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Functional limb anatomy in a refugee species: The endangered Patagonian huemul deer (*Hippocamelus bisulcus*)

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Abstract

Early naturalists already considered huemul rare, refuged and a stocky, short-legged mountain deer, 163 years before declared endangered (1972). Anatomically, huemul do not overlap with rock-climbers previously considered analogous, as corroborated in this paper by including additional huemul cases. Assertions that population declines are caused principally via livestock infections remain unfounded. Instead, osteopathology in multiple populations across 1,000 km, affecting 57% among dead and 86% among live specimens, may relate to micronutrient deficiencies. Historically classified a mountain deer, widespread osteopathology, micronutrient deficiencies and lack of recovery qualify huemul as a refugee species. Recovery strategies thus must include repopulating historical distribution sites.

KEYWORDS

anatomy, cervid, deer, epidemiology, huemul, morphometry, osteology, pathology

1 | INTRODUCTION

Early European naturalists described Patagonian huemul (*Hippocamelus bisulcus*) as stocky, massive and short-legged mountain deer, comparing them to their ibex (*Cabra ibex*) and chamois (*Rupicapra rupicapra*). Similarly, Americans compared huemul to their mountain sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*). Recent authors (e.g. Eisenberg, 1987; Riquelme et al., 2018) used similar descriptions referring to early writings; moreover, government agencies responsible for conservation in Argentina currently describe huemul as deer adapted to mountains, having stocky bodies with short and strong limbs (APN, 2020; Biodiversity Information System of Argentina, 2020). Historic interpretations thus have fomented these persisting claims that huemul are mountain deer, with Andean mountains being their natural range, as evidenced by the current distribution: yet this is but a snapshot of the original natural distribution (Flueck & Smith-Flueck, 2012). Significant impacts from these assertions, although never substantiated, are on conservation policies: extant huemul found in such environments are considered to have survived there because it is their most optimal habitat (Riquelme et al., 2018), and efforts thus concentrate on Andean mountains.

Current recovery efforts are distinctly based on assumptions that prevailing ecological interpretations of huemul are correct, despite a review showing that even the basic ecology is little known or unknown (Flueck & Smith-Flueck, 2006). However, basic aims in studying endangered huemul are to identify factors limiting population recovery. No reasoning exists to assume that extant huemul are occupying all-encompassing (i.e. optimal) habitat or are healthy and vigorous. Conversely, having become endangered implies that severe constraints limit the natural tendency of healthy populations to increase and spread (Taber, 1978). If constraints are suboptimal nutrition, it may be manifested in immunodepression, below-normal skeletal size and development, or reduced rate of recruitment. Thus, increasing knowledge about huemul anatomy and its functional interpretation benefits clinical and biomedical research, teaching (Salinas, Núñez-Cook, et al., 2020; Salinas, Arenas-Caro, et al., 2020) and, importantly, achieving recovery of huemul (Taber, 1978).

Evolutionary traits are preferably evaluated based on reliable parameters for inferring about adaptations for locomotion, rather than relying on prior vague intuitive inferences based on overall similarities and phylogenetic affinities. This paper aims to expand comparisons of appendicular morphometry between huemul and other ungulates (Flueck & Smith-Flueck, 2011a) by including huemul cases used in Salinas, Núñez-Cook, et al. (2020) and Salinas, Arenas-Caro, et al. (2020), to assist with ecological interpretations and future conservation measures towards recovering this species.

2 | MATERIALS AND METHODS

The morphometric analysis of leg bones from huemul was based on complete leg assemblies from the collection at DeerLab (Research Collections, http://deerlab.yolasite.com). Measurements (mm) taken with callipers were recorded for total length, articular width, and width (lateral) and depth (anteroposterior) of shafts at the most narrow section. Circumference was obtained with a flexible tape measure. Red deer (*Cervus elaphus*) samples were from work in Patagonia (Flueck & Smith-Flueck, 2013). For other species with no published data, samples were measured at the Basel Naturhistorisches Museum, Switzerland: *Rupicapra rupicapra* (specimens C.III.386, C.3607, C.3667, C.728/729, C.9635, C.2279) and *Hemitragus jemlahicus* (specimen 10753).

3 | RESULTS AND DISCUSSION

3.1 | Anatomy of huemul: understanding the enigma

Salinas, Arenas-Caro, et al. (2020) state that there is no literature about anatomical and morphometric characteristics of huemul, although Flueck and Smith-Flueck (2011a) reported allometric comparisons between huemul and 12 other species. However, these were considered erroneous (Salinas, Núñez-Cook, et al. 2020), and importantly, they incorrectly claim that this study describes huemul as having short and stocky limbs, comparable to mountain ungulates such as ibex, chamois, bighorn sheep and mountain goat, and that huemul is a mountain deer with structural characteristics typical of climbing animals that live at high altitudes. However, that study (op. cit.; Huemul Task Force, 2012) evidenced exactly the opposite: (a) paleontological comparisons were rejected as they were based on a new fossil labelled as mountain deer which, however, has been shown to be a construct and declared “nomen nudum”; (b) leg morphometrics of huemul and 12 other ungulates revealed that huemul cannot be associated with rock-climbing species; (c) huemul morphology does not overlap with rock-climbing species previously considered analogous, but falls *within* the range of cervids (Figure 1). Importantly, some populations of reindeer (*Rangifer* spp.) and even white-tailed deer (*Odocoileus virginianus*) have much shorter legs than huemul (Flueck & Smith-Flueck, 2011a) and clearly are not considered mountain deer. These conclusions are corroborated by additional research based on rearlimb ecomorphology, showing that huemul is adapted to open habitat (unforested) areas (Curran, 2012, 2015).

Several proportional appendicular morphometric indicators are very similar between the huemul cases used in Salinas, Núñez-Cook, et al. (2020), Salinas, Arenas-Caro, et al. (2020) and Flueck and Smith-Flueck (2011a) (Table 1). Moreover, among true rock-climbers, tibia are the longest bone, and metatarsals range from just over, to just under half of tibial length (Whistler & Webb, 2005), again placing huemul far from true rock-climbers (Table 2). Additionally, arranging metatarsals according to proportional length as main indicator of locomotor use (Scott, 1985), there are clear groupings of “true rock-climbers” (Whistler & Webb, 2005), followed by potential ‘inhabitants of rocky areas' like Bighorn sheep or chamois, to black antelope (*Antilope cervicapra*) considered to be the fastest runner (Garland & Janis, 1993).

Among ungulates, the tibia/femur and radius/humerus ratios are rather uniform and corroborate that differences in leg proportions relate mainly to metapodials (Christiansen, 2002; Scott, 1985). Among comparisons (Table 3), standardized tibias varied by 18%, whereas the metatarsals varied considerably by 53%. Also,

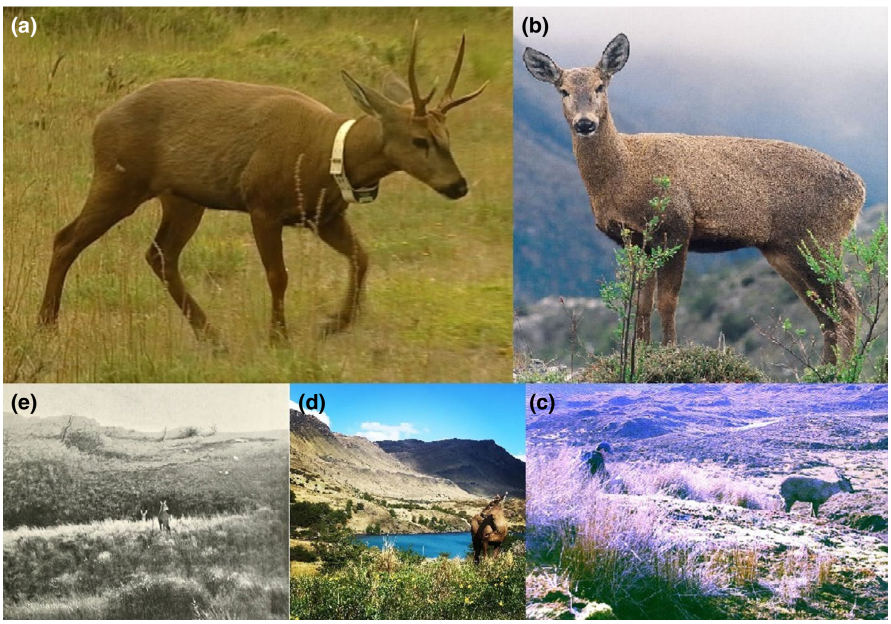

FIGURE 1 Huemul in summer coat resembling other cervids in body proportions (a, b). Very few more recent examples of huemul in Patagonian ecotone or steppe (c, d) corroborate historical encounters (Allen, 1905) some 200 km from forest (e), a likely scenario during the last glacial maximum (Flueck & Smith-Flueck, 2012)

TABLE 1 Proportional appendicular morphometric indicators for Patagonian huemul deer

Metatarsal/femur	Radius/ humerus	Tibia/ metatarsal	Source
0.786	0.856	1.664	Salinas, Núñez-Cook, et al. (2020) and Salinas, Arenas-Caro, et al. (2020)
0.736	0.920	1.560	Flueck & Smith-Flueck (2011a)

TABLE 2 Percentage difference between half the tibial and total metatarsal lengths (means), as an indication of affinity to a true rock climber[a]

	Mountain goat	Ibex	Chamois	Bighorn sheep	Huemul	Red deer
Tibia	426	290	413	403	305.2	373
Metatarsal	180	142	255	256	195.767	291
% diff	+15.5	+2.1	−23.5	−27	−28.3	−56

[a]Whistler & Webb (2005).

proportions between segments of the hind leg are very similar to those of the front leg in the same individual. As metapodials are important for gait dynamics, Table 3 shows the tibia/metatarsal ratio among ungulate species. A larger ratio means that metapodials are shorter, and the pattern largely coincides with proportional metatarsal length. Again, the group of 'true rock-climbers' has the largest tibia/metatarsal ratios.

3.2 | Complementary information useful for huemul recovery policies

Species severely reduced numerically often lack fundamental information (Povilitis, 1978; Taber, 1978; Thornback & Jenkins, 1982), since studies are logistically challenging. Thus, existing reliable, although limited information, must be disseminated correctly, to avoid establishing heresies and their influence over conservation policies.

IUCN did not declare huemul as endangered in 2003 (Salinas, Arenas-Caro, et al., 2020), but did so already in 1972 (Goodwin & Holloway, 1972; Thornback & Jenkins, 1982), and huemul had thus been on CITES appendix since 1975 (UNEP-WCMC, 2014). Also incorrect are assertions that currently huemul are absent between 34°–41°S in both countries (Salinas, Núñez-Cook, et al., 2020). One of the most important, and northern-most population occurs there in Chile, having received ample conservation actions since 1970s and in actuality (Povilitis, 1978; Thornback & Jenkins, 1982); several populations occur in Argentina (Jiménez et al., 2008). Similarly, asserting that 1,500–2,000 huemul remain in Chile (Salinas, Núñez-Cook, et al., 2020) disagrees with reiterated conclusions of IUCN that Chilean huemul may number up to 1,000 (Black-Decima et al., 2016; Jiménez et al., 2008; Povilitis, 1978). Lastly, Salinas, Núñez-Cook, et al. (2020) refer to high prevalences of skeletal injuries and diseases in Chile (87%) and Argentina (57%): no available information corroborates this high prevalence in Chile. Rather it likely stems from sources stating that prevalences of osteopathology in Argentina in dead huemul were 57%, and 86% based on live and intact specimens (Escobar et al., 2018; Flueck & Smith-Flueck, 2017, 2018, 2020; Smith-Flueck et al., 2018).

3.3 | Magnitude of intraspecific variation in biology, health, disease adaptations

Generalizations often mask important variations from that supposed norm, whereas in practice there is tremendous phenotypic plasticity, with variation in morphology, physiology, social organization and behaviour of any one deer species. The extraordinary degree of intraspecific variation which may be recorded within species has important consequences for conservation of endangered deer (Putman & Flueck, 2011).

The bold, candid assertion regarding huemul, that "undoubtedly, the greatest impact on population decline is caused by infections transmitted by domestic livestock" (Salinas, Núñez-Cook, et al., 2020; Salinas, Arenas-Caro, et al., 2020) remains unfounded. Diseases are common among any wild deer, yet simply listing these is insufficient to draw epidemiological conclusions. The mentioned parapoxvirus refers to the first-ever infection recorded in one single huemul (Vila et al., 2019). Significantly, parapoxvirus in bovids do not usually result in clinical disease as described in those huemul (Friederichs et al., 2015; Howerth et al., 2018). This atypical symptomology may relate to having presumed that parapoxvirus was correctly identified, but moreover, huemul cases occurred in areas without cattle, whereas areas in Argentina with coexisting huemul, cattle and red deer have not resulted in this disease (Flueck, 2020). For South America, this huemul with presumed parapoxvirus is first among native and exotic cervids and thus undescribed for the remaining > 100 huemul subpopulations.

Caseous lymphadenitis (CLA) (Salinas, Núñez-Cook, et al., 2020; Salinas, Arenas-Caro, et al., 2020) was first identified in huemul in 2015 (Morales et al., 2017). It resulted surveying another population in 2018, although clinical symptoms described there 1999–2007 (Guineo et al., 2008) did not elicit sanitary concerns until CLA was diagnosed in 2015 (Flueck & Smith-Flueck, 2020). However, described in 1888, CLA is well known with global distribution, common in Argentina by 1913, and notably, CLA recognized early in Chile resulting by 1937 in obligatory reporting to governments (Flueck & Smith-Flueck, 2020). Huemul,

TABLE 3 Proportional length of appendicular bones from various ungulate species, using the femur for a standard length (arranged according to metatarsal length)

	Mountain goat	Ibex	Tahr (1)	Bighorn sheep	Huemul (2)	Huemul (3)	Navaho (4)	Chamois	(5) Ovis ammon	Tule elk (6)	Mule deer (7)	Odoc. lucasi (8)	Red deer (9)	Black antelope
Femur	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Tibia	1.09	1.16	1.11	1.18	1.14	1.31	1.07	1.26	1.18	1.19	1.15	1.1	1.14	1.23
Metatarsus	0.48	0.57	0.57	0.70	0.73	0.79	0.79	0.79	0.79	0.80	0.82	0.84	0.85	1.01
Tibia/metatarsus	2.27	2.04	1.95	1.69	1.56	1.66	1.14	1.59	1.49	1.19	1.4	1.31	1.34	1.22

Note: (1) Thar, *Hemitragus jemlahicus*. (2) Huemul, *Hippocamelus bisulcus*, from Flueck & Smith-Flueck (2011a). (3) Huemul, *Hippocamelus bisulcus*, from Salinas, Núñez-Cook, et al. (2020), Salinas, Arenas-Caro, et al. (2020). (4) Mountain deer, *Navahoceros fricki*. (5) Argali or Marco Polo sheep. (6) Tule elk, *Cervus canadensis nannodes*. (7) Mule deer, *Odocoileus hemionus*. (8) American mountain deer, *Odocoileus lucasi*. (9) Red deer, *Cervus elaphus*.

therefore, have been with CLA for much of its existence in South America, due to their being in contact with species affected with CLA, namely sheep, goats, mules, horses, cattle, alpaca, other deer species, hares and also native guanaco (Wernery & Kinne, 2016). Infected cervids are well known in other continents, and infections in huemul are thus to be expected (Matos et al., 2015; Pepin & Paton, 2010; Valli et al., 2016). Also highly relevant, selenium deficiency has been shown to negatively affect antibody responses in sheep against CLA (Larsen et al., 1988).

Lastly, regarding bovine paratuberculosis, clinical disease in wild deer has only recently (2002) been reported in Florida, and a single case (2009) in Virginia (Sleeman et al., 2009). Common symptoms include emaciation and consistent chronic diarrhoea (Sleeman et al., 2009). The huemul case, based on sampling 14 groups of solid faecal pellets (i.e. no diarrhoea), had six positives (Salgado et al., 2017). Importantly, stressors, such as high deer density and low selenium levels, may contribute to the development of clinical disease (Mackintosh et al., 2004; Sleeman et al., 2009). Generally for cervids, there is minimal mortality, almost invariably diarrhoea, and besides sheep and cattle, there are other sources from wildlife like rabbits, foxes, stoats, ferrets and others (Mackintosh et al., 2004). Finally, additional studies mention two huemul having antibodies against bovine viral diarrhoea; and four huemul carrying sheep scab.

The limited data on these diseases in huemul render doubtful that they present the greatest impact on population decline, as asseverated by Salinas, Núñez-Cook, et al. (2020); Salinas, Arenas-Caro, et al. (2020). The strongest epidemiological conclusions come from studies that use large populations with precise measurements of exposure and disease; repeated observations of event (A) which is followed by another (B) enabling to hypothesize why A causes B; biological plausibility explaining the reasonability that A causes B; proper temporal relationship—an absolute requirement, where the exposure must precede the disease; consistency as shown by the association being repeated in many studies (large effect size); and by determining the causal inference (Steenland & Moe, 2016). According to these epidemiological principles, the infections listed for huemul qualify solely as local case reports.

3.4 | Widespread disease complex: osteopathology and micronutrient deficiency

Nutritional ecology has been proposed as the most parsimonious explanation regarding osteopathology, especially due to micronutrient deficiencies. Important aspects of this disease pattern include its corroboration in multiple populations over large geographical scales, spanning 1,000 km (Flueck, 2015, 2018, 2020; Flueck & Smith-Flueck, 2008, 2011b, 2017). Osteopathology concurrent with micronutrient deficiency in huemul has also been shown (Flueck, 2015) and substantiated by soil analyses (Flueck et al., 2014). Moreover, hair analyses of huemul with osteopathology revealed tissues levels well deficient in selenium, copper and manganese as compared to other cervids (Flueck, 2020).

The widespread occurrence of osteopathology, including crippled antlers, with concomitant micronutrient deficiencies, lack of recovery and population expansion, all indicate that huemul qualify as a refugee species (Faurby & Araujo, 2018; Lomolino & Channell, 1995). Additionally, naturalists described huemul as rare, as refugee, disappearing and in danger of extinction as early as 1857 (Flueck & Smith-Flueck, 2011a), and all non-mountain sites with historically reported huemul do not have them anymore. Lastly, the first-ever group of huemul radiocollared in Argentina (Flueck & Smith-Flueck, 2018) clearly reveals that these animals are all-year residents in summer ranges, a clear artefact from anthropogenic impact. It calls for strategically installing salt licks fortified with micronutrients as practiced in other cases of periled wild ungulates.

4 | CONCLUSIONS

Functional analysis and interpretation of limb anatomy in huemul based on comparing 12 ungulate species with an ample diversity of locomotive behaviour indicates that huemul cannot be associated with rock-climbing species, and their morphology falls within the range of other cervids. Moreover, rearlimb ecomorphology demonstrate their adaption to open unforested habitat. Regarding infectious diseases, the limited available data preclude an epidemiological assessment of impacts at population levels, nor is it possible to ascertain that they are paramount factors. The one disease complex noticed in multiple populations over a wide geographical area presents clinical bone problems and is accompanied by nutritional deficiencies, which likely present the underlying cause. Historic claims that huemul is a mountain deer, and the currently prevailing micronutrient deficiency is compatible with huemul being classified as a refugee species. Strategies towards numerical recovery thus must include repopulating historical distribution sites.

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CONFLICTS OF INTEREST

The author declares no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, upon reasonable request.

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