

Huemul heresies: beliefs in search of supporting data. 2. Biological and ecological considerations

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Abstract. Scarce information from remnant huemul (*Hippocamelus bisulcus*) populations in marginal habitats can lead to erroneous interpretations of the species' natural history, such as assumptions of being a highly inflexible species. We evaluated discrepancies between historical accounts and recent interpretations regarding biological and ecological traits to better understand factors preventing recovery of highly endangered huemul. Early information supports the theory that huemul are currently living under suboptimal conditions. We find variability to be the norm for huemul, as with other cervids, in regard to antler characteristics, group size and density, sexual segregation, and social and feeding behaviours. No evidence supports competition and disease from livestock or red deer as having caused declines or preventing recovery. Instead, livestock management, particularly presence of people and dogs, creates incompatibilities. Where red deer are sympatric with huemul, red deer are outnumbered by livestock by 2100%, and being regularly inspected at slaughter, livestock provide a good proxy for diseases afflicting red deer. Inadequate antipredator responses due to evolutionary absence of cursorial predators are unsupported as several *Canis* species coexisted with huemul, overlapping with dogs that arrived with Paleoindians. Three populations have increased despite high predator density. Age at maturity for huemul is 1 year, with evidence that fawns may also breed. Reported twinning needs confirmation, but occurs in congeneric taruca (*H. antisensis*) and other Odocoelinae, and huemul frequently raise fawns successfully every year; life cycle calculations should apply these parameters. Like taruca, dominance group breeding systems have been described repeatedly. Although huemul bucks were recently claimed unique by displaying territoriality year-round, data do not support such behaviour. Two sole dispersal records (8 and 15.5 km) are unlikely to represent maximum dispersal capacity and do not support barriers assumed from few kilometres of unsuitable habitat. Huemul using 500 ha could predictably disperse up to 90 km, well within the ranges of other cervids. Mistakenly assuming barriers and underestimating reproductive capacity may distract from discovering the factors affecting recolonisations. Sustained recovery may depend on re-establishing source populations on more productive habitats, guided by zooarcheological and historical data.

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Introduction

In the accompanying paper (Flueck and Smith-Flueck 2012b), we analysed information regarding historical conditions showing how it has influenced the current interpretation of the biology and ecology of huemul (*Hippocamelus bisulcus*). The two papers together aim at improving our understanding of huemul and its conservation. Here we focus on interpretations of antlers, group size and density, predation, diet, competition, diseases and reproduction to reveal currently accepted beliefs that do not stand up under closer scrutiny. The detailed analysis and completed list of cited sources are in Flueck and Smith-Flueck (2011a, 2011b, 2011c).

Methods

Securing reliable data is difficult on species highly reduced in numbers and remaining mainly in remote refuge areas. We review

available literature on huemul and other related deer species and use a comparative approach to interpret questionable information that originated in the historic literature and continues to be used to describe huemul.

Results

Antlers

Antler phenotypes relate principally to age, nutrition, animal condition and social environment. Age results in predictable antler growth patterns, but as luxury tissue, antler growth is secondary to optimising body mass and other needs, and nutrition thus has a large effect on antler size and number of tines (Bubenik and Bubenik 1990). Being regrown annually, unique among mammals, antlers provide a phenomenal tool for interpreting myriad biological and ecological relationships.

Their correct interpretation therefore is not a trivial issue. Yet 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. Kurtén (1975) even claimed that huemul differed from *Navahoceros* by having two, and not three antler tines. The claim has repeatedly been made (Redford and Eisenberg 1992; Webb 2000; Lord 2007; Guérin and Faure 2009), moreover, that forks are typical and 20–25 cm long (Povilitis 1985; Nowak and Walker 1999; Vila *et al.* 2010). In contrast, three tines are still common in some localities, representing 43% of samples we measured ($n = 47$, W. Flueck and J. M. Smith-Flueck, unpubl. data), while antlers with four tines have been found repeatedly with lengths >34 cm (Fig. 1). Although antlers with five tines were also documented previously (Philippi 1895; Osgood 1923; Magne de la Croix 1937), antlers beyond forks were, and still are, labelled ‘abnormal’ (Rusconi 1936; Vila *et al.* 2010). Instead, previously larger antlers with multiple tines likely represented fully developed bucks that had reached older ages, having used traditional areas that provided access to good nutrition. In comparison, some extant remnant populations have very young age structures, lacking individuals older than 4 years old (Smith-Flueck and Flueck 2001), and are restricted to small fractions of the previously used ranges (Flueck and Smith-Flueck 2011*d*).

Group size and density

Group size and density of huemul are often stated categorically, yet these data only represent particular remnant subpopulations occurring in subsets of former habitats. Maximal group sizes are commonly stated as solitary, one to five, or up to eight during winter (Redford and Eisenberg 1992; De Nigris 2004; Fernández 2008; Vila *et al.* 2010). However, groups of 10 in summer (Grosse 1949) and 11 in autumn (Díaz and Smith-Flueck 2000) occurred even recently, and huemul formed wintering groups of 100 or more during Prichard’s (1902*a*) study. Larger groups were reported from more open and particularly treeless landscapes, in concordance with behaviour of other cervids (Putman and Flueck 2011). Considering past and extant observations, huemul group compositions and sizes are dynamic and are likely determined by factors like density, sex and age structure, habitat type, season, and reproductive patterns.

Similarly, densities are given as 0.002–1.2 huemul/km² (Redford and Eisenberg 1992; Belardi and Otero 1998; Fernández 2008); however, even some extant populations have densities of nine huemul/km² (Wensing 2005). Although lacking estimates for historic times, we can deduce that densities commonly must have been substantial. For instance, Juan Ladrillero reported huemul from Chile in 1558: ‘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’ – and

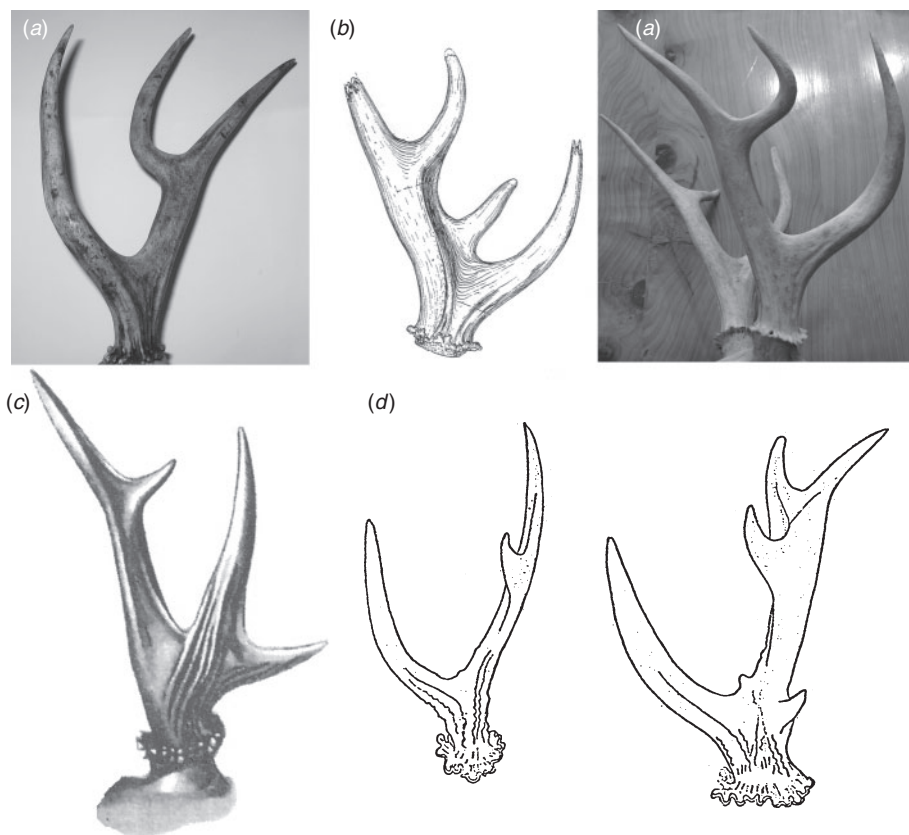


Fig. 1. Huemul antlers still commonly have three tines, and had up to five in the past. (a) Extant specimens from Patagonia, (b) Rusconi (1936), (c) Philippi (1892), and (d) Colomés (1978).

they were using weaponry that was less accurate than the bow and arrow! Early naturalists regularly mentioned huemul occurring in great numbers together with guanaco in the ‘Patagonian pampas’. Patagonians knew the huemul well, hunting it frequently and preferentially, with skins traded at the Atlantic coast. Prichard stated that he ‘could have very easily shot 10 huemul in a day’, yet natives assured him that these deer were at one time even more numerous (Prichard 1902a; Hatcher 1903). Early expeditions still found numerous huemul such that hunting was easy and provided large crews with fresh meat daily for weeks while travelling. Grosse (1949) saw groups every day and so many tracks that he concluded that there were huge herds (‘riesige Herden’). Later, however, during colonisation, huemul were killed by the thousands per year for human consumption, and to feed dogs, chicken and pigs, while skins were used to construct shelters for people and domestic animals (Gigoux 1929; Giai 1936; Krieg 1940; Madsen 1948; Grosse 1949; Iglesias 1965). When first settling the large Rio Manso valley, a colonist reported finding old shed antlers while first plowing riparian areas. Considered competition to livestock, huemul were killed and consumed whenever spotted; one neighbour shot nine deer in one day (A. Andrade, pers. comm.).

Instructively, high capacity habitat in eastern foothills and grasslands was quickly filled with a large biomass of livestock. In 1900, Argentina already had 120 million sheep and 28 million fenced cattle. Then between 1908 and 1952, Argentine Patagonia went from 10 to 25 million sheep and from 0.83 to 3.92 million cattle. There were 0.5 million horses and mules by 1908 (Willis 1914; Fernández and Busso 1997; von Thüngen and Lanari 2010). Today, ecotonal ranges formerly used by huemul produce 3000–5000 kg/km² of exotic ruminant biomass (Flueck 2010), equivalent to 40–60 huemul/km² if they would forage similarly, as would be expected from mixed feeders.

Predation

Predation events in severely reduced subpopulations, as with some extant huemul, are important due to dynamics of small populations (Caughley 1994). Nonetheless, equally important is to understand underlying causes of supposedly excess predation. ‘Overabundant predators’ and ‘inadequate antipredator behaviour’ were implied as major impediments for huemul, 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. The main predator is puma (*Puma concolor*); foxes (*Lycalopex culpaeus*) may kill fawns, and dogs have killed huemul. However, even puma scavenge appreciably, treating carrion as they would their own kills; 8–12 puma scavenged 19 of 44 placed deer carcasses during a mean of 5 days, even when rotting and maggot-infested, spending up to 50% of feeding time on carrion (Bauer *et al.* 2005; Knopff *et al.* 2010) and a healthy female puma fed exclusively on four carcasses during >22 days (Nowak *et al.* 2000). Interestingly enough, a puma was already documented to have scavenged deer – a huemul that was killed earlier by Prichard (1910).

Frequently, dog predation is implied as causing declines or preventing recovery, yet only occasional kills have been reported.

The impact on recruitment has not been quantified conclusively in any population, and differentiating kills from scavenging remains enigmatic. The assumed highly effective dog predation is asserted to stem from huemul having evolved in, and still inhabiting, areas lacking large cursorial predators (Saucedo and Gill 2004; Corti *et al.* 2010, 2011; Vila *et al.* 2010). Yet this contradicts known facts. Firstly, cervids radiating to South America were accompanied by Canidae, including at least three species of *Canis*. Dire wolf co-existed with huemul into the Holocene, i.e. existing until after man arrived with domestic dogs. These dogs, providing hunting assistance, transportation as well as emergency food, arrived in South America together with Paleoindians, with records dating back to the late Pleistocene. Pre-Columbians 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). Secondly, a large fox considered analogous to *Canis latrans* in appearance and habits (Hershkovitz 1972) is sympatric with huemul. This cursorial fox also pursues large prey (Novaro *et al.* 2009). Although occasionally killed, huemul have escaped dogs by taking advantage of obstacles, outrunning dogs uphill, or mothers leading dogs away from bedded young (Jiménez *et al.* 2008). These behaviours are similar to observations of northern deer encountering dogs. Considering continuous exposure to cursorial predators for millennia, huemul likely have retained appropriate antipredator behaviour. Furthermore, prey–predator interactions do not appear to specialise due to prevailing multi-prey and multi-predator systems, and reintroductions of large predators have resulted in rapid readjustments of prey behaviours (Breitenmoser and Haller 1993; Molinari-Jobin *et al.* 2002; Flueck 2004). Other Odocoelines besides huemul employ the same escape strategies: they hide and freeze, bolt or run off at close encounter, or take to water. Huemul are known to snort, stomp the ground, run, trot or race away uphill or downhill, and also bound like mule deer (*Odocoileus hemionus*). Although a fox was observed killing a fawn (Wensing 2005), successful cooperative defence by adult females has also been documented, and remains of huemul were absent in a fecal study of foxes sympatric with huemul (Smith-Flueck *et al.* 2011).

Severely reduced huemul populations, however, might not be able to sustain additional losses from native predators, and temporary predator control might allow recovery as documented for bighorn sheep (Williams 2010). Regardless, two huemul populations in southern Chile recovered despite high-density puma (6/100 km²) and fox populations (Jiménez *et al.* 2008; Flueck 2010). Moreover, the Fjord Tempango valley, which in 1940 was still covered with glacial ice, now contains one of the largest populations at the high density of 9 huemul/km², together with foxes and puma. This is possible in adequate habitat and with appropriate antipredator responses as evidenced by huemul evading attacks by a puma with kittens (Prichard 1902a), or chasing puma into trees (Murillo and Ramb 1975), similar to female red deer, which, notably, is a species that did not evolve with puma (Flueck 2004).

Ungulates may form larger mixed-species groups due to foraging advantages and predator avoidance. Accordingly, in open areas huemul mix with guanaco (Prichard 1902b), and historically huemul commonly ended up in corrals with

livestock having been herded down to winter ranges (Flueck and Smith-Flueck 2011d). Recently, a female huemul found among ranch cattle in southern Chile was lassoed and kept in a stable for a month (Vidal *et al.* 2011). Moreover, open habitats with shallow slopes offer the benefit of diminished risks as it provides little hiding cover for puma (Atwood *et al.* 2007). Thus, open lowlands east of the Andes likely presented source areas of huemul where puma as the only main predators would have had limited impact on a prey that formed large group sizes, including mixed-species groups. Accordingly, the large biomass of herbivores was able to be sustained in such habitat.

Diet

Circular reasoning is used to explain huemul diet. It was asserted that huemul, having brachyodont molars – supposedly indicative of browsers – require forests and browse species (Vila *et al.* 2010); the assumption is then made that huemul are therefore not apt to utilise Patagonian grasslands. However, nearly all cervids have brachyodont teeth, yet even small-sized species thrive exclusively in treeless grasslands, like Pampas deer (*Ozotoceros bezoarticus*) and roe deer (*Capreolus capreolus*) (Pérez *et al.* 2008). Many cervids, including *Odocoileus*, are extremely versatile in food exploitation and successfully utilise grasslands, steppes and deserts (Putman and Flueck 2011), quite independently of cranial and dental features (Ozaki *et al.* 2007; Codron and Clauss 2010). For instance, mule deer eat forage of unexpected low digestibility, but compensate with faster gut passage rates. However, variance in diet between individual deer was greater than between elk, sheep and deer (Hobbs *et al.* 1983). Also, in autumn–early winter, roe deer from the most forested landscapes fed on poorer quality diet and adjusted by having heavier stomachs than their counterparts from the most open landscapes, and stomach mass of roe deer can increase by 50% when food quality is reduced in winter (Serrano Ferron *et al.* 2012). Moreover, strong support indicates that leaf-grass mixed feeding was the original feeding style of cervids (DeMiguel *et al.* 2008). Importantly, deer in steppes or grasslands do not solely rely on fibrous portions of grasses, but also heavily use nutrient-rich seed heads, particularly in winter. Huemul occurring 270 km east of the Andes (Prichard 1902a; Anon. 1904) were described as grazing there (Allen 1905). One population of extant huemul ate 16% grass (Sierralta 2003), while congeneric taruca had ~60% of grass in the diet (15 species, Gazzolo 2006). Furthermore, the Patagonian steppe contains a large component of shrubs and forbs, and maintains important green grass production throughout winter. In comparison, similar-sized *Odocoileus* also live in broken table grassland (<300 mm precipitation) and deserts (74 mm precipitation) (Flueck and Smith-Flueck 2011b). Irrespective of this, huemul are still asserted to avoid grasslands and steppes and thus are claimed not to have been there. Consequently, according to Cruz *et al.* (2010), a huemul antler found near the Atlantic was suggested to stem instead from Paleoindians having walked 250 km from the Andes and bringing the antler along. In contrast, Barberena *et al.* (2011) recently found that huemul inhabiting forested areas did not mainly consume closed-canopy plants, but showed highly selective and biased foraging behaviour towards plants from open areas within forests or forest edges. Moreover, huemul could not

be differentiated from steppe guanaco on the basis of $\delta^{13}\text{C}$ collagen values, in contrast to pudu, whose range was within the values for guanacos from forests but not from steppes. These observations are consistent with historic records of huemul far from the Andes and their current success in burnt-over areas.

Gut morphophysiology does not impede feeding in alternate niches because a range of different adaptations may serve for utilising the same dietary niche (Codron and Clauss 2010; Serrano Ferron *et al.* 2012). Ingestions of other plant resources are physical and physiological possibilities and often only translate into slight differences in chewing efficiency. Within the adaptive capacity of ruminants, 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). Lastly, the extent of possible adjustments to different forage conditions, while assuring species persistence, is very broad, and includes morphophysiological changes and varying the body size by several orders of magnitude. This occurs by altering the extent of selective feeding, by increasing forage retention in the rumen, by varying gut length and gastrointestinal anatomy, by changing gut microbial communities, and/or changing reproductive output, among others (Putman and Flueck 2011).

Competition

Declines in distribution and abundance, and lack of recovery of huemul are frequently attributed to competition from exotic herbivores. The red deer especially is claimed to outcompete and displace the huemul (Miller *et al.* 1983; Lever 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, Díaz 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 Jiménez *et al.* 2008; Flueck 2010). In contrast, huemul have disappeared in several areas lacking cattle, sheep, or exotic red deer (Smith-Flueck 2003). Moreover, feral cattle have co-existed with huemul for several hundred years, and >113 years with ranches in one case (Jiménez *et al.* 2008). Whereas red deer in southern forests ate many of the same plants and had similar preferences as huemul (Smith-Flueck 2003), this is relevant only if it reduces the population growth rate of huemul to <1. Considering huemul diet breadth (at least 191 plants, J. M. Smith-Flueck and W. Flueck, unpubl. data), they can likely shift diet without necessarily affecting recruitment, as is known for other cervids (Codron and Clauss 2010; Putman and Flueck 2011). Then, considering the impressive densities of exotic domestic and wild herbivores on former huemul habitat, it is unlikely that such areas were, or still would be, limiting to huemul in terms of energy and major plant nutrients (Krieg 1940; Flueck 2001). Moreover, mammalian herbivore communities commonly are multi-species assemblages, and presence *per se* of other herbivores is unlikely to be problematic for huemul, as evidenced by long-term coexistence with livestock, pudu and guanaco. Taruca also coexist with pudu, mazama, white-tailed deer (*Odocoileus virginianus*), several camelids, cattle and other livestock (Jungius 1974). On the other hand, ecosystems can be

affected negatively if overabundance of herbivores occurs, be it through livestock, exotic or native wild herbivores (Nugent *et al.* 2011).

Many remaining huemul populations share habitat with livestock (some even with red deer), but no studies show conclusively a spatial displacement from avoidance. In contrast, huemul used to mingle with livestock and were commonly driven with them to winter ranges. However, spatial avoidance could result from activities related to livestock production, such as human harassment and hunting, and from accompanying unleashed dogs. Lastly, a principal difference in habitat use exists in that currently only livestock and red deer inhabit lowlands and valley bottoms, whereas migratory behaviour of huemul to their former winter ranges was eliminated. Moreover, anthropogenic pressures today do not allow huemul to return to and persist in the lowlands and valley bottoms.

Diseases

Huemul are frequently asserted to be highly susceptible to cattle diseases: *Cysticercus tenuicollis*, foot-and-mouth disease (FMD), coccidiosis, parasites, or actinomycosis (Povilitis 1978; Redford and Eisenberg 1992; Simonetti 1995; Wemmer 1998; McCallum and Dobson 2002; Uhart and Chang Reisig 2006; Lord 2007). However, such assertions have been based on hearsay, guesses, or misquoting of original sources. In one case, though the original source stated that the presence of *C. tenuicollis* was not considered to have caused death (Texera 1974), Simonetti (1995) wrote '*C. tenuicollis* when transmitted by livestock is fatal to huemul'. McCallum and Dobson (2002) wrote that *C. tenuicollis* is highly pathogenic to huemul, with 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. To the contrary, in other cervids and ungulates the presence of *C. tenuicollis* is considered trivial (Leiby and Dyer 1971). This would also appear to be the case for huemul judged by several centuries of coexistence with livestock, millennia with guanaco that also harbor this larval-stage parasite, and absence of direct evidence. Similarly, the only report on coccidiosis (Texera 1974) was subsequently misinterpreted, thus erroneously blaming coccidiosis for the death of huemul individuals. FMD was also claimed to have wiped out huemul; however, 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 (Flueck and Smith-Flueck 2012a), and a recent review of FMD in susceptible wild South American 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 red deer and commonly in livestock are mostly considered nonthreatening. Although red deer are suggested to present special disease threats to huemul, they harbor diseases commonly associated with livestock; red deer and livestock, having coexisted for >100 years, play epidemiological roles regarding shared diseases. While livestock are commonly sympatric with huemul (nearly 100%), sympatry with red deer occurs in <2%

of known huemul populations, and in recent time. Even in these latter cases, livestock 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 2012a).

Reproduction

The general lack of huemul recovery immediately raises questions about population dynamics including vital rates, and other parameters essential for diagnosing factors limiting recovery. Age at maturity has been asserted to be 3 years, although without supportive data (Corti *et al.* 2011). Instead, huemul irrefutably breed as yearlings (Texera 1974; Guineo *et al.* 2008; Vidal *et al.* 2011), with good evidence that fawns can breed (Giai 1936; Texera 1974; Vidal *et al.* 2011), as known for other Odocoileines. It is therefore unrealistic to classify females <3 years old as juveniles and base calculations of intrinsic population growth rates on 'adult' females (Wittmer *et al.* 2010). Whereas a delay in reaching maturity can result from nutritional constraints as documented for other cervids (Putman and Flueck 2011), such constraints have not been documented for low-density huemul. Another deceptive asseveration refers to females having fawns only every second year, unless the fawn dies early on (García *et al.* 2008). Huemul indisputably breed every year and frequently raise fawns successfully during several consecutive years (Guineo *et al.* 2008; Vidal *et al.* 2011). Lastly, huemul have been reported to have twin fawns (Magne de la Croix 1937; Housse 1953; Whitehead 1993), as occurs in congeneric taruca under good conditions (Barrio 2010), as well as in *Odocoileus*. No recent cases, however, have been recorded, and twinning needs to be confirmed.

Sexual segregation

Huemul social structure is commonly stated to differ from other cervids by forming mixed-sex groups not only during rut, but throughout the year (Povilitis 1983, 1985; Vila *et al.* 2010). However, sexual segregation, including single animals, multiple males (Fig. 2), and multiple female groups, has also been documented (Serret and Borghiani 1997; Frid 1999; Wensing 2005). Moreover, in one population, sexes were mainly segregated, with adult males and females associating only twice out of 104 group sightings (Frid 1994).

The degree of sexual segregation (social or spatial separation) is highly variable between different cervid populations (Putman and Flueck 2011). In red deer, with sexes usually considered highly segregated outside the rut, in some populations even among mature animals, only 18–20% of stags and 50–56% of hinds were seen in segregated parties. In fallow deer, males remain in female areas long after the rut, with frequent aggregations of both sexes throughout the year. In white-tailed deer, some populations formed mixed groups year round, while among mule deer mixed groups made up 13–30% of all groups. In roe deer, home ranges of adult males and females overlap all year and mixed-sex groups can be common all year. Moose (*Alces alces*), considered a rather solitary species, may nonetheless occur in mixed groups throughout the year. Thus,

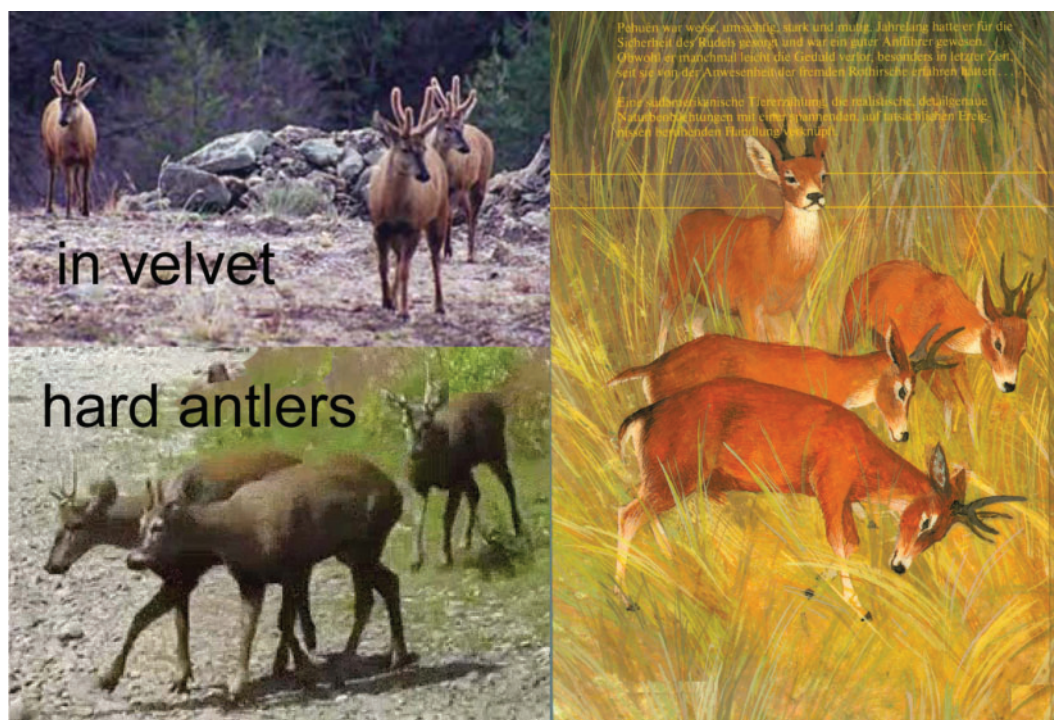


Fig. 2. Groups of multiple huemul bucks. The painting is from 'Der Kampf der Andenhirsche' (courtesy of Milada Krautmann).

mixed-sex groups in huemul are as variable as in numerous other cervids, all of which also form single-sex groups, with several known factors accounting for these variations.

Territoriality

Breeding systems are important in reduced populations (Stephens and Sutherland 1999). Until recently, only dominance group mating has been observed for huemul (Povilitis 1985; Díaz and Smith-Flueck 2000; Wensing 2005; Fundación RA Philippi 2009), consisting of multi-male aggregations (up to six males, Wensing 2005) with one male dominant over all others. Subordinate males are tolerated, male aggression is low, and during a 10-year study, no indications of huemul territoriality with active defence were found (Guineo *et al.* 2008). Congeneric taruca also exhibit dominance systems and lack of territoriality (Barrio 2010). However, huemul bucks were recently asserted to be strongly territorial, thus displaying behavioural characteristics unusual for most cervids (Corti *et al.* 2010, 2011). Territoriality involves expelling potential competitors from defended areas using defence behaviours at the boundaries that include scent marking, displays, retreats, chases and fights, and agonistic or aggressive behaviour in general (Maher and Lott 1995). Huemul bucks were considered territorial, defending their areas all year and throughout their lives, and were asserted to defend and monopolise female groups in their areas and sire most offspring, while non-territorial bucks rarely sired offspring. Specifically, 50% of sexually mature bucks ($n = 16$) sired no offspring (2005–07), and 44% of all the fawns born were sired by two bucks (Corti *et al.* 2011).

Territoriality as described for huemul would indeed be unusual among cervids. Previous instances of territoriality in cervids related to male rutting behaviour in only a few species (Putman and Flueck 2011). Red and fallow deer can adopt strategies of defending mating territories, as determined by population density and resource patchiness. In roe deer, the only species with delayed implantation, bucks often maintain larger breeding territories, especially in forests, but not in open-field habitats. Such bucks mark peripheries and interiors of their areas. However, adult males of these facultatively territorial cervids also form mixed groups year round with highly variable group sizes depending on density, habitat and sex structure, which determine the type of breeding system adopted (Putman and Flueck 2011). However, no other cervid is known to exhibit territoriality during the whole year as asserted for huemul.

Male behaviour makes up only part of the mating strategy. Although roe bucks maintain territories, up to 55% of females left home ranges for several days during peak rut (0.6–3.0 km), commonly acquired extra-pair matings, and 14% of polytocous litters were sired by >1 buck. Multiple paternity also occurs in white-tails where subadult bucks (1.5–2.5 years old) collectively fathered one-third of the offspring in all studied populations, even when mature males were present (DeYoung *et al.* 2009). Similarly flexible mating occurs in red deer (Stopher *et al.* 2011) and also in huemul, where subordinate males did all the siring in consecutive years in areas of supposedly territorial males, with females being bred by neighbouring males, and females moving into areas of other males to return after mating (Povilitis 1983, 1985; Wensing 2005; Corti 2008).

Observations, at least once a month, provided 25.7 spatial points on average from 18 males and 23 females to estimate home ranges and spatial overlap (Corti 2008). Males were considered territorial if they appeared dominant and held a specific area; non-territorial and juvenile males were considered subordinates; however, dominance was not defined nor measured. The 7–20 spatial points/male indicate that not all individuals were seen every consecutive month. The 50% core areas of dominant males (based on 15.6 spatial points on average) were considered defended territories (averaging 55.7 ha, range 25–114 ha). However, as these locations were determined during 33 months, with large intervals between readings, the core areas and overlaps do not indicate spatio-temporal relationships. Moreover, little or no overlap of home ranges is not evidence for territorial defence behaviour (Grant *et al.* 1992). Additionally, 50% of ‘territorial’ males had their core areas overlapping with another ‘territorial’ male, and life-long territoriality was based on three adults monitored 2–3 years. The few observed interactions included ‘territorial’ males chasing subadults five times, and one parallel walk of ‘territorial’ males. Parallel walking, however, is common among cervids, unrelated to territoriality, and is interpreted as assessment of opponents. A ‘territorial’ and a juvenile male with broken limbs were considered evidence of aggressive territoriality. This seems unlikely given that no direct interactions between ‘territorial’ males were seen, given that juveniles do not engage in fights with mature males (Geist 1981; Povilitis 1983, 1985; Anderson and Wallmo 1984; Guineo *et al.* 2008), and also given the absence of such reported injuries from rutting in other cervids. Although fighting accidents might result in broken legs, a more plausible scenario would be pursuing dogs (Packard 1947), which frequented that area. Frayed trees and shrubs were interpreted as territorial markings; however, this common behaviour of non-territorial cervids is described as innate extra-rut behaviour, velvet shedding, marking behaviour, and conspecific communication. *Odocoileus*, and likely the related huemul, have much fewer forehead skin glands than territorial *Capreolus* (Quay and Müller-Schwarze 1970, 1971). Intensive rubbing and thrashing, also called horning, is known for huemul (Geist 1998), and is very common in non-territorial *Odocoileus*. Lastly, territoriality was inferred from skewed parentage: polygynous males attend several oestrus females sequentially, and 13% of mature males sired 44% of all fawns (Corti *et al.* 2011). Thus, few ‘territorial’ males would be able to monopolise breeding by maintaining strong associations with many females within their reduced core areas. However, association indices were very weak, ranging from 0.00 to 0.03 for males and 0.01 to 0.03 for females, indicating that most huemul spent only short periods of time in small groups or were solitary, especially adult males. Furthermore, at only 1.7 huemul/km², the supposedly exclusive 50% core areas (56 ha on average) would require a very clumped distribution, with most females having to remain principally in these reduced areas of ‘territorial’ bucks. In contrast, in other cervids at low density and few males, females started to wander in search of breeding opportunities, multiple fathers are common, and non-dominant males frequently breed successfully. Huemul actually exhibited similar variations: (1) one of seven ‘territorial’ males never sired fawns; (2) one subordinate entered the area of a ‘territorial’ male in consecutive years and sired all fawns; (3) five females had

offspring sired by males inhabiting neighbouring areas; (4) and three females were directly observed leaving their areas and moving to areas with other males before returning after mating (Corti 2008). Other huemul groups (Povilitis 1983; Wensing 2005) and taruca (Barrio 2010) were also found to be very fluid with members coming and going, and Povilitis (1985) described females being courted by two or three males intermittently, another female being mainly courted by one male but mounted by another, a dominant male chasing a subordinate after the latter had mounted the female, and dominant males leaving females for prolonged times in apparent search for other oestrus females. Thus, the reported skewed breeding success among male huemul seems at odds with these other observations and is evaluated below.

Paternity assignments had low confidence and were considered to possibly generate bias (Corti 2008). To reduce bias, putative fathers were only assigned if they were near mothers; yet indices of overlap of fathers’ 50% core area with mothers’ home range were low (average of 0.29, range 0.00–0.67). Relative success of ‘territorial’ males breaks down to siring only ~45% of fawns observed in their social group, while siring another 41% of fawns to wandering females, and importantly, their social groups also ‘lost’ 32–45% of observed fawns to outside males. From the one ‘territorial’ male who did not sire, all fawns stemmed from a subordinate male coming in from another social unit. Within social units, 22% of females were bred by other males, 11% of females had inconclusive mates, and 33% of female had no data. The 13% of mature males (two ‘territorial’ bucks) siring 44% of all fawns (Corti *et al.* 2011) were responsible for only 26% of fawns in their respective social groups. However, when using 1 year as age at maturity (Guineo *et al.* 2008; Vidal *et al.* 2011) instead of 3 years, then there are potentially 28 fawns unaccounted for, aside from the 23 sampled ones (Table 1). Thus, probably <50% of all neonates were sampled, which presents yet another bias.

Genetic isolation and dispersal

Genetic isolation requires either absolute barriers, or an absence of immigration due to factors like the lack of conspecifics through a discrepancy between maximal dispersal distance and distances separating neighbouring populations. It can also result from neighbouring populations being too small to produce dispersers, possibly being influenced by the Allee effect on behaviour (Stephens and Sutherland 1999) and population density (e.g. Kokko and Lopez-Sepulcre 2006).

Table 1. Potential offspring production during 2 years (capture data from Corti 2008), based on the age at maturity of 1 year and assuming successful breeding each year

	Females	Captured fawns	Missing fawns
Females with fawns captured each year	6	13 ^A	
Females with only one fawn captured	10	10	10
Females resulting in zero captures	9	0	18
Total	25	23	28

^AOne female resulted in three sampled fawns over 3 years.

Genetic isolation of a huemul population was suggested due to a valley 5 km wide (Fig. 3), asserting that its flat and open characteristic present a barrier (Corti *et al.* 2011). However, such habitat should not present an obstacle to movements, and extant huemul are known to occupy open grasslands, with some populations using them 48% of the time, and males nearly exclusively so (Frid 1994, 1999), and huemul used open, flat areas hundreds of kilometres from forests historically (reviewed in Flueck and Smith-Flueck 2012b). Furthermore, the valley contained guanaco, a species sympatric with huemul elsewhere and commonly so in the past (Prichard 1902a, 1902b; Hatcher 1903; Osgood 1923), such that Prichard collected a guanaco and huemul with two consecutive shots. Moreover, a description of the nature reserve containing this valley states this Chacabuco Valley contains a population of 150 huemul deer shared with the neighbouring huemul reserve (www.conservacionpatagonica.org, verified 21 June 2012).

To further support implied genetic isolation, a very limited dispersal capacity of adult huemul was asserted. Citing Gill *et al.* (2008), a single case of dispersal of 8 km by a subadult female was used to support that the study population cannot receive dispersers from populations 10 km away, thus resulting in an absence of gene flow (Corti *et al.* 2011). However, given the low density, very small groups and short-term study (Gill *et al.* 2008), this single dispersal recording most likely does not represent the maximum distance nor the norm for huemul. In fact, a second case of dispersal was recently documented for a marked male that dispersed 15.5 km (Uribe 2011). This too unlikely represents a maximum. Huemul certainly disperse effectively considering their rapid postglacial occupancy of a huge region of South America (30–55°S). White-tailed deer disperse 50 km on average in some areas (but may exceed 200 km, Brinkman *et al.* 2005); small roe deer disperse 120 and 51 km on average in northern Sweden and interior Norway, respectively; and *Alces alces* disperse a minimum of 20 and up to 150–200 km (reviewed in Hjeljord 2001).



Fig. 3. Valley of 5 km width containing guanaco (*Lama guanicoe*), a species which coexists with huemul adjacent to this area and elsewhere.

Discussion

Knowledge of historical ranges is important regarding endangered species, due to its potential to contribute to the understanding of evolutionary history and the interpretation of biological and ecological traits. For instance, although common today, considering greater than two times in huemul 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 development with up to five times, and thus antler expression to be closer to the species' norm? Of plausible historical changes, the strongest effect likely stems from lack of access to nutritionally superior places, followed by males not reaching prime age. This effect on antlers and skull size has been shown for white-tailed deer historically displaced from favourable habitat by colonists (Wells and Stangl 2003). It is also reminiscent of red deer in primaeval Europe when Lords forced 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).

Historical and current cases indicate that densities and group sizes can be substantially larger than orthodox descriptions of huemul, which are based on some current remnant populations in marginal habitats. Reliance on such biased information results in circular reasoning when interpreting zooarchaeological data, paleodiets, prehistoric distribution, and the ecology of huemul in general. The frequent claim that natives hardly hunted huemul due to their leanness, contradicts insights from other northern cervids which accumulate >50% of energy as fat by autumn. Instead, due to extreme ease of killing huemul in autumn–winter, their past large winter concentrations, and strong incentives to hunt for accessing these rich fat reserves, natives likely influenced huemul distributions and density on winter ranges, particularly once they possessed horses for mobility (reviewed in Flueck and Smith-Flueck 2012b). Based on current biomass of exotic herbivores and densities of cervids in similar habitat elsewhere, huemul abundance must have been substantial. As Cabrera and Yepes (1940) observed: historically, huemul was one of the most frequently hunted by Patagonians who traded their skins at Atlantic ports. North American game species were similarly affected when adoption of horse nomadism led to abandonment of traditional hunting 5–6 generations before the first literate explorers arrived, resulting in absent eyewitness accounts or credible oral traditions about the past, particularly regarding densities and the loss of seasonal migration patterns of the animals (Benedict 1999, 2005). Thus, this discrepancy between current and past group sizes and densities is related to the displacement of huemul from former portions of the distribution which, also by livestock standards, would be more favourable.

As marginal habitat results in fragmentation and reduced subpopulations, any mortality factor becomes more important, including predation. Determining causes of mortality becomes a central challenge like differentiating predation from scavenging and species involved, yet rarely are applied methodologies reported, nor are data provided to support asserted causes of death. Lastly, the possibility of underlying debilitating factors (physical condition, disease, etc) has to be analysed, as these

factors might be concealed by predation. Although most studies on effects of feral dog predation on healthy deer populations suggested that the influence is minimal (Reed 1981), predation events in severely reduced subpopulations like huemul may be important due to dynamics of small populations and might call for temporary native predator (and dog) control to allow recovery to sustainable numbers. Importantly, three huemul populations have increased despite very high-density puma populations, foxes, incursions by dogs, and poaching: 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.

Cold-temperate ecosystems contain several ungulate species, with competition expressed as adjustments in spatio-temporal habitat use and feeding behaviour, 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 showing that competition, particularly from red deer, or livestock, have caused declines in distribution and abundance in the past century, or prevented recovery of huemul. Instead, huemul have disappeared in numerous areas lacking livestock or red deer, while persisting in other areas with livestock for several hundred years. Intra- and interspecific food habits in cervids vary greatly, due to numerous adjustments which can be made in behaviour, physiology and morphology, allowing even small deer (*Ozotoceros*, *Capreolus*), but also *Odocoileus* and taruca, to persist in grasslands and steppes. Huemul also exhibit flexible feeding behaviour, utilising 200–300 plant species when also considering historical habitat use and exotic food received in zoos. 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) recognised *Hippocamelus* as pastoral and only secondarily adapted to sylvan habitats, which agrees with habitats associated with past glacial events and with historic evidence of huemul still living far from Andean forests. Co-existence of huemul (as well as taruca) with other cervids and camelids for millennia, and with bovids and equids for centuries, casts doubts on recent emphasis on competition as cause for the absence of recovery. Thus, competition *per se* appears to be of minor importance, and more likely, incompatibilities relate to management associated with livestock production, particularly the presence of people and their dogs, which exert heavy pressure on wildlife.

There is no evidence that huemul is exceptionally susceptible to livestock diseases, nor that these affect population dynamics or have caused extinctions. Emphasising red deer is not warranted as they have shared diseases with livestock for >100 years, which in turn have coexisted with huemul for several hundred years. Red deer, where sympatric with a couple of huemul populations, are still outnumbered by 2100% by cattle, which, therefore, dominate epidemiological relationships. Hence, for huemul the primary factor regarding contagious diseases are feral and free-ranging livestock, and regular research and slaughter inspections of livestock provide a good proxy for pathogens afflicting sympatric red deer or huemul. It should not be overlooked that there is a latent risk from uncontrolled translocations of ungulates

including cervids, raising concerns about new exotic diseases like transmissible spongiform encephalopathy of cervids. The appearance of this disease could be disastrous for South America due to the large variety of endemic and threatened cervids (Flueck and Smith-Flueck 2012a).

Several factors affect the age at maturity, like food limitation resulting in proportionally smaller offspring and juvenile weights below the norm (Putman and Flueck 2011). Age at maturity of huemul is at 1 year, with evidence that fawns may breed as well. Moreover, they breed every year and frequently raise fawns in successive years. For calculations of intrinsic growth rates or life tables we recommend these parameters be used. Applying unrealistic parameters may cover up underlying processes and lead to spurious conclusions, such as underestimating reproductive potential and consequently, underestimating mortality events, or overvaluing other processes. Reports of twinning in huemul, as known for congeneric taruca and other *Odocoileus*, needs confirmation. Mixed-sex groups during all seasons, segregation of sexes, single or multiple male and female groups are all expressed by several cervids including huemul. Mixed-sex groups in huemul all year are neither a consistent trait nor unique among cervids, instead, variation in social group composition is common, which will assist in reinterpreting the historically much larger group sizes and densities, use of other habitat types, and potential variations in behaviour and ecology.

Huemul bucks were characterised as strongly territorial during all seasons and throughout their lives, defending and monopolising female groups and siring most offspring. Spatial overlap was used as the surrogate for territoriality, which, however, is considered inappropriate (Grant *et al.* 1992). Home range overlap in cervids is strongly tied to animal density and vegetation structure (Tufto *et al.* 1996; Jepsen and Topping 2004; Kjellander *et al.* 2004). Also, the few spatial points cannot reveal spatio-temporal relationships, as for huemul it took 600% more spatial points before estimated home-range sizes became asymptotic (Gill *et al.* 2003). Due to very few interactions seen between 'territorial' males, defence of areas against other males could not be established conclusively, and half of the core areas of 'territorial' bucks overlapped. The low breeding success of such bucks within their social units, regular success by subordinate males, females wandering to breed elsewhere, do not support territoriality in huemul which, together with congeneric taruca, are reported to have a dominance male group breeding systems. Moreover, the very low inbreeding coefficient of 0.009 found in this huemul population implies a random mating system (Corti *et al.* 2011).

Genetic isolation requires either absolute barriers, or an absence of immigration due to other factors. Two sole records of dispersal (8 and 15.5 km) unlikely represent maximal dispersal capacity of huemul, which disperse effectively considering their rapid postglacial occupation of a large South American region. Dispersal distances of mammals have been found to be proportional to home-range size (Bowman *et al.* 2002). Huemul using 500 ha could predictably disperse up to 90 km (at reported 1300 ha, it would be up to 144 km), well within ranges of other cervids as reviewed in Hjeljord (2001). In comparison, mountain goats (*Oreamnos americanus*), which are true rock specialists with extremely short legs, still manage to travel up to 25 km during spring and summer to get to low elevation mineral licks,

crossing large stretches of habitat considered completely unsuitable, like flat forests (Brandborg 1955; Poole *et al.* 2010). Visits to such highly specific places, and lasting <2 days are clearly a result of vertical traditions, which are considered vulnerable to anthropogenic impacts (Benedict 1999, 2005; Poole *et al.* 2010). Similarly, reduced movements in huemul may be due to past elimination of traditions to utilise areas settled by man. Still, to influence the genetics of a given population, the one-migrant-per-generation rule has been shown to be valid and robust (Wang 2004). For instance, Vila *et al.* (2003) documented the large genetic impact from a single male wolf immigrant on a bottlenecked population. Thus, erroneously considering landscape features as barriers may distract from discovering the factors underlying the lack of recolonisations generally observed in currently reduced huemul populations.

In conclusion, anthropogenic displacement seems to be a unifying pattern explaining the performance of most huemul populations (Flueck and Smith-Flueck 2011*d*, 2012*b*), with additional factors playing roles in some populations. 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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References

- Allen JA (1905) 'The Princeton University expeditions to Patagonia, 1896–1899. Volume 3. Zoology. Part 1. Mammalia of Southern Patagonia.' (E. Schweizerbart'sche Verlagshandlung: Stuttgart)
- Anderson AE, Wallmo OC (1984) *Odocoileus hemionus*. *Mammalian Species* **219**, 1–9. doi:10.2307/3504024
- Anon. (1904) Excursión del gobernador del Chubut. *Caras y Caretas* **7**, 8.
- Atwood TC, Gese EM, Kunkel KE (2007) Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison range. *The Journal of Wildlife Management* **71**, 1098–1106. doi:10.2193/2006-102
- Barberena R, Méndez C, Mena F, Reyes O (2011) Endangered species, archaeology, and stable isotopes: Huemul (*Hippocamelus bisulcus*) isotopic ecology in Central-Western Patagonia (South America). *Journal of Archaeological Science* **38**, 2313–2323. doi:10.1016/j.jas.2011.04.008
- Barrio J (2010) Taruka *Hippocamelus antisensis*. In 'Neotropical Cervidology'. (Eds JM Barbanti Duarte, S González) pp. 77–88. (FUNEP: Jaboticabal, Brazil)
- Bauer JW, Logan KA, Sweaner LL, Boyce WM (2005) Scavenging behavior in puma. *The Southwestern Naturalist* **50**, 466–471. doi:10.1894/0038-4909(2005)050[0466:SBIP]2.0.CO;2
- Belardi JB, Otero JG (1998) Anatomía económica del Huemul (*Hippocamelus bisulcus*): una contribución a la interpretación de las evidencias arqueológicas de su aprovechamiento en Patagonia. *Anales del Instituto Patagónico* **26**, 195–207.
- Benedict JB (1999) Effects of changing climate on game-animal and human use of the Colorado High Country (USA) since 1000 BC. *Arctic, Antarctic, and Alpine Research* **31**, 1–15. doi:10.2307/1552617
- Benedict JB (2005) Tundra game drives: an Arctic-Alpine comparison. *Arctic, Antarctic, and Alpine Research* **37**, 425–434. doi:10.1657/1523-0430(2005)037[0425:TGDAAC]2.0.CO;2
- Beninde J (1937) 'Zur Naturgeschichte des Rothirsches.' (Verlag Dr. Paul Schoeps: Leipzig, Germany)
- Bowman J, Jaeger JA, Fahrig L (2002) Dispersal distance of mammals is proportional to home range size. *Ecology* **83**, 2049–2055. doi:10.1890/0012-9658(2002)083[2049:DDOMP]2.0.CO;2
- Brandborg SM (1955) 'Life history and management of the mountain goat in Idaho.' (State of Idaho Department of Fish and Game: Boise, ID)
- Breitenmoser U, Haller H (1993) Patterns of predation by reintroduced European lynx in the Swiss alps. *The Journal of Wildlife Management* **57**, 135–144. doi:10.2307/3809010
- Brinkman TJ, Deperno CS, Jenks JA, Haroldson BS, Osborn RG (2005) Movement of female white-tailed deer: effects of climate and intensive row-crop agriculture. *The Journal of Wildlife Management* **69**, 1099–1111. doi:10.2193/0022-541X(2005)069[1099:MOFWE]2.0.CO;2
- Bubenik GA, Bubenik AB (1990) 'Horns, pronghorns, and antlers.' (Springer-Verlag: New York)
- Cabrera A, Yepes J (1940) 'Mamíferos sudamericanos.' (Compañía Argentina de Editores: Buenos Aires)
- Caughley G (1994) Directions in conservation biology. *Journal of Animal Ecology* **63**, 215–244. doi:10.2307/5542
- Codron D, Clauss M (2010) Rumen physiology constrains diet niche: linking digestive physiology and food selection across wild ruminant species. *Canadian Journal of Zoology* **88**, 1129–1138. doi:10.1139/Z10-077
- Colomé AA (1978) Biología y ecología del huemul Chileno (*Hippocamelus bisulcus*). Estudio de sus hábitos alimentarios. PhD Dissertation, Universidad de Chile, Santiago.
- Corti P (2008) Organisation sociale, dynamique de population, et conservation du cerf huemul (*Hippocamelus bisulcus*) dans la Patagonie du Chili. PhD Dissertation, Université de Sherbrooke, Canada.
- Corti P, Wittmer HU, Festa-Bianchet M (2010) Dynamics of a small population of endangered huemul deer (*Hippocamelus bisulcus*) in Chilean Patagonia. *Journal of Mammalogy* **91**, 690–697. doi:10.1644/09-MAMM-A-047.1
- Corti P, Shafer AB, Coltman DW, Festa-Bianchet M (2011) Past bottlenecks and current population fragmentation of endangered huemul deer (*Hippocamelus bisulcus*): implications for preservation of genetic diversity. *Conservation Genetics* **12**, 119–128. doi:10.1007/s10592-009-9997-7
- Cruz I, Muñoz AS, Caracotche M (2010) A huemul (*Hippocamelus bisulcus*) antler artefact in archaeological deposits of the Atlantic coast. Implications for human mobility and species distribution. *Magallania* **38**, 287–294.
- De Nigris ME (2004) Guanaco and huemul in Patagonian hunter-gatherers diet. In 'Zooarcheology of South America. BAR International Series 1298'. (Ed. GL Mengoni Gonalons) pp. 11–21. (Archaeopress: Oxford, England)
- DeMiguel D, Fortelius M, Azanza B, Morales J (2008) Ancestral feeding state of ruminants reconsidered: earliest grazing adaptation claims a mixed condition for Cervidae. *BMC Evolutionary Biology* **8**, 13. doi:10.1186/1471-2148-8-13
- DeYoung RW, Demarais S, Gee KL, Honeycutt RL, Hellickson MW, Gonzales RA (2009) Molecular evaluation of the white-tailed deer (*Odocoileus virginianus*) mating system. *Journal of Mammalogy* **90**, 946–953. doi:10.1644/08-MAMM-A-227.1
- Díaz NI, Smith-Flueck JM (2000) 'The Patagonian huemul. A mysterious deer on the brink of extinction.' (Literature of Latin America: Buenos Aires)
- Dolman PM, Wäber K (2008) Ecosystem and competition impacts of introduced deer. *Wildlife Research* **35**, 202–214. doi:10.1071/WR07114
- Fernández PM (2008) Taphonomy and zooarchaeology in the Neotropics: a view from northwestern Patagonian forest and steppe. *Quaternary International* **180**, 63–74. doi:10.1016/j.quaint.2007.08.012
- Fernández OA, Busso CA (1997) Arid and semi-arid rangelands: two thirds of Argentina. In 'Proceedings from an international workshop in Iceland. Rala Report No. 200'. (Eds O Arnalds, S Archer) pp. 41–60. (Agricultural Research Institute: Reykjavik, Iceland)

- Flueck WT (2001) Body reserves and pregnancy rates of introduced red deer in Patagonia (Argentina) after a period of drought. *Ecologia Austral* **11**, 11–24.
- Flueck WT (2004) Observations of interactions between Puma, *Puma concolor*, and introduced European Red Deer, *Cervus elaphus*, in Patagonia. *Canadian Field Naturalist* **118**, 132–134.
- Flueck WT (2010) Exotic deer in southern Latin America: what do we know about impacts on native deer and on ecosystems? *Biological Invasions* **12**, 1909–1922. doi:10.1007/s10530-009-9618-x
- Flueck WT, Smith-Flueck JM (2011a) Huemul heresies: beliefs in search of supporting data. 1. Historical and zooarcheological considerations. *Animal Production Science* **51**, cx1–cliv. [Short Communication]
- Flueck WT, Smith-Flueck JM (2011b) Huemul heresies: beliefs in search of supporting data. 2. Biological and ecological considerations. *Animal Production Science* **51**, clv–clxxx. [Short Communication]
- Flueck WT, Smith-Flueck JM (2011c) Huemul heresies: beliefs in search of supporting data. 3. Reproduction. *Animal Production Science* **51**, clxx–clxxx. [Short Communication]
- Flueck WT, Smith-Flueck JM (2011d) Recent advances in the nutritional ecology of the Patagonian huemul: implications for recovery. *Animal Production Science* **51**, 311–326.
- Flueck WT, Smith-Flueck JM (2012a) Diseases of red deer introduced to Patagonia and implications for native ungulates. *Animal Production Science* **52**, 766–773. doi:10.1071/AN11342
- Flueck WT, Smith-Flueck JM (2012b) Huemul heresies: beliefs in search of supporting data. 1. Historical and zooarcheological considerations. *Animal Production Science* **52**, 685–693. doi:10.1071/AN11344
- Frid A (1994) Observations on habitat use and social organization of a huemul (*Hippocamelus bisulcus*) coastal population in Chile. *Biological Conservation* **67**, 13–19. doi:10.1016/0006-3207(94)90003-5
- Frid A (1999) Huemul (*Hippocamelus bisulcus*) sociality at a periglacial site: sexual aggregation and habitat effects on group size. *Canadian Journal of Zoology* **77**, 1083–1091.
- Fundación RA Philippi (2009) Mamíferos de Chile. Huemul. Available at <http://www.fundacionraphilippi.cl> [Verified 7 June 2012]
- García K, Jara A, Ortiz JC, Victoriano P (2008) Evaluation of an extinction scenario for the last population of *Hippocamelus bisulcus* (Molina, 1782) in Central Chile. *Interciencia* **33**, 152–159.
- Gazzolo C (2006) Botanical composition of taruka (*Hippocamelus antisensis*) diet during rainy season in Huascarán national park, Peru. In 'Advances in deer biology'. (Eds L Bartos, A Dusek, R Kotrba, J Bartosova) p. 216. (Research Institute of Animal Production: Praha, Czech Republic)
- Geist V (1981) Behavior: adaptive strategies in Mule deer. In 'Mule and black-tailed deer of North America'. (Ed. OC Wallmo) pp. 157–223. (University of Nebraska Press: Lincoln, NE)
- Geist V (1998) 'Deer of the world.' (Stackpole Books: Mechanicsburg, PA)
- Giai AG (1936) Huemul, inofensivo venado de las soledades cordilleranas de la Patagonia. *La Chacra (Arg.)* **6**, 99–101.
- Gigoux EE (1929) El huemul. *Revista Chilena de Historia Natural (Valparaíso, Chile)* **23**, 573–582.
- Gill R, Saucedo C, Montero E, Millacura R (2003) Ranging behavior and habitat use of huemul (*Hippocamelus bisulcus*). In 'Huemul ecology research for conservation planning'. (Darwin Initiative: Cochrane, Chile)
- Gill R, Saucedo C, Aldridge D, Morgan G (2008) Ranging behavior of huemul in relation to habitat and landscape. *Journal of Zoology* **274**, 254–260. doi:10.1111/j.1469-7998.2007.00378.x
- Grant JW, Chapman CA, Richardson KS (1992) Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology* **31**, 149–161. doi:10.1007/BF00168642
- Grosse A (1949) El huemul – ciervo de los Andes y emblema del escudo Chileno. *The Condor* **12**, 10–12. [Revista Chileno Alemana]
- Guérin C, Faure M (2009) The Cervidae (Mammalia, Artiodactyla) of the Upper Pleistocene/Lower Holocene deposits of the Serra da Capivara National Park Region (Piauí, Brazil). *Geobios* **42**, 169–195.
- Guineo P, Guineo Garay R, Garay G (2008) 'Conociendo al huemul de Torres del Paine.' (La Prensa Austral: Punta Arenas, Chile)
- Hatcher JB (1903) 'Reports of the Princeton University expeditions to Patagonia, 1896–1899. Vol. I: Narrative of the Expeditions. Geography of Southern Patagonia.' (E. Schweizerbart'sche Verlagshandlung: Stuttgart)
- Hershkovitz P (1972) The recent mammals of the neotropical region: a zoogeographic and ecological review. In 'Evolution, mammals, and southern continents'. (Eds A Keast, FC Erk, B Glass) pp. 311–431. (State University New York Press: Albany, New York)
- Hjeljord O (2001) Dispersal and migration in northern forest deer – are there unifying concepts? *Alces (Thunder Bay, Ont.)* **37**, 353–370.
- Hobbs NT, Baker DL, Gill RB (1983) Comparative nutritional ecology of montane ungulates during winter. *The Journal of Wildlife Management* **47**, 1–16. doi:10.2307/3808046
- Housse PR (1953) 'Animales salvajes de Chile en su clasificación moderna: su vida y sus costumbres.' (Ediciones de la Universidad de Chile: Santiago, Chile)
- Iglesias RE (1965) El huemul. *La Montaña (Arg.)* **7**, 26–28.
- Jaksic FM, Iriarte JA, Jimenez JE, Martinez DR (2002) Invaders without frontiers: cross-border invasions of exotic mammals. *Biological Invasions* **4**, 157–173. doi:10.1023/A:1020576709964
- Jepsen JU, Topping CJ (2004) Modelling roe deer (*Capreolus capreolus*) in a gradient of forest fragmentation: behavioural plasticity and choice of cover. *Canadian Journal of Zoology* **82**, 1528–1541. doi:10.1139/z04-131
- Jiménez J, Guineo G, Corti P, Smith J, Flueck W, Vila A, Gizejewski Z, Gill R, McShea B, Geist V (2008) *Hippocamelus bisulcus*. In '2008 IUCN Red List of threatened species'. (International Union for Conservation of Nature: Gland, Switzerland) Available at www.iucnredlist.org/details/10054 [verified 7 June 2012]
- Jungius H (1974) Beobachtungen am Weisswedelhirsch und an anderen Cerviden in Bolivien. *Zeitschrift für Säugetierkunde* **39**, 373–383.
- Kjellander P, Hewison AJM, Liberg O, Angibault JM, Bideau E, Cargnelutti B (2004) Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. *Oecologia* **139**, 478–485. doi:10.1007/s00442-004-1529-z
- Knopff KH, Knopff AA, Boyce MS (2010) Scavenging makes cougars susceptible to snaring at wolf bait stations. *The Journal of Wildlife Management* **74**, 644–653. doi:10.2193/2009-252
- Kokko H, Lopez-Sepulcre A (2006) From individual dispersal to species ranges: perspectives for a changing world. *Science* **313**, 789–791. doi:10.1126/science.1128566
- Krieg H (1940) 'Als Zoologe in Steppen und Wäldern Patagoniens.' (J.F. Lehmanns Verlag: München, Germany)
- Kurtén B (1975) A new pleistocene genus of American mountain deer. *Journal of Mammalogy* **56**, 507–508. doi:10.2307/1379377
- Leiby PD, Dyer WG (1971) Cyclophyllidean tapeworms of wild carnivores. In 'Parasitic diseases of wild mammals'. (Eds JW Davis, RC Anderson) pp. 174–234. (Iowa State University Press: Ames, IA)
- Lever C (1985) 'Naturalized mammals of the world.' (Longman Inc.: New York)
- Lord RD (2007) 'Mammals of South America.' (JHU Press: Baltimore, MD)
- Madsen A (1948) 'Patagonia Vieja.' (Zagier & Urruty: Buenos Aires)
- Magne de la Croix P (1937) El huemul. *Caras y Caretas* **40**, 117.
- Maher CR, Lott DF (1995) Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behaviour* **49**, 1581–1597. doi:10.1016/0003-3472(95)90080-2
- McCallum H, Dobson A (2002) Disease, habitat fragmentation and conservation. *Proceedings. Biological Sciences* **269**, 2041–2049. doi:10.1098/rspb.2002.2079
- Miller S, Rottman J, Raedeke K, Taber RD (1983) Endangered mammals of Chile: status and conservation. *Biological Conservation* **25**, 335–352. doi:10.1016/0006-3207(83)90069-1

- Molinari-Jobin A, Molinari P, Breitenmoser-Wursten C, Breitenmoser U (2002) Significance of lynx *Lynx lynx* predation for roe deer *Capreolus capreolus* and chamois *Rupicapra rupicapra* mortality in the Swiss Jura Mountains. *Wildlife Biology* **8**, 109–115.
- Murillo J, Ramb AM (1975) 'Der Kampf der Andenhirsche.' (K. Thienemann Verlag: Stuttgart, Germany)
- Navas JR (1987) Los vertebrados exóticos introducidos en la Argentina. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* **14**, 7–38.
- Novaro AJ, Moraga CA, Briceno C, Funes MC, Marino A (2009) First records of culpeo (*Lycalopex culpaeus*) attacks and cooperative defense by guanacos (*Lama guanicoe*). *Mammalia* **73**, 148–150. doi:10.1515/MAMM.2009.016
- Nowak MC, Taylor TE, Witmer GW (2000) Prolonged scavenging by a female mountain lion in Northeastern Oregon. *Northwestern Naturalist (Olympia, Wash.)* **81**, 63–65. doi:10.2307/3536666
- Nowak RM, Walker EP (1999) 'Walker's mammals of the world.' (JHU Press: Baltimore, MD)
- Nugent G, McShea WJ, Parkes J, Woodley S, Waithaka J, Moro J, Gutierrez R, Azorit C, Mendez Guerrero F, Flueck WT, Smith-Flueck JM (2011) Policies and management of overabundant deer (native or exotic) in protected areas. *Animal Production Science* **51**, 384–389.
- Osgood WH (1923) The Marshall Chilean Field Expedition 1922–1923. Field notes. Available at <https://sites.google.com/a/fieldmuseum.org/bruce-pattersons-lab/Home/collections/osgood-files> [verified 7 June 2012]
- Ozaki M, Suwa G, Kaji K, Ohba T, Hosoi E, Koizumi T, Takatsuki S (2007) Correlations between feeding type and mandibular morphology in the sika deer. *Journal of Zoology* **272**, 244–257. doi:10.1111/j.1469-7998.2006.00264.x
- Packard FM (1947) A study of the deer and elk herds of Rocky Mountain National Park, Colorado. *Journal of Mammalogy* **28**, 4–12. doi:10.2307/1375489
- Pérez W, Clauss M, Ungerfeld R (2008) Observations on the macroscopic anatomy of the intestinal tract and its mesenteric folds in the Pampas deer (*Ozotoceros bezoarticus*, Linnaeus 1758). *Anatomia, Histologia, Embryologia* **37**, 317–321. doi:10.1111/j.1439-0264.2008.00855.x
- Philippi RA (1892) El guemul de Chile. *Anales del Museo Nacional de Chile* **2**, 1–9.
- Philippi RA (1895) 'Drei Hirsche der Anden.' (F.A. Brockhaus: Leipzig, Germany)
- Pinto AA (2004) Foot-and-mouth disease in tropical wildlife. *Annals of the New York Academy of Sciences* **1026**, 65–72. doi:10.1196/annals.1307.008
- Poole KG, Bachmann KD, Teske IE (2010) Mineral lick use by GPS radio-collared mountain goats in Southeastern British Columbia. *Western North American Naturalist* **70**, 208–217. doi:10.3398/064.070.0207
- Povilitis A (1978) The Chilean Huemul Project – a case history (1975–1976). In 'Threatened deer'. pp. 109–128. (International Union for Conservation of Nature: Morges, Switzerland)
- Povilitis A (1983) The huemul in Chile: national symbol in jeopardy? *Oryx* **17**, 34–40. doi:10.1017/S003060530001838X
- Povilitis A (1985) Social behavior of the huemul (*Hippocamelus bisulcus*) during the breeding season. *Zeitschrift für Tierpsychologie* **68**, 261–286. doi:10.1111/j.1439-0310.1985.tb00129.x
- Prichard HH (1902a) Field notes upon some of the larger mammals of Patagonia made between September 1900 and June 1901. *Proceedings of the Zoological Society of London* **1**, 272–277.
- Prichard HH (1902b) 'Through the heart of Patagonia.' (D. Appleton and Co.: New York)
- Prichard HH (1910) 'Hunting camps in wood and wilderness.' (William Heinemann: London)
- Putman R, Flueck WT (2011) Intraspecific variation in biology and ecology of deer: magnitude and causation. *Animal Production Science* **51**, 277–291. doi:10.1071/AN10168
- Quay WB, Müller-Schwarze D (1970) Functional histology of integumentary glandular regions in black-tailed deer (*Odocoileus hemionus columbianus*). *Journal of Mammalogy* **51**, 675–694. doi:10.2307/1378294
- Quay WB, Müller-Schwarze D (1971) Relations of age and sex to integumentary glandular regions in Rocky Mountain mule deer (*Odocoileus hemionus hemionus*). *Journal of Mammalogy* **52**, 670–685. doi:10.2307/1378915
- Redford KH, Eisenberg JF (1992) 'Mammals of the Neotropics: the southern cone. Volume 2. Chile, Argentina, Uruguay, Paraguay.' (The University of Chicago Press: Chicago)
- Reed DF (1981) Conflicts with civilization. In 'Mule and black-tailed deer of North America'. (Ed. OC Wallmo) pp. 509–535. (University of Nebraska Press: Lincoln, NE)
- Rottmann JS (2003) Experiencias con huemules en cautividad. In '4ta Reunión Chileno-Argentina sobre Estrategias de Conservación del Huemul'. (Ed. G Acosta-Jamett) pp. 40–42. (CONAF and CODEFF: Las Trancas, Chile)
- Rusconi C (1936) Anomalías en las cornamentas del huemul. *Anales Sociedad Científica Argentina* **122**, 288–296.
- Saizar P (1987) La estación de cría del pudu. *Vida Silvestre* **5**, 56–58.
- Saucedo C, Gill R (2004) The endangered huemul or south Andean deer *Hippocamelus bisulcus*. *Oryx* **38**, 132–133.
- Serrano Ferron E, Verheyden H, Hummel J, Cargnelutti B, Lourtet B, Merlet J, Gonzalez-Candela M, Angibault JM, Jonathan A, Hewison M, Clauss M (2012) Digestive plasticity as a response to woodland fragmentation in roe deer. *Ecological Research* **27**, 77–82. doi:10.1007/s11284-011-0872-x
- Serret A, Borghiani F (1997) Registros de avistajes y comportamiento de huemules en el seno Moyano, Parque Nacional Los Glaciares. *Boletín Técnico Fundación Vida Silvestre Argentina* **35**, 1–24.
- Sierrala D (2003) La microhistología de fecas para el estudio de dieta del huemul. In 'Huemul ecology research for conservation planning'. (Darwin Initiative: Cochrane, Chile)
- Simonetti JA (1995) Wildlife conservation outside parks is a disease-mediated task. *Conservation Biology* **9**, 454–456. doi:10.1046/j.1523-1739.1995.9020454.x
- Smith-Flueck JM (2003) The ecology of huemul (*Hippocamelus bisulcus*) in Andean Patagonia of Argentina and considerations about its conservation. Doctoral Dissertation, Universidad Nacional Comahue, Bariloche, Argentina.
- Smith-Flueck JM, Flueck WT (2001) Natural mortality patterns in a population of southern Argentina huemul (*Hippocamelus bisulcus*), an endangered Andean cervid. *European Journal of Wildlife Research* **47**, 178–188.
- Smith-Flueck JM, Barrio J, Ferreyra N, Nuñez A, Tomas N, Guzman J, Flueck WT, Hinojosa A, Vidal F, Garay G, Jimenez J (2011) Advances in ecology and conservation of *Hippocamelus* species in South America. *Animal Production Science* **51**, 378–383. doi:10.1071/AN10287
- Stephens PA, Sutherland WJ (1999) Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution* **14**, 401–405. doi:10.1016/S0169-5347(99)01684-5
- Steward JH (1946) Handbook of South American Indians. Volume 1. The marginal tribes. (Smithsonian Institution: Washington, D.C.)
- Stophor KV, Nussey DH, Clutton-Brock TH, Guinness F, Morris A, Pemberton JM (2011) The red deer rut revisited: female excursions but no evidence females move to mate with preferred males. *Behavioral Ecology* **22**, 808–818. doi:10.1093/beheco/arr052
- Texera WA (1974) Algunos aspectos de la biología del huemul (*Hippocamelus bisulcus*) (Mammalia: Artiodactyla, Cervidae) en cautividad. *Anales del Instituto Patagónico* **5**, 155–188.
- Tufto J, Andersen R, Linnell J (1996) Habitat use and ecological correlates of home range size in a small cervid: the roe deer. *Journal of Animal Ecology* **65**, 715–724. doi:10.2307/5670

- Uhart M, Chang Reisig E (2006) Ungulados exóticos: amenaza sanitaria para el huemul? In '5ta Reunión Binacional Argentino-Chilena sobre Estrategias de Conservación del Huemul'. pp. 25–27. (Adm. Parques Nacionales: Bariloche, Argentina)
- Uribe LS (2011) Los Dominios de 'Silencio' en el Baker. *Informativo: Coordinación Nacional Del Plan de Conservación del Huemul Chile* **4**, 1–22.
- Urrutia AB, Ojeda AA (2008) 'Manual de Plagas y Enfermedades del Bosque Nativo en Chile.' (Editora e Imprenta Maval Ltda: Santiago, Chile)
- Vidal F, Smith-Flueck JM, Flueck WT, Arias E (2011) The Patagonian huemul (*Hippocamelus bisulcus*) under captive conditions: past and current experiences. *Animal Production Science* **51**, 340–350. doi:10.1071/AN10226
- Vila C, Sundqvist AK, Flagstad O, Seddon J, Björnerfeldt S, Kojola I, Casulli A, Sand H, Wabakken P, Ellegren H (2003) Rescue of a severely bottlenecked wolf (*Canis lupus*) population by a single immigrant. *Proceedings. Biological Sciences* **270**, 91–97. doi:10.1098/rspb.2002.2184
- Vila AR, Saucedo C, Aldridge D, Ramilo E, Corti P (2010) South Andean huemul *Hippocamelus bisulcus* (Molina 1782). In 'Neotropical Cervidology'. (Eds JM Duarte, S González) pp. 89–100. (FUNEP: Jaboticabal, Brazil)
- von Thüngen J, Lanari MR (2010) Profitability of sheep farming and wildlife management in Patagonia. *Pastoralism* **1**, 274–290.
- Wang J (2004) Application of the One-Migrant-per-Generation rule to conservation and management. *Conservation Biology* **18**, 332–343. doi:10.1111/j.1523-1739.2004.00440.x
- Webb SD (2000) Evolutionary history of New World Cervidae. In 'Antelopes, deer, and relatives'. (Eds ES Vrba, GB Schaller) pp. 38–64. (Yale University Press: New York)
- Wells KW, Stangl FB (2003) Superior size and antler development in populations of white-tailed deer (*Odocoileus virginianus*) from the North Texas rolling plains. *The Texas Journal of Science* **55**, 337–346.
- Wemmer C (1998) 'Deer: status survey and conservation action plan.' (IUCN/SSC Deer Specialist Group: Gland, Switzerland)
- Wensing D (2005) Conservation study of the huemul (*Hippocamelus bisulcus*) within the Bernardo O'Higgins National Park, Chile. Thesis report NWS-I-2005–6, Utrecht University, Utrecht, The Netherlands.
- Whitehead GK (1993) 'The Whitehead encyclopedia of deer.' (Swan Hill Press: Shrewsbury, England)
- Williams D (2010) Bighorn success. *New Mexico Wildlife* **55**, 1–15.
- Willis B (1914) 'El norte de la Patagonia.' (Ministerio de Obras Publicas: Buenos Aires)
- Wittmer HU, Corti P, Saucedo C, Galaz JL (2010) Learning to count: adapting population monitoring for endangered huemul deer (*Hippocamelus bisulcus*) to meet conservation objectives. *Oryx* **44**, 516–522. doi:10.1017/S0030605310001018