy* deer populations suggested that the influence is minimal (Reed 1981). However, predation events in severely reduced subpopulations, as now found with huemul, may be important due to dynamics of small populations. Thus, even puma predation in such circumstances might call for temporary predator control to allow huemul recovery to sustainable numbers. Importantly, of the two huemul populations documented to have increased, one recovered despite a high-density puma population (Guineo *et al.* 2008; Flueck 2010), whereas the other recovered despite puma and frequent incursions by dogs from nearby settlers and a town only 3km away (Díaz and Smith-Flueck 2000). The lack of recovery in other populations therefore might indicate other ongoing processes including excess morbidity, or other more important causes of mortality unrelated to predation. Lastly, certain areas in the past allowed large aggregations of huemul, forming mixed groups with guanaco in areas which today produce a large amount of herbivore biomass, and therefore likely represented source areas for huemul.

Cold-temperate ecosystems contain several ungulate species, with competition expressed as adjustments in spatio-temporal habitat use and feeding behavior, and modulated by factors like predation. Competition thus affects parameters like: distribution, recruitment, morphology and physiology, yet persistence of multi-species assemblages is the rule. There is no data supporting claims that competition, particularly from red deer, have caused declines in distribution and abundance in the past century, or prevented recovery of huemul. In contrast, huemul have disappeared in areas lacking livestock or exotic red deer (Vogel 1969; Smith-Flueck 2003). Moreover, huemul have also remained in coexistence with livestock over several hundred years, besides coexisting with guanaco and pudu. Intra- and interspecific food habits in cervids vary greatly and quite independently from dental and gastrointestinal features, due to numerous adjustments which can be made in behavior, physiology and morphology. This is even true for small deer (*Ozotoceros*, *Capreolus*), but also *Odocoileus* and taruca persist in grasslands and steppes. Huemul exhibit very flexible feeding behavior considering the use of at least 145 plant species, apart from species used historically in Patagonian steppe far from forests, and exotic food received for several years in subtropical Buenos Aires (Flueck 2010). In Chile, captive huemul accepted fruits, concentrates for heifers, ground oats, alfalfa hay, exotic willow and poplar, but given the choices they did not consume native *Nothofagus* (*lenga*, *cohiue*) (Rottmann 2003). Hershkovitz (1972) recognized *Hippocamelus* as pastoral and only secondarily adapted to sylvan habitats, which accords with habitats associated with past glacial events and with historic evidence of huemul still living far from Andean forests.

There are no data supporting claims that huemul is exceptionally susceptible to livestock diseases, nor that these affect population dynamics or have caused extinctions. Parasites found in huemul were at very low levels and are generally considered nonthreatening. Regarding epidemiology, emphasizing red deer is not warranted as they share diseases with livestock, having coexisted for >100 years. Livestock in turn have coexisted with huemul for several hundred years. Currently, most all huemul populations are exposed to livestock, but practically none are sympatric with red deer, in which cases livestock still determine the epidemiology since they outnumber red deer by 2100%. Thus, for huemul the primary factor regarding contagious diseases are feral and free-ranging livestock.

CONCLUSION

Huemul antlers frequently are simple forks, but rather than claiming it to be the norm, we need to determine what conditions in the past allowed much larger antlers. Orthodox descriptions of density and group size stems from biased data. To avoid circular reasoning when interpreting zooarcheology or past distribution, historical data on abundance need to be considered. Having co-evolved with cursorial and ambush predators, huemul have adequate antipredator tactics, and any current predator impacts

would relate to dynamics of small populations or to other underlying problems. Although competition from other herbivores can shift spatio-temporal habitat use and affect performance, persistence of multi-species assemblages including huemul/guanaco/pudu is the rule. There is no evidence that livestock or the red deer in particular have caused declines or are preventing the recovery of huemul. In contrast, huemul have disappeared in numerous areas lacking livestock or red deer, while persisting in other areas with livestock for several hundred years. Cervid feeding behavior varies greatly due to flexibility in behavior, physiology and morphology. Thus, competition *per se* appears to be of minor importance, more likely incompatibilities relate to management associated with livestock production, particularly the presence of people and their dogs which exert heavy pressure on wildlife. Concerning contagious diseases from exotic ungulates, the overwhelming primary factor would be livestock given their numbers and degree of overlap with huemul. Regular research and slaughter inspections of livestock provide a good proxy for pathogens afflicting sympatric red deer or huemul.

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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Figure 1. Huemul antlers still commonly have three tines, and up to five in the past.



Figure 2. 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.

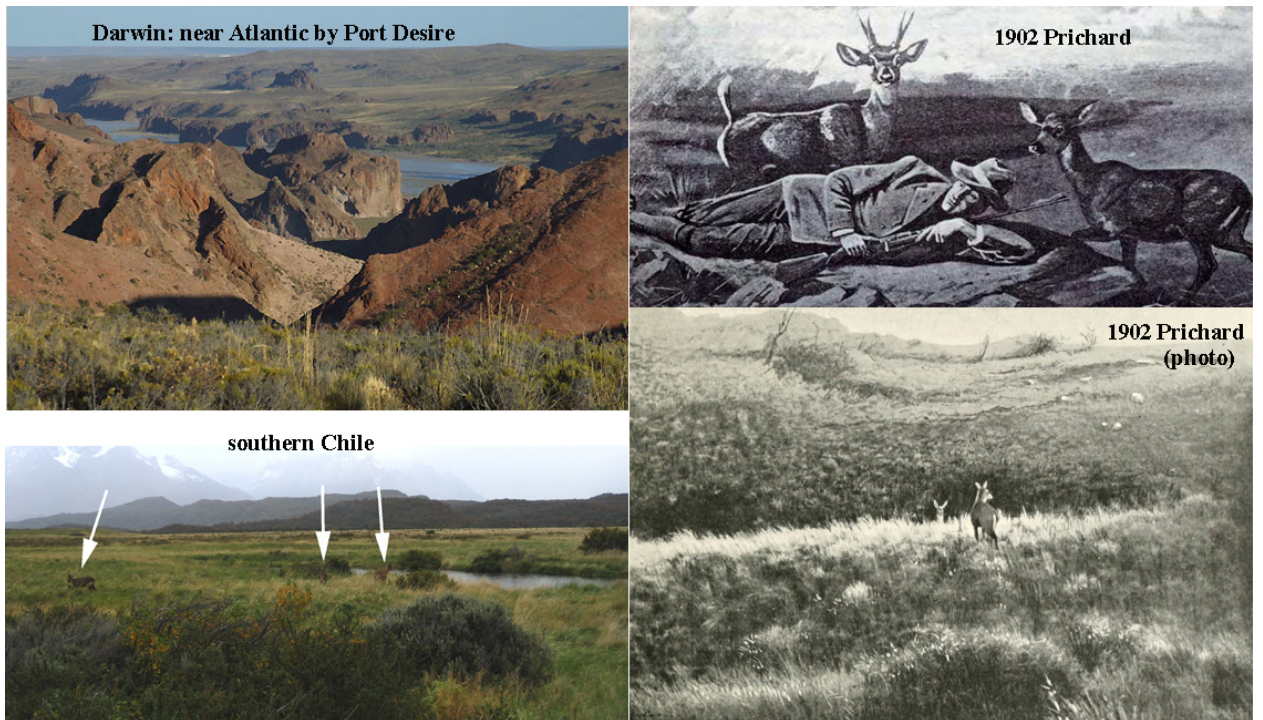


Figure 3. Huemul shot at 270 km from the Andes at Sierra Piré Mahuida (with courtesy of N. Díaz).



Figure 4. Similar sized *Odocoileus* and taruca (*H. antisensis*) also live in broken table grassland (<300mm precipitation) and deserts (74mm precipitation).

