

Misinterpretation of historical data for determining past huemul (*Hippocamelus bisulcus*) distribution and migratory patterns may threaten their conservation: A critique of Flueck *et al.* (2022)

Malinterpretación de datos históricos para determinar la distribución pasada y patrones migratorios del huemul (*Hippocamelus bisulcus*) puede amenazar su conservación: Una crítica a Flueck *et al.* (2022)

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ABSTRACT

Historical accounts documenting the presence of a species, despite several known spatial and temporal weaknesses, are useful to understand distribution patterns, to establish conservation baselines, and to develop effective conservation strategies. An article by Flueck *et al.* (2022), based on historical records, proposes to reinterpret the past distribution, population dynamics, and migratory behaviour of the huemul (*Hippocamelus bisulcus*), an endangered deer endemic of the southern Andes. Our analysis of the same historical data revealed a range of questionable interpretations of the sources. Because of this, we argue that the conservation strategies for huemul proposed by Flueck *et al.* (2022) may be counterproductive and even potentially harmful.

Keywords: Andean mountains, historical records, Neotropical deer, migratory behavior, Patagonian steppe.

RESUMEN

Los relatos históricos escritos que documentan la presencia de especies son útiles para comprender los patrones de distribución y establecer medidas de conservación, aunque pueden presentar debilidades espaciales y temporales. Un artículo de Flueck *et al.* (2022), basado en esta fuente de información, propone reinterpretar la distribución pasada, la dinámica poblacional y el comportamiento migratorio del huemul (*Hippocamelus bisulcus*), un ciervo endémico y amenazado de los Andes del sur. Nuestro análisis de esos mismos datos históricos revela interpretaciones cuestionables de dichas fuentes. Debido a esto, argumentamos que las estrategias de conservación del huemul propuestas por Flueck *et al.* (2022) pueden ser contraproducentes e incluso potencialmente perjudiciales.

Palabras clave: ciervo neotropical, conducta migratoria, Cordillera de los Andes, estepa patagónica, registros históricos.

The use of historical accounts is widely applied to assist reconstructing past wildlife features, despite several interpretational challenges related to the quality of that information (Boshoff & Kerley 2013; Zielinski *et al.* 2005; Forman & Russell 1983). Records of early chroniclers present both advantages and drawbacks, not providing a full spatial and/or temporal picture of the events reported (Miller *et al.* 2007). Main weaknesses include inaccuracies due to personal perceptions (Clavero *et al.* 2022; Tingley & Beissinger 2009), species misidentifications, assumed presences and absences, and lack of geographical precision (Peterson *et al.* 2004), leading to errors in historical distribution maps (Clavero *et al.* 2022; Tingley & Beissinger 2009).

Correct interpretation of historical ecological records is crucial, both for developing conservation baselines and for implementing effective conservation strategies for threatened species (Clavero & Delibes 2013). Huemul (*Hippocamelus bisulcus*, Molina 1782) is an endangered South American deer (Black-Décima *et al.* 2016) associated with the southern Andes mountains of Chile and Argentina. Huemul have declined dramatically in both numbers (Riquelme *et al.* 2020; Corti *et al.* 2010) and distribution (Riquelme *et al.* 2018) since the arrival of Europeans (Redford & Eisenberg 1992; Povilitis 1983). Today, huemul only occur from central Chile (Nevados de Chillán; 36° S) to the Magellan Strait (53° S) in highly fragmented, small groups and populations (Riquelme *et al.* 2018; Marín *et al.* 2013; Corti *et al.* 2011), numbering < 2,000 individuals in total (Black-Décima *et al.* 2016; Vila *et al.* 2006).

We analysed the main historical sources as well as interpretations and ecological conclusions of a recent study by Flueck *et al.* (2022), who propose historical changes in our understanding of the past huemul distribution and of their population dynamics, highlighting the presumed loss of migratory behaviour as a serious conservation concern. Based on our re-analysis of the same sources, we address and critique the issues raised by Flueck *et al.* (2022), including huemul migration across landscape patterns and past occurrences in steppe grasslands, range limits, presence/absence observations, abundance, coexistence with other ungulates in different habitats, past huemul abundances and dynamics, and potential causes for extinction in assumedly optimal habitats.

HUEMUL ALTITUDINAL MIGRATIONS AND OCCURRENCES IN STEPPE GRASSLANDS

Flueck *et al.* (2022) argued that early observers “described huemul to descend to valleys and/or out into the grasslands during winter where they formed large groups of over 100 huemul”, despite the existence of multiple references (i.e.,

Housse 1953; Wolffsohn 1910; Moreno 1898; Sclater 1875; Claraz 1864; Gay 1847) not making any reference to altitudinal movements. Some authors (Krieg 1940; Giai 1936; Gigoux 1929; Neveu-Lemaire 1911; Prichard 1902; Lydekker 1898) indeed referred to seasonal migrations but without suggesting that huemul migrated off the Andean foothills. Even if some explorers of the 19th and 20th centuries observed huemul relatively far from the Andes, they also considered the Andean forests and clearings to be the primary habitat for huemul (i.e., Osgood 1943; Krieg 1940; Brown in Allen 1905; Prichard 1902, 1910; Onelli 1905; Hatcher 1903; Steffen 1900; Moreno 1899; Lydekker 1898; Burmeister 1873).

About the huemul's past presence in the steppe grasslands, Flueck *et al.* (2022) incorrectly referred to several authors: Von Colditz (1925; p. 352), Claraz (1864; p. 247), Sclater (1875; p. 44), and Wolffsohn (1910; p. 233) indicated gallery forests and cordillera valleys as the primary huemul habitat, and both Claraz (1864) and Burmeister (1873) emphasised that huemul rarely descend to flat country. During Steffen's (1900) explorations in Patagonia, deer hunting provided them fresh meat, but they did not travel across open plains as Flueck *et al.* (2022) implied, because they explored rivers along the Chilean Andes. Other citations pertaining to the presence of huemul near the Atlantic coast of South America contain errors. At Puerto San Julian and Deseado, Pigafetta and Van Noort observed guanacos and not huemul (Eastman 1915; p. 353); Pennant (1793) confused huemul with guanaco, a mistake mentioned in “The Colonial Journal” (1817, no. 5, March, p. 9); and Roulin (1835) does not mention deer at Puerto San Julián. Although Díaz (1993) suggested that historical records from 1592 to 1960 point out to huemul presence in the steppe, the available evidence is too scarce to confirm that this deer naturally occurred as far east as the Atlantic coast. Further, archaeological sites with huemul remains are present between 38°53' S and 53°37' S in Patagonia, with the exception of Tierra del Fuego: Huemul records on the steppe represented only 15% and the remaining 85% were associated with Andean forest (n = 24 records), forest/steppe ecotone (n = 42), and other forest habitats of Chilean coastal Patagonia (n = 30) (Fernández *et al.* 2016), thus coinciding with the currently occupied huemul habitat (Riquelme *et al.* 2018; Vila *et al.* 2009).

RANGE LIMITS OF HUEMUL

The known northernmost range of huemul was the Cachapoal River (34° S), according to Cabrera & Yepes (1960) but Flueck *et al.* (2022) propose that it reached some 680 km further north. Nevertheless, archaeological sites with huemul remains in Chile and Argentina are all located south of 38°53' S (Fernández *et al.* 2016). Indeed, a recent taxonomic

and taphonomic analysis of the Laguna de Tagua-Tagua site (34°30' S) did not reveal the presence of *Hippocamelus* spp. (Labarca *et al.* 2020) as previously reported by Casamiquela (1976). The same applies to the southernmost range proposed by Flueck *et al.* (2022). Specifically, the presence of huemul on Tierra del Fuego Island is largely speculative. Darwin (1860) reported the presence of a “deer” in 1834, and Lista (1881) included “*Cervus chilensis*” in their records of the Island’s species. Up to the present, there is general agreement on the absence of *Hippocamelus* spp. on Tierra del Fuego Island (Pallo 2017; Fernández *et al.* 2016; Martín *et al.* 2009; Borrero 2007; Muñoz 2005; Morello *et al.* 1999), who regarded as misidentified the remains reported by Laming-Empeaire *et al.* (1972).

COEXISTENCE WITH OTHER SPECIES ON OPEN STEPPE GRASSLANDS

The evidence on the coexistence of guanaco (*Lama guanicoe* Müller 1776) and huemul on open grasslands proposed by Flueck *et al.* (2022) is weak: Cox (1863) is wrongly cited, and during Osgood’s (1923) expedition, they did not report huemul coexisting with guanacos on the steppe. Indeed, Osgood (1943; p. 226) stated that huemul appear to be a mountain animal that preferentially lives near timberlines, while De Agostini (2010) considered guanaco a steppe species and huemul a mountain dweller, thus not providing support for their coexistence. The rock paintings at Cueva de las Manos (Santa Cruz, Argentina) that include guanaco and deer depictions were interpreted by Flueck *et al.* (2022) as evidence for the coexistence of both species. Nevertheless, the integration of guanaco and deer in the same pictorial scenes may only be attempts to incorporate prey animals exploited by the early peoples (Aschero 2012).

HUEMUL ABUNDANCES AND CAUSES OF POPULATION DECLINES

The examination of the historical records cited by Flueck *et al.* (2022) reveals that the evidence provided is too scarce to adequately estimate past huemul abundance and group sizes, due to misrepresentations of prior estimates. Prichard (1902; p. 249) was told by Mr. Cattle, a pioneer living near Lake Argentino, that he had seen a large herd of over a hundred huemul. However, Onelli, then a member of the Boundary Commission (in Gigoux 1929; p. 581), said that he had not found huemul in such great abundance as claimed in the earlier account.

Assessing the scale of a species decline is challenging when historical information is incomplete or inaccurate. Flueck *et al.* (2022) argued that one putative cause of huemul extinction on the steppe was overhunting due to fur trade, stating that huemul was listed as early as 1883 as an important species utilised by humans (Simmonds 1883; p. 61), but this

attribution is erroneous because the latter author did not refer to this issue. Philippi (1873; p. 721) referred to huemul fur trade, but not as an intense activity, and Behm (1880) did not make comments on huemul fur trade in Punta Arenas. Although Claraz (in Hux 1975) mentioned that indigenous people often went to Viedma (Río Negro, Argentina) to sell huemul furs, huemul seemed not to be an important trade species, with explorers referring mostly to the guanaco fur trade (i.e., Viedma 1972; Villarino 1972; Guinnard 1947; Hatcher 1903; Musters 1871; Cox 1863; Falkner 1835).

Another putative cause of huemul extinction in steppe suggested by Flueck *et al.* (2022) was hunting pressure from indigenous people. Still, it must be regarded that humans have been hunting guanaco and rhea (*Rhea* spp.) in that environment over the last 3500 years without causing their extinction (Carballido *et al.* 2021). Indeed, guanaco were the staple terrestrial prey for hunter-gatherer societies throughout the Holocene in terms of both their caloric contribution to human diet and their representation in local archaeofaunal records (De Nigris & Mengoni Goñalons 2004; Mengoni Goñalons 1999; Miotti & Salemme 1999). To the contrary, the zooarchaeological record shows that huemul were hunted only exceptionally during the Holocene, with an increase of remains after 9500 BP, and a further increase after 2200 BP (Fernández *et al.* 2016). Even then, the comparatively low frequency of bone remains suggests that hunting of huemul may have been opportunistic and with little influence on the species’ regional distribution. Still, we recognise that progressive human presence in some forested areas towards the end of the Holocene could have affected huemul populations at a local scale.

HUEMUL BEHAVIOUR, HABITAT, AND CLIMATE CONDITIONS IN PATAGONIA

Flueck *et al.* (2022) seem to assume that deer species behave similarly despite differences in body size, preferred habitat type, and climate conditions, although all variables are known to influence feeding behaviour and social organisation of ungulates (Jarman & Jarman 1979; Jarman 1974). Flueck *et al.* (2022) expect that huemul undertake marked migrations similar to those that occur in some deer species in the northern hemisphere and argue that huemul lost their migratory behaviour due to human impacts (i.e., habitat loss, hunting, livestock competition, dog attacks). However, philopatry has been reported in several huemul populations throughout their distribution (Riquelme *et al.* 2020; Sandvig *et al.* 2016; Briceño *et al.* 2013; Corti *et al.* 2010; 2011; Vila *et al.* 2009; Gill *et al.* 2008; Povilitis 1983; 1998), together with lack of sexual segregation (Corti *et al.* 2010; 2011; Frid 1999; Povilitis 1983). In addition, Flueck *et al.* (2022) neglect to mention evolutionary processes causing migration in

huemul. Although migration can be plastic, recent research on the evolution of this behaviour in herbivorous ungulates indicates that some specific traits must be present to trigger it: large body size and a diet mostly based on graminoids, in a context of large environmental fluctuations (Abraham *et al.* 2022). These traits are not found among huemul, which is a medium-sized deer (69 kg body-mass; Corti & Arnemo 2021), with a diet mostly composed of shrubs and forbs, which it browses (i.e., Vila *et al.* 2009; Galende *et al.* 2005; Frid 1994); with no anatomical adaptations to feed solely on graminoids (e.g., brachyodont molars; Pérez-Barbería & Gordon 2001); and requiring high-quality forage (Demment & Van Soest 1985), which is scarce in the steppe (Radic *et al.* 2021). Finally, climate conditions in southern South America are comparatively stable (Neukom *et al.* 2011). Here, temperature oscillations are much smaller between summer and winter than in North America at the same latitudes (Radic *et al.* 2021; Kang *et al.* 2015). In southern South America, although there is snow cover in some areas in winter, the amount is much lower than in the northern hemisphere, often lasting just a few months (Kang *et al.* 2015).

Flueck *et al.* (2022) claim that climate conditions in southern South America resemble those in the northern hemisphere by using references summarising guanaco research (e.g., Puig *et al.* 2011), which have a vastly different life history than huemul (González *et al.* 2006). Current research on huemul population dynamics indicates that mortality occurs mostly in summer, so winter is not critical (Corti *et al.* 2010), and thus the increase in temperature due to climate change may negatively affect huemul due to lack of snow and higher temperature in winter (Riquelme *et al.* 2020). It should be noted that huemul survived the Last Glacial Maximum in refugia at both sides of the Andes, including mountains surrounding the Nevados de Chillán volcano in the central Chilean Andes (Marín *et al.* 2013). Finally, current descriptions of huemul niche (Riquelme *et al.* 2018; Quevedo *et al.* 2017) match it to lenga beech (*Nothofagus pumilio*) distribution, a tree species historically associated to the Andes mountains (Ignazi *et al.* 2019), supporting huemul preference for mountainous forested habitats and not for steppe.

CONCLUSIONS

Historical accounts can provide useful insights into species distributions, habitat use, and animal behaviour. Their value can be enhanced when combined with an understanding of known ecological requirements of a species. But problems arise when data are not used and interpreted with caution, and without considering all available evidence. The evaluation of the historical record made by Flueck *et al.* (2022) highlighted several misinterpretations and what appears

to be preconceived assumptions. By analysing the same historical sources combined with our current understanding of huemul ecology, we argue that Flueck *et al.*'s conclusions are not supported by the data and that they would lead to the development of counterproductive and perhaps even harmful conservation strategies. We do agree with Flueck *et al.* that without a thorough review of historical documents, determining the past distribution of a species may be difficult. However, for future conservation strategies to be effective we need to understand both past and present causes of huemul decline (*sensu* Caughley 1994). Currently, research suggests that huemul are at risk from the following causes of decline (also see Black-Décima *et al.* 2016 for a summary): Unsustainable predation in the form of apparent competition (Wittmer *et al.* 2013; Corti *et al.* 2010), habitat loss and fragmentation (Riquelme *et al.* 2018; Corti *et al.* 2011), poaching (Briceño *et al.* 2013; Corti *et al.* 2010), diseases from and competition with domestic livestock (Corti *et al.* 2020, 2013; Frid 2001), dog predation and introduction of exotic species (Corti *et al.* 2010). Focussing on conservation of huemul in open grasslands and the reestablishment of migrations as suggested by Flueck *et al.* (2022) is, in our opinion, not only misguided but will not lead to the recovery of the huemul.

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