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Osteological comparisons of appendicular skeletons: a case study on Patagonian huemul deer and its implications for conservation

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Abstract. Early explorers described huemul (*Hippocamelus bisulcus*) as stocky, massive and short-legged deer of mountains, comparing them to ibex (*Cabra ibex*), chamois (*Rupicapra rupicapra*), mountain sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*). Subsequent key paleontological work also claimed that huemul are mountain deer. However, all these comparisons of huemul to other ungulates were done without any supporting data. These historic events lead to: (i) the continued prevailing claim that huemul are mountain deer; and (ii) that their natural range is the Andean mountains, as evidenced by the current distribution. We found that early writings about huemul generally reported their rareness, disappearance or near extinction. References to stocky and short-legged huemul were casual remarks made about deer found mainly in refuge areas. Paleontological comparisons were based on a new fossil labelled as mountain deer which, however, has been shown to be a construct and declared a ‘*nomen nudum*’. Behaviour like the aggressive horseshoe stance and thick long hair dissimulate stockiness by distorting body shape. Comparing leg morphometrics of huemul and 12 other ungulates revealed that huemul cannot be associated with rock climbing species. Intraspecific proportional leg length is not static and is influenced by ecogeography, nutrition, physiology and factors affecting exercise. Thus, climate, altitudinal hypoxia and locomotor pattern employed according to terrain, predation and forage affect the appendicular skeleton. Nutritional deficiencies occurring in Andean mountains are notorious for affecting bone development, causing osteopathology and altering body shape. Frequent underdeveloped huemul antlers and high incidence of osteopathology support the effect from mineral deficiencies. Skeletal proportions are affected by numerous factors, causing large intraspecific variation. Relative metapodial length varies up to 70% in better studied cervids, and populations from different environments can be clearly distinguished. Huemul morphology does not overlap with rock climbing species previously considered analogous, but falls within the range of other cervids. We caution against the rigid application of modern huemul occurrences in interpreting past habitat use. The few historic extra-Andean accounts cannot be considered abnormal outliers. Huemul ecology must be interpreted in terms of first principles rather than applying direct analogues from the present. This allows us to begin to use the past to understand the present instead of repeating the fallacy of imposing the present on the past. Current efforts to recover remaining huemul are distinctly based on the assumption that huemul foremost belong in rugged mountains, because of their supposed special adaptations and resemblance to stereotype ungulates, also erroneously believed to only occur in rugged mountains elsewhere. We conclude that the present empirical comparisons support many other lines of evidence that huemul existed in treeless habitat and colonised Andean forests and higher altitudes secondarily. Habitat breath of huemul is thus more like that found in other closely related Odocoelines, promising tremendous new opportunities for recovery efforts.

Additional keywords: adaptation, epigenetics, *Hippocamelus bisulcus*, morphometry, skeletal ratios.

Introduction

Early European explorers and naturalists described huemul (*Hippocamelus bisulcus*) as stocky, massive and short-legged deer of mountains, comparing them to ibex (*Cabra ibex*) and chamois (*Rupicapra rupicapra*) in their homeland. They assumed huemul to be a mountain deer, just as was the interpretation of ibex and chamois at that time, ungulates which by then were mainly surviving in remote alpine areas. Similarly, North

American workers compared huemul to mountain sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*). More recent authors,^{1–6} often referring to these early writings, make similar statements. Although Diaz showed already in 1993 how history erroneously ‘led to the assumption that the huemul was a deer of the mountains and that it had always inhabited areas in proximity to rugged topography’,⁷ the importance has remained largely unrecognised and the paper mentioned only a few times

in passing. Moreover, huemul being a mountain deer is often reiterated and supported by referencing key paleontological work, a study which, however, was erroneous (see below). Problems with interpretations based on nonmetric traits include high degrees of inter- and intraobserver subjectivity of qualitative descriptions and thus proneness to false dichotomies. Main results of these historic influences are 2-fold, by fomenting persisting claims that: (i) huemul are mountain deer, specialised to rugged terrain; and (ii) that their natural range are the Andes mountains, as evidenced by the current distribution, even while acknowledging the currently reduced and fragmented distribution.

Current efforts to recover remaining huemul subpopulations are distinctly based on the assumption that prevailing ecological interpretations of huemul are correct, despite a recent review showing that even the basic ecology is little known or unknown.⁸ The evolutionary history of huemul has major implications for the prospects of successful species recovery, which so far has failed. Evolutionary history is preferably evaluated having some reliable parameters for inference of adaptations for locomotion, as more vague intuitive inferences based on overall similarities and phylogenetic affinities are often not applicable. The functional morphology of mammalian postcranial remains can be used to infer locomotor adaptations and, by association, habitat relations. All references we have found, comparing huemul to other ungulates, have been statements without any supporting data. We analysed various observations and assumptions related to huemul body shape and its relation to adaptations to mountains, and compared huemul to other ungulates with the objective to determine if huemul can justifiably be considered a mountain specialist and if not, to describe the relation of its morphology to available habitat.

Methods

We review past and more recent claims of huemul being stocky, massive and short-legged and living principally in high Andean mountains; analyse phylogeny, particularly with regards to the only empirical paleontological work, from which huemul received the vernacular name 'mountain deer'; and review behavioural and physical aspects of huemul contributing to the appearance of stockiness.

We provide the first morphometric analysis of leg bones from huemul based on complete leg assemblies. Measurements (mm) taken with calipers were recorded for total length, articular width, and width (lateral) and depth (antero-posterior) of shafts at the most narrow section. Circumference was obtained with a flexible tape measure. Samples stemmed from Chile (Punta Arenas) and Argentina (province of Rio Negro, specimens cmhp316 and 345; province of Chubut, CITES permit No. 020729, permits 37/06, 38/06 and 03/07 issued by the Dirección de Fauna y Flora Silvestre; and National Parks, permit 915/08).

Data from huemul were compared with other ungulates: *Navahoceros*;⁹ *Odocoileus lucasi*;¹⁰ mule deer *O. hemionus*;^{11,12} ibex;^{13,14} chamois, measured in Basel Naturhistorisches Museum, Switzerland: specimen numbers C.III.386, C.3607, C.3667, C.728/729, C.9635, C.2279 and;^{12,13} tahr *Hemitragus jemlahicus*,

measured in Basel Naturhistorisches Museum: specimen numbers 10753, and;¹³ Marco Polo sheep *Ovis ammon*;¹³ bighorn sheep *O. canadensis*;^{13,15} mountain goat;^{12,13} red deer *Cervus elaphus*, our collection from Patagonia and;¹² and black antelope *Antilope cervicapra*.¹³ Finally, factors which are known to affect body proportions are summarised.

Results

Initial written accounts on huemul can only be understood correctly by acknowledging the concurrently reported rareness, or reference to being already endangered. Most early observers noted the already unnatural state and remarked that huemul were rare, disappearing and becoming extinct: e.g. 1857,¹⁶ 1897,¹⁷ 1910,¹⁸ 1935,¹⁹ 1941,²⁰ 1946,²¹ 1949,²² 1968.²³ In 1929 the Chilean government made a law providing total protection, and in 1932, the Argentine government employed a German scientist to start a breeding station aimed at avoiding extinction of huemul.²⁴

References to stocky, massive and short-legged huemul

According to Krieg in the 1920s, huemul in Argentina remained only in remote areas, hiding in brush above the treeline, whereas only very few people living on the western side of the Andes had seen huemul, although they had lived there for many decades.²⁵ He also noted the very thick fur, comparing it to mountain goats, and compared the hind legs to those of chamois, a comparison also made by Kolliker Frers.²⁶ In 1897, Heck compared appearance and behaviour of *Hippocamelus* to ibex.²⁷ Then, in Kurten's²⁸ technical paper, *Hippocamelus* was referred to as mountain deer based on (unquantified) short legs, being related to the ancestral cervid *Navahoceros*, and comparable to ibex and chamois. More recently, huemul were described as well adapted to broken, difficult terrain with a stocky build and short legs (^{29,30}, <http://www.wikipedia.org>, <http://www.ambiente.gov.ar>, verified 21 January 2011); or as having very short legs and found in rugged terrain and steep slopes of the Andes (<http://www.arkive.org>, verified 21 January 2011). Eisenberg¹ also considered huemul a typical high-altitude form by claiming that body proportions 'are reminiscent' of bighorn sheep (however, no data provided), appearing to occupy a similar niche as bighorn sheep. Argentine governments and National Parks (³¹, <http://www.ambiente.gov.ar>) and recent natural history accounts^{2,4,5} concur with his statements that huemul have a restricted distribution exclusively inhabiting the forests and sub-Andean grassland of the Patagonian Andes and are short-legged. Clearly, since the first descriptions of remnant huemul groups right up to the present, huemul has foremost been considered a mountain deer based on subjective descriptions of physiognomy and distribution in recent times.

Evolutionary phylogeny

Kurten,⁹ describing a new fossil North American cervid *Navahoceros fricki*, pointed out its 'highly unusual adaptive characters' among cervids, specifically referring to very thick-set limb bones, short metapodials, and simple antlers. Providing leg bone measurements of this fossil, he interpreted the sizes as extreme adaption to mountains, thereby applying the common

name ‘mountain deer’ for *Navahoceros*. Further, he stated that the plump limb bones are reminiscent of those from alpine chamois and ibex, claiming them to be adaptations to an alpine rock climbing mode of life. He contrasted *Navahoceros* to another fossil deer which he had described as *Sangamona*, a long-legged deer located east of the former,²⁸ thus reinforcing his new ‘mountain deer’ *Navahoceros*. He made the explicit correlation that *Hippocamelus* was related to *Navahoceros*, only differing by having two, instead of three antler tines:²⁸ he thus considered *Hippocamelus* implicitly to be homologous to chamois and ibex. Subsequently, Webb³² looked at one partial cranium of *Navahoceros* to interpret phylogenetic relationships. Referring to Kurten’s⁹ interpretation of *Navahoceros* as mountain deer, he further stated that ‘clearly, *Navahoceros* shares with *Hippocamelus* very short metapodials’, however, without offering data or references; and that ‘the correlation of skeletal proportions with mountain habitat is certain’, again without data or references. Later on New World cervids, Webb³³ reconfirmed close cranial relationships between *Navahoceros* and *Hippocamelus*, reiterated the very short metapodials of both, and concluded that soon after the Panama land bridge was established, this lineage of ‘mountain deer’, being better adapted to the high Andes, thus became established there. Webb reiterated (2007, pers. comm.) ‘that the North American mountain deer *Navahoceros* was phylogenetically affiliated with *Hippocamelus*, but surely could not have remained rigidly tied to alpine settings if, during the Plio-Pleistocene, they extended their range through the isthmian region’. Clearly, immigration of temperate species from North America was filtered through a subtropical-tropical barrier.³⁴ Regardless, huemul continued to be claimed to be ‘mountain deer’ based on ancestral *Navahoceros*, which contributed to further reinforcing contemporary claims that the current remnant populations in high elevation central Andes are there, and have survived, because it is their prime habitat.

However, a necessary closer look at Kurten’s original paper⁹ reveals major methodological flaws. For example, no standard deviations on leg bone measurements ($n = 9-52$) of *N. fricki* were provided, nor any indication as to sex or age. Thus, his averages cannot be interpreted, being well known that age and sex influence the size of leg bones in dimorphic ungulates.¹⁴ Furthermore, bones in the consulted multi-species collections are disarticulate individual bones, not complete sets of legs, and mixtures of ovids and cervids are prone to be confused (C. Dailey, pers. comm.). As Kurten did not provide collection identification numbers, it was impossible to duplicate his work.¹⁰ For comparisons, Kurten referred to measurements taken on only one single *O. hemionus*, without providing the origin, sex nor age. Notably, this specimen was near the extreme of long-leggedness for this species (metatarsal/femur = 0.97), compared with the reported range (0.82–1.00).^{11,12}

The most comprehensive analysis of fossil records pertaining to origins of huemul was provided by Morejohn and Dailey,¹⁰ which was based on detailed descriptions of new complete fossil finds, reconfirming the ancestral form *O. lucasi* as a North American endemic species. In addition, a painstaking reanalysis of many museum collections, particularly the ones consulted by Kurten, was summarised as follows:

- (1) All bones labelled as *Navahoceros*, and all skeletons in various museums, assembled from piles of disarticulated bones, were confirmed to be *Odocoileus*;
- (2) *N. fricki* is considered a ‘*nomen nudum*’; and
- (3) *Sangamona fugitiva* was also confirmed to be *Odocoileus*. *Sangamona* was declared a *nomen nudum* already in 1984,³⁵ as a construct of diverse and disparate skeletal elements, all of which derive from other and usually better known taxa, and except in the minds of men, never existed.

Thus, *N. fricki* and ‘mountain deer’ have been invalidated, and the focus remains on *O. lucasi* as ancestral form for *Hippocamelus*. Another fossil species, *O. brachyodontus*, recently shown to fall within the variation of other *Odocoileus*, was also declared ‘*nomen nudum*’.³⁶ Thus, *O. lucasi* remains the likely primary link to *Hippocamelus*.

Behavioural and physical factors affecting huemul body shape

Huemul at a glance can appear stocky and short-legged, especially males. For one, a peculiar behavioural trait portrays a stance which distorts body proportions. Huemul appear naturally unafraid of humans since they frequently do not run, or even walk away when approached, allowing people to get extremely close (Fig. 1a).³⁷ Such curiosity and apparent lack of fear in approaching humans is also known for several other ungulates including mountain goats³⁸ and bighorn sheep.³⁹ Nevertheless, Povilitis²⁹ first described an aggressive posture of huemul at close range: when first alarmed, huemul remain still and keep the front legs parallel and inclined posteriorly, and hind legs in a forward position (Fig. 1b). We posit that this stance is a homologous behaviour to that called the horseshoe posture which involves shifting of the back hooves towards the front hooves with the legs now forming a triangle with the abdomen. According to Cowan and Geist,⁴⁰ it involves a hunched posture, with flexed hind legs having the effect of lowering the height of the animal. The flexure of the hind legs is greater than that of the forelegs, resulting in an arched back and low-rumped position, leading to the impression that the animal is stocky and short-legged. This aggressive behaviour is common among Capreolinae⁴¹ such as *Alces alces*,⁴² *Rangifer tarandus*,⁴¹ *Odocoileus* with most exaggeration in periglacial *O. h. sitkensis*,⁴⁰ and huemul (Fig. 1b), but also occurs in mountain goats.³⁸

A further feature adding to apparent stockiness and short legs is related to the thick hair coat, which in winter provides thermoneutrality down to -50°C .⁴³ This results from a dense woolly underfur keeping the 7–9-m-long hair straight.⁴⁴ The appearance of a shedding huemul has repeatedly been compared with sick animals as hair comes out in clumps, similar to other mammals from cold climates. The extremely thick hair coat thus contributes substantially to the perceived stockiness of huemul (Fig. 1c).

Morphometrics of huemul and other ungulates

Although a shaved huemul would be instructive to reveal musculoskeletal relationships, body proportions can also be deduced from bone measurements (Table 1). Data from adult males were encountered more frequently and huemul bucks also provided the largest set of complete leg assemblies.

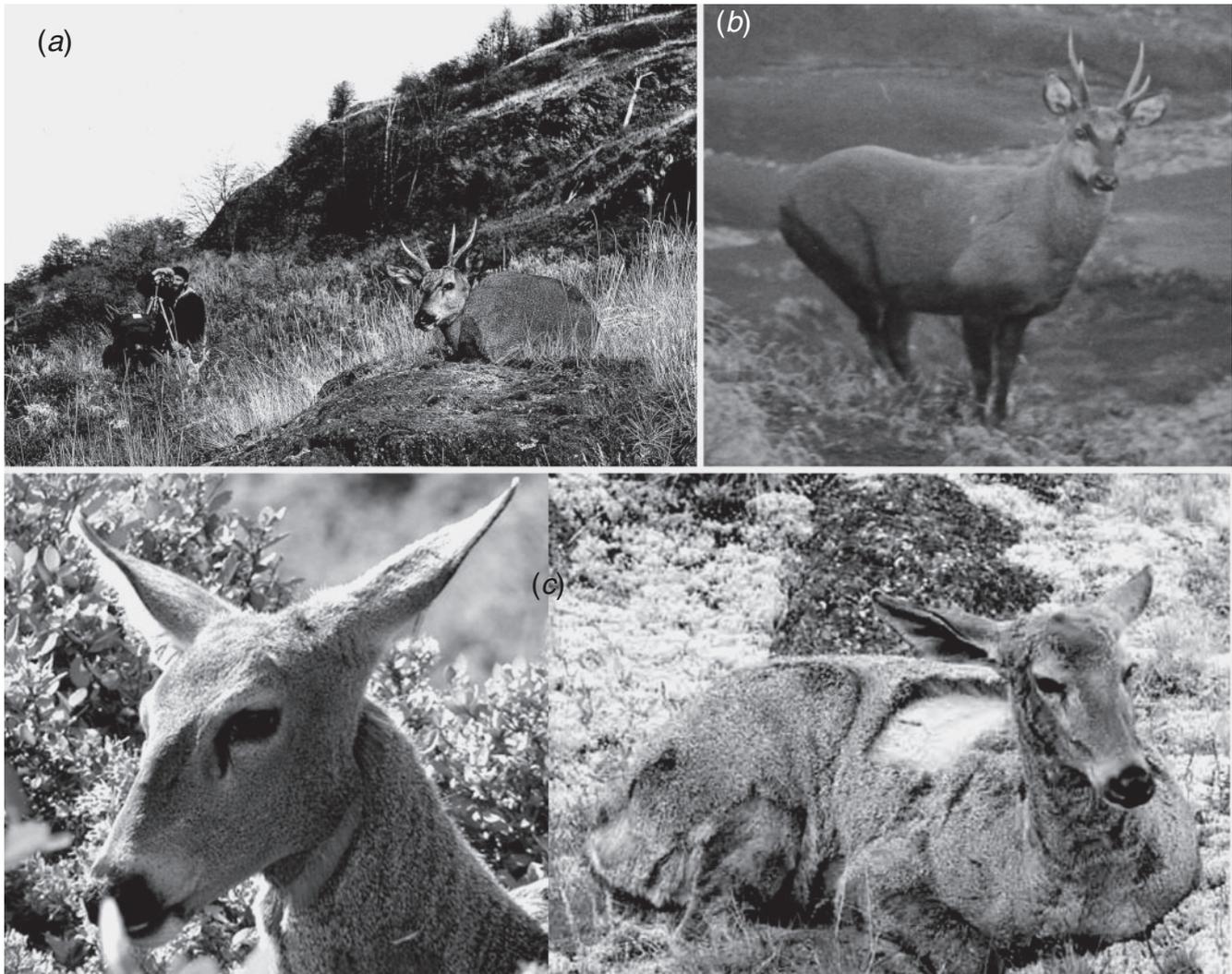


Fig. 1. (a) Huemul unaccustomed to humans frequently have very short flight distances (photo by J. M. Smith-Flueck). (b) The aggressive stance of huemul at close range, known as the horseshoe posture. (c) The 7–9-cm-thick hair coat is best appreciated when being shed (courtesy of G. Garay). Note in the left photo that the diameter of the upper neck is substantially less than further down in the unshed portion.

Table 1. Lengths and articular width (mm) of appendicular bones from adult male and female huemul

	<i>n</i>	Length	s.d.	Males				<i>n</i>	Length	s.d.	Females			
				Distal	s.d.	Proximal	s.d.				Distal	s.d.	Proximal	s.d.
Humerus	7	237	69	47.2	1.6	65	3.1	2	217	43	50.8	1.06		
Radius	10	214	53	40	1.5	41	0.9	4	205	47	40	37		
Metacarpus	12	172	43	37	0.5	35	0.7	4	163	40	32.5	31		
Femur	11	276	54	71.5	1.5	65	2.3	4	257	81	53.4	1.43	58.5	0.71
Tibia	16	315	103	43.3	1.2	64	1.9	8	294	86	40.7	1.49	62	1.83
Metatarsus	13	201	71	37	0.7	33	1.2	5	192	21	35.5	1.05	31.1	1.46

Interspecific proportional appendicular bone lengths were compared by standardising femur length (Table 2). Arranging metatarsals according to their proportional length as the main indicator of locomotor use,¹³ there is a clear grouping of ungulates

living in extreme steepness and rockiness ('true rock climbers'¹⁵), followed by species merely potential 'inhabitants of rocky areas' like bighorn sheep or chamois, to black antelope considered to be the fastest running ungulate.⁴⁵ The widely

Table 2. Proportional length of appendicular bones from various ungulates, using the femur for a standard length (arranged according to metatarsal length)

	Mountain goat	Ibex	Tahr	Bighorn sheep	Huemul	Navahoceros	Chamois	<i>Ovis ammon</i>	Tule elk	Mule deer	<i>Odocoileus lucasi</i>	Red deer	<i>Antelope cervicapra</i>
Femur	1	1	1	1	1	1	1	1	1	1	1	1	1
Tibia	1.09	1.16	1.11	1.18	1.14	1.07	1.26	1.18	1.19	1.15	1.10	1.14	1.23
Metatarsus	0.48	0.57	0.57	0.70	0.73	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	1.14	1.59	1.49	1.19	1.40	1.31	1.34	1.22
<i>n</i>	3	26–32	6	2	11–16	9–52	7	15	1	1	1	2	4
Sex	Male	Male	Mixed	Unknown	Male	Unknown	Male	Male	Unknown	Unknown	Male	Male	Mixed

accepted rock specialists (mountain goats, ibex, tahr) are clearly far different even from bighorn sheep. Speedy Black antelope on the other extreme are also separated distinctly by proportionally much longer metatarsals.

Among ungulates, the tibia : femur and radius : humerus ratios are rather uniform and corroborate that differences in leg proportions relate mainly to metapodials^{13,46} (Fig. 2a). Among species compared here (Table 2), standardised tibias varied by only 4.7%, whereas the metatarsals varied by 19.6%. Also, 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 2 shows the tibia : metatarsal ratio among ungulates. 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.

Stoutness refers to bone length in relation to thickness or articular width, with smaller ratios indicating stouter bones. Stout bones are the physiological reaction to forces, and would go in parallel with larger muscle masses. Table 3 presents the ratios of appendicular bone length in relation to articular width. Huemul are compared with ibex (‘true rock climber’) and red deer as originating from steppes.⁴⁷ Out of the 12 possibilities (six leg bones × two ends), huemul only once had the stoutest, yet three times the least stout articulate ends. Remarkably, ibex were stoutest, and red deer the least stout, for all metapodial ends (Table 3). Additionally, in true rock climbers tibia are the longest bone, and metatarsals range from just over, to just under half of tibial length,¹⁵ again placing huemul far from true rock climbers (Table 4).

Finally, bone circumference as a measure of bone strength is highly correlated with body mass in bones primarily supporting

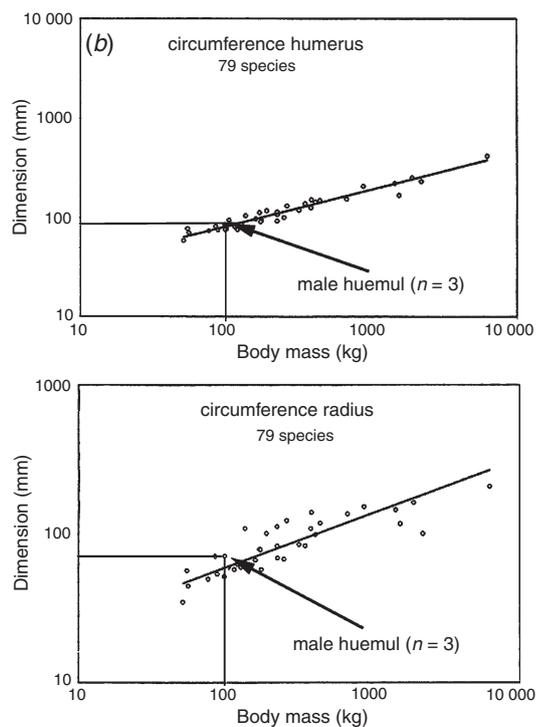
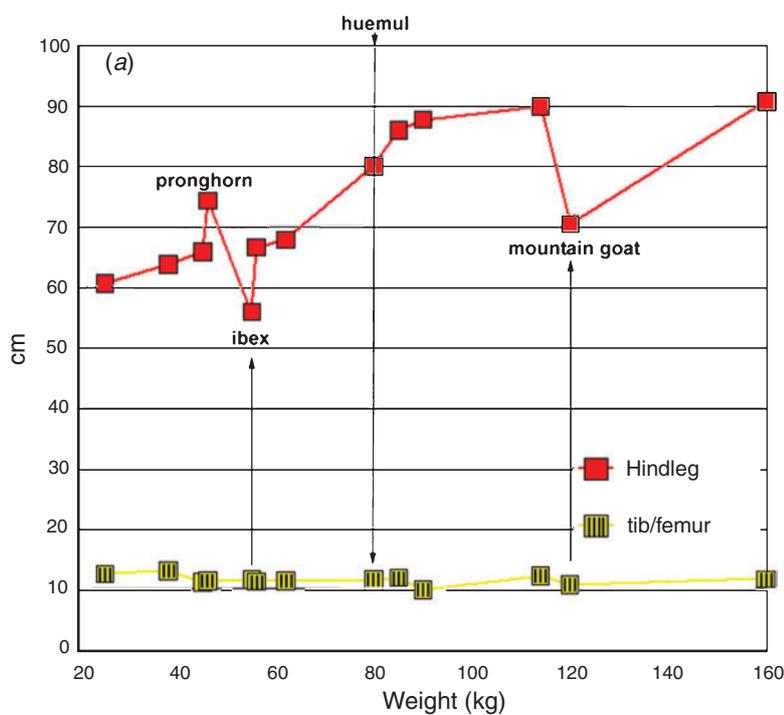


Fig. 2. (a) Tibia : femur ratios among ungulates mentioned in the text, in relation to leg length and arranged according to bodyweights⁴⁶, huemul from present study). (b) Bone circumference in relation to body mass in 79 different species analysed by⁴⁸ and adult male huemul from the present study.

Table 3. Comparison of stoutness among huemul, ibex and red deer: ratios of appendicular bone length to articular width at distal and proximal ends

	Ibex	Huemul	Red deer	Comparative stoutness	
				Maximal	Minimal
<i>Length/distal articular width</i>					
Femur	4.81	3.85	3.47	Red deer	Ibex
Tibia	8.5	7.27	8.97	Huemul	Red deer
Metatarsal	4.3	5.43	6.83	Ibex	Red deer
Humerus	4.85	5.02	4.67	Red deer	Huemul
Radius	4.74	5.35	5.59	Ibex	Red deer
Metacarpal	3.64	4.65	6.25	Ibex	Red deer
<i>Length/proximal articular width</i>					
Femur	4.06	4.23	3.63	Red deer	Huemul
Tibia	5	4.92	4.61	Red deer	Ibex
Metatarsal	5.26	6.09	6.99	Ibex	Red deer
Humerus	3.67	3.65	3.34	Red deer	Ibex
Radius	4.6	5.22	4.97	Ibex	Huemul
Metacarpal	4.05	4.91	6.07	Ibex	Red deer

Table 4. Percentage difference between half the tibial and total metatarsal lengths, as an indication of affinity to a true rock climber¹⁵

Mountain goat	Ibex	Chamois	Bighorn sheep	Huemul		Red deer
				Male	Female	
+15.5%	+2.1%	-23.5%	-27%	-27.6%	-30.7%	-56%

body mass such as femur, tibia, humerus, and radius. Measurements on forelegs of three adult male huemul coincide closely with correlations among 79 species analysed by Christiansen⁴⁸ (Fig. 2b).

Factors affecting body proportions

Constraints regarding body proportions are set by genetics, however, intraspecific variation is due to adaption following ecogeographical rules, nutritional and physiological limitations.^{49,50} According to Flueck,⁵¹ skeletal muscles are extremely plastic in their capacity to remodel according to alterations in physical demands, such as in response to average needed muscle work as a function of terrain, disturbances, and food density. As most species fill the landscape along the full spectrum of habitat qualities, from source to sink areas, body shape will vary within a species.⁵² Scott⁵³ observed that cervid leg long bones are highly variable depending on habitat used, predator avoidance strategy used, gait and locomotor pattern employed. It is the distal limb segments (metapodials), however, which undergo more length modification than proximal segments.^{12,13,54-56}

A most relevant ecogeographical pattern known since 1877, Allen's rule, is found between climate and morphology as a thermoregulatory adaptation. This principle explains changes in ratios of body surface area to body mass in hot and cold climates and predicts short and broad limb proportions for animals in colder climates. For instance, bighorn sheep in cold climate have shorter legs than bighorns in warm deserts.⁵⁷ Besides ample empirical cases, adaptations were shown experimentally in pig

litter mates raised at 35, 20 and 5°C (Fig. 3a),⁵⁸ or rats raised at 28 and 5°C:⁵⁴ colder temperature resulted in increased hair density and stockiness, and shorter proportional leg length. Furthermore, oxygen pressure has also been recognised to influence bone growth. With higher altitude, increasing hypoxia results in reduced growth of distal limb bones already at the fetal stage and thus proportionally shorter legs.^{59,60}

Certain nutritional factors play well known roles in shaping body proportions. Iodine deficiency affects bone growth by decreasing muscle function and thereby affecting bone remodelling, and by direct effects on bone growth metabolism,^{50,61,62} including shortening of metapodials and joint disease,^{63,64} cretinism in its worst form including in sheep and deer.⁶⁵ Selenium deficiency has a synergistic effect and produces shorter bones and overt osteopathology like Kasin-Beck disease.^{66,67} Andean mountains are deficient in iodine and selenium and may relate to high incidences of such osteopathology in huemul.⁶⁸⁻⁷⁰ Similarly, a high prevalence of osteoarthritis has been noted in moose (*A. alces*), which was correlated with shorter metatarsals from nutritional constraints.⁷¹ Corroborating trace mineral deficiency in huemul is the puny antler development noted in many remaining populations,⁷⁰ when considering the clear relationship between such deficiencies and reduced antler growth in other wild Odocoelinae.⁷²

Discussion

'Mountain deer' remains as a misconception about huemul. It originated from early explorers stressing the resemblance to ibex, chamois, mountain sheep and mountain goats. However, early on huemul were described as rare and endangered, and many observations came from remote Andean refuge areas. In addition, the peculiar aggressive behaviour of huemul, the horseshoe posture, and the very long hair coat may give an impression of stockiness. These early casual statements about body shape were later reinforced by key paleontological work, linking huemul to the fossil 'mountain deer' *Navahoceros*.⁹ This was an unfortunate error, since the fossil was later shown to be a *nomen nudum* and corresponding to ancestral *O. lucasi*.¹⁰ Kurten also stated that huemul differed from *Navahoceros* by having two, and not three, tines on the antlers: yet huemul have up to five points.^{6,73} Strikingly, all of Kurten's comparisons to huemul were also done only as casual statements without supporting data, yet his *Navahoceros* continues to enter phylogenetic interpretations.^{32,33,74}

The present morphometric analysis shows for the first time that huemul appendicular morphology is completely different from that of ungulates considered true rock climbers. Thus, neither the proportional metapodial lengths, nor tibia : metatarsal ratio, nor measures of bone stoutness have any resemblance to rock climbers. Although bighorn sheep or chamois are considered at times as 'inhabitants of rocky areas',¹⁵ this applies equally well to red deer,^{75,76} and even to American bison (i.e. 'mountain buffalo'), which 'used precipices so steep that hunters could not follow them and even for dogs it was doubtful if they could have followed unharmed'.⁷⁷ In little time, exotic red deer have invaded all habitat types used now and in the past by huemul,⁷⁸ confirming that both species can equally occupy Andean habitat types. In fact, of all species considered in this

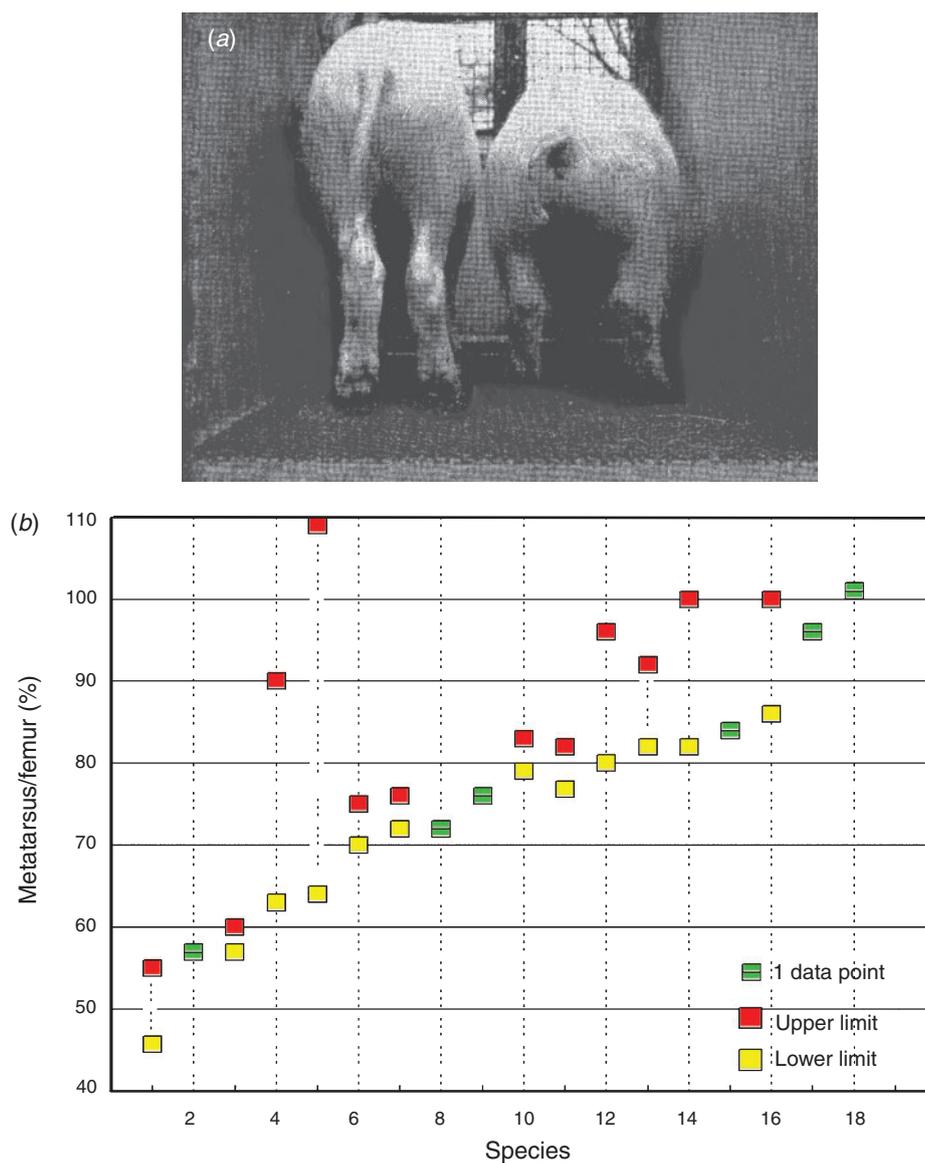


Fig. 3. (a) Body proportions of pig litter mates raised at 35 and 5°C, fed to the same weights.⁵⁸ (b) Intraspecific variation in proportional leg length among several ungulates. Sources are listed in Table 5. The species are: mountain goat (1), tahr (2), ibex (3), *Odocoileus virginianus* (4), *Rangifer tarandus* (5), Bighorn sheep (6), huemul (7), *Ovis dalli* (8), *Navahoceros* (9), *Ovis ammon* (10), chamois (11), red deer (12), *Dama dama* (13), *Odocoileus hemionus* (14), *O. lucasi* (15), *Capreolus capreolus* (16), *Antilocapra americana* (17), and *Antelope cervicapra* (18).

paper, those with proportional metatarsal length of 0.7–0.85 (Table 2) are all well known to successfully inhabit rocky areas. Instructively, bighorn sheep and all species with longer proportional metapodials including chamois, huemul, and mule deer (Table 2) are also found in flat open areas. Bighorns are well known to inhabit, or have inhabited, low, flat, deserts and grasslands,^{79,80} and sheep in general can do without rocks or cliffs. Similarly, chamois as an ‘alpine’ species is an artefact of past human-induced displacements⁸¹ since remains have been found down to near sea level,^{82–84} as well as in rolling, forest-covered hills, which they currently repopulate rapidly (now called ‘forest chamois’).^{85,86} Lastly, even Alpine ibex is a misnomer:

extermination was much easier and much earlier at low and medium altitude, resulting in a prejudice in earlier years by reintroducing them to high elevations because that was where the last remaining groups were known from.⁸⁷ Recognised only recently, these reintroductions have actually created an artificial model of an animal of high altitude, living there in all seasons above the tree line.^{87–89} In contrast, paleozoological data now indicate that ibex occupied many additional topographic positions than they do today.⁸⁹ Although ibex may remain in areas with some cliffs, many fossils have been found down to sea level, sometimes as dominant prey species in archeological sites, and altitude clearly was not a factor in ibex ecology.⁸⁸ At

low elevation sites, ibex were associated with all the other main ungulate species also exploited by humans. Recent reintroductions to very low elevation areas were thus successful, and there are cases of natural recolonisation, from high elevation populations to low elevation areas.⁹⁰ Therefore, historic comparisons of huemul to ibex and chamois were done under the misbelief that both latter species are specialists for high altitudes and extreme rocky areas: the only link between these three species, however, appears to be historic anthropic displacement from favourable habitats. Observations by Scott⁵³ coincide in that no cervids are occupying the type of cliff habitat as do Caprini and at times *Rupicapra*. Moreover, it is no surprise that the only sister species to huemul, *Hippocamelus antisensis*, is considered osteologically indistinguishable and even considered a mere subspecies,^{16,25,91} yet besides using some forest types,⁹² its current habitat is mainly treeless grasslands with high affinity to Patagonian grasslands, coexisting with several camelid species.

The literature is replete with empirical and experimental data showing intraspecific variation in proportional bone growth, and several causative factors are well known. As the metapodials undergo major length modifications compared with the proximal leg bone segments, we would expect to find large intraspecific variation in proportional leg length, which in turn has been substantiated (Table 5). For instance, relative leg length is considerably greater in forest reindeer than in mountain

reindeer,⁹³ and shoulder height is reported to differ by 15 cm between forest- and alpine-wintering groups, without differences in other body measurements or proportions.^{94,95} Importantly, changes in leg proportions in *Rangifer* have been observed within one single population after only 30–35 years of nutritional stress^(96, also see⁴⁹). *Odocoileus virginianus* from two different environments had proportionally different hind foot lengths such that populations could be distinguished with $r = 0.92$ at $P < 0.0001$,⁹⁷ similar to studies on mule deer⁹⁸ and *Capreolus capreolus*.⁹⁹ The currently small sample size of huemul, and mainly from one reduced population, shows only small variations, however, other better studied ruminants give an indication of possible variability of proportional leg length (Fig. 3b). Importantly, some populations of *Rangifer* and even *O. virginianus* have much shorter legs than our huemul sample, with metatarsals proportionally 14% shorter than huemul (Table 5).

Skeletal proportions are affected by numerous factors. Some morphological differences of proportional limb bone lengths result from adaption to different environmental regimes rather than reflecting phylogeny.^{10,13,56} Van der Meuleun and Carter¹⁰⁰ concluded that long bone scaling is not a result of intrinsic genetic factors but is the result of highly conserved extrinsic biophysical processes whereby bone tissue strains modulate skeletal morphogenesis. This is due to epigenetic components of skeletal design that is continuously updated in response to the

Table 5. Variation of proportional metatarsal or hind foot length (HL), among various cervid species, and some comparative ratios from other ungulates

Species	Sex	Femur/metatarsus	% difference	Reference
<i>Cervids</i>				
<i>Rangifer tarandus</i>	Male	100:89–100:108	21	96
<i>R. tarandus</i>	Female	100:93–100:109	17	96
<i>R. tarandus</i>	Unknown	100:64–100:99	55	12
<i>R. tarandus</i>	Mixed	100:64–100:109	70	12,96
<i>Odocoileus virginianus</i>	Unknown	100:63–100:90	43	12
<i>O. hemionus</i> ^A	Unknown	100:86–100:100	16	9,11,46
<i>O. hemionus</i>	Unknown	100:82	22	11,12
<i>O. lucasi</i>	Unknown	100:84	–	10
<i>Dama dama</i>	Unknown	100:82–100:92	12	12,46
<i>Cervus elaphus</i>	Unknown	100:80–100:96	20	12,46
<i>Capreolus capreolus</i>	Unknown	100:86–100:100	16	12,46
<i>Hippocamelus bisulcus</i>	Male	100:72–100:75	4	$n = 8$, this study
<i>H. bisulcus</i>	Female	100:73–100:76	4	$n = 3$, this study
<i>Other ungulates</i>				
<i>Oreamnos americanus</i>	Unknown	100:46–100:55	20	12,13,46
<i>Capra ibex</i>	Mixed	100:57–100:60	5	14
<i>Ovis ammon</i>	Unknown	100:79–100:83	5	13,46,106
<i>Rupicapra rupicapra</i>	Unknown	100:77–100:82	7	12,46
<i>O. canadensis</i>	Unknown	100:70–100:75	7	12,13
<i>O. dalli</i>	Unknown	100:72	–	12
<i>Antilocapra americana</i>	Unknown	100:96	–	46
<i>Antilope cervicapra</i>	Unknown	100:101	–	13
Species	Sex	Body length/HL	% difference	Reference
<i>Rangifer tarandus</i>	Male	100:20–100:62	310	96
	Female	100:26–100:34	31	96

^AData as HL in reference¹¹ was adjusted by halving to approximate metatarsal length.

mechanical forces exerted on the bones.^{51,101} Muscle force is the single most important factor in determining the amount of force the bones must resist as these forces surpass several fold the stress imposed from static weight.^{48,101–103} Major forces result from locomotion, and the change in limb posture accounts for most of the reduction in bone stress among small to rather large mammals.^{48,101} Only a short duration of mechanical loading is necessary to initiate an adaptive bone response, and extending the loading duration has a diminishing effect on further bone adaptation.¹⁰¹ Furthermore, long bones lose considerable bone mass when they are not mechanically loaded. Lastly, strong effects on proportional leg length result from nutritional constraints, which in central Andean habitats of huemul are notably deficiencies of phosphorous, iodine and selenium. These and other analyses clearly show the extraordinary degree to which the skeleton can adapt to differences in mechanical loading, as induced from different habitat types and locomotor needs, and to nutritional constraints.^{51,100,104} The nutritional ecology of remnant huemul populations⁷⁰ and the climatic and topographic features of localities where huemul currently remain indicate that leg proportions of huemul from these sites would be expected to be at the low end of the potential range of variations for the species in response to local adaption. In contrast, populations which in the past existed in more open rolling landscapes would be expected to have had individuals with notably longer proportional leg lengths. Nonetheless, extant huemul, particularly if not in an alert stance and in summer coat, often can hardly be qualified as being short-legged (Fig. 4).

Conclusion

Huemul had a much wider distribution in pre-Spanish times than in more recent times of explorations and settlement

of Patagonia. Accordingly, a few historic accounts still documented presence in the eastern treeless lowlands indicating that huemul was well suited to exploit those areas (Fig. 5).⁷ We caution against the rigid application of modern huemul habitat use in interpreting past habitat use and simply ignoring the few historic extra-Andean accounts as abnormal outliers. Clear evidence,⁷ even if rare, of past presence has to be accepted and should not be dismissed as shown for chamois and ibex. Indeed, huemul ecology must be interpreted in terms of first principles rather than applying direct analogues from the present. This allows us to begin to use the past to understand the present instead of repeating the fallacy of imposing the present on the past.

Current efforts to recover remaining huemul are distinctly based on the assumption that huemul foremost belong in rugged mountains, because of their supposed special adaptations and resemblance to stereotype ungulates erroneously believed to only occur in rugged mountains elsewhere. However, such a supposed specialisation is not reflected by the evolutionary history of huemul, and current ecological realities were recently created from human impacts. These claims also underscore the continuous ignoring of historic accounts of huemul in steppes far from the Andean forests, condemned to be at most a footnote. Anecdotal and inconclusive physical data are often used to assess the current ranges of rare or elusive species. However, the use of such data for species conservation can lead to large errors of omission and commission, which can influence the efficacy of subsequent conservation efforts.¹⁰⁵ The present empirical comparisons show huemul leg morphology to fall well within that of other cervids and can be expected to vary substantially if they were to live in habitats formerly used. It supports many other lines of evidence that huemul existed in treeless habitat and colonised Andean forests and higher altitudes



Fig. 4. Body shapes of several extant huemul that are not in an alert stance and with summer coat.



Fig. 5. Huemul habitat far from forests and in flat or rolling landscapes. (a) Landscape by Port Desire at Atlantic coast ($47^{\circ}44'S$, $65^{\circ}54'W$), where several reports mentioned huemul.⁷ (b) Huemul in steppe, approached by gaucho, from Onelli 1904. (c) Huemul photographed in the 1920s by A. Grosse. (d, e) Princeton expeditions, late 1800s, hunting huemul as far as 200 km from forests. (f) Extant huemul: periglacial Pacific coast, old moraines, flat wide valley bottoms.

secondarily, and habitat breadth of huemul is thus more like that found in other closely related *Odocoileus*. This promises tremendous new opportunities for recovery efforts by considering reintroductions to other portions of the landscape used formerly by huemul, which tend to be more productive sites than those currently occupied by many huemul groups.

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