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Diseases of red deer introduced to Patagonia and implications for native ungulates

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Abstract. The red deer (*Cervus elaphus*) invasion in Patagonia has been continuing for nearly a century, with occurrence in all habitats between 34°S and 55°S. Their distribution, movement patterns and locally high densities raise concerns over their potential epidemiological role in maintaining disease reservoirs or transmitting diseases such as foot-and-mouth disease or tuberculosis, with potential severe health and economical impacts at the interface of humans, livestock or native wildlife. Among adult females collected by rifle and radio-collared deer that died naturally, no ectoparasites were found (n = 73). *Fasciola hepatica* was encountered in three surveys at prevalences ranging from 9% to 50% (n = 108). *Taenia ovis krabbei* was identified, and *Cysticerus tenuicollis* was found at a prevalence of 8% (n = 12). *Ostertagia* sp., *Bunostomum* sp. and *Dictyocaulus* sp. had a prevalence of 75%, 25% and 13% (n = 9), respectively. Several gastrointestinal parasites reported at low prevalence in endangered Patagonian huemul (*Hippocamelus bisulcus*) are common in livestock and considered commensals in domestic ruminants. Sympatry of huemul with livestock is commonplace, whereas with red deer it occurs in <2% of known populations, in which case there were 1.2 red deer, but 25.2 livestock per huemul, making livestock the determining epidemiological factor regarding disease transmission or reservoir. As red deer have been coexisting with livestock for >100 years in Argentina, both red deer and livestock play epidemiological roles for shared diseases. Research, conservation and management efforts should be directed towards livestock herd health programs or restriction of free livestock movements, particularly if diseases are shown to have an impact on recruitment of endangered natives. Livestock are routinely researched and inspected at slaughter and thus provide a proxy for diseases afflicting co-existing ungulates. Testing for antibodies to foot-and-mouth disease viral antigen was negative (n = 41). A tentative diagnosis of mycobacterial infection was based on typical visceral lesions. Antler damage occurred on 73% of shed antlers, with 36% having major breaks of tines and main beams, possibly indicating mineral imbalances. One male had both antlers, including pedicles with portions of frontal, parietal and occipital bones, broken off the skull, causing his death. The prevalence of 0.9% of campylognathia (n = 776) indicates that the disease is unlikely to be inheritable, because the founding stock of 20 animals would have had a prevalence of at least 5%. Among deer, handedness of scoliosis related significantly to the hemisphere where specimens originated ($P < 0.001$, n = 131). Coriolis forces are known to affect early stages of development, such as the innervation pattern of the mammalian vestibular system, or the plane of bilateral symmetry. It is, therefore, conceivable that the networks processing these environmental cues, or the mechanisms responsible for compensation, are malfunctioning and thus result in a preponderance of facial scoliosis in accordance to the earth's rotation.

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Introduction

Argentina has a long tradition of animal introductions, beginning with livestock that reached millions of feral cattle, horses and goats shortly after Spanish settled in the 16th century (Torrejon 2001; Flueck and Smith-Flueck 2012*a*). Exotic wildlife were introduced later and included red deer (*Cervus elaphus*), which are considered to be one of the world's 14 worst mammalian invasive species (IUCN, www.issg.org, accessed April 2012). The expansion of red deer in the southern cone of South America began less than a century ago, and has yet to reach a state of equilibrium (Flueck and Smith-Flueck 1993; Flueck *et al*. 2003).

Feral red deer have established themselves in all mayor habitats of Patagonia and are currently established in most forested habitat types encountered between ~34°S and 55°S, including semi-captive deer in southern Tierra del Fuego (Flueck and Smith-Flueck 2012*b*). The area occupied in 2003 was estimated at >51 000 km^2, consisting of 29% forest habitat, 57% Patagonian steppe habitat, and 14% of non-forested habitat such as wet meadows and riparian habitat, brush or grasslands of anthropogenic origin, and high-altitude vegetation above the tree line (Flueck *et al*. 2003). In Chile, they were estimated to occupy ~7700 km^2 (also see review in Flueck and Smith-Flueck 2012*b*). The distribution of red deer had the following environmental characteristics: it covers the latitudes between 37°42′S and 54°55′S (non-contiguous), longitudes between 73°36′W and 69°50′W (non-contiguous) and altitudes from sea level to >2450 m (Flueck *et al*. 2003). Within the present distribution, feral red deer may number >100 000 animals at an average density of ~2 deer/km^2. This appears to be a conservative estimate, considering that favourable ecotonal habitats have revealed densities of ~100 deer/km^2, whereas in steppe areas they reached 40–50 deer/km^2 (Flueck *et al*. 1995; J. Amaya, pers. comm.). After liberation, red deer initially formed resident populations, but decades later also have established migratory segments, with individuals traveling 25 km, and with cases of dispersal reaching as far as 40 km (Flueck 2005). In the study area reported here, red deer are commonly sympatric with cattle, horses, sheep, goats and wild species such as fallow deer (*Dama dama*), European boar (*Sus scrofa*), guanaco (*Lama guanicoe*), and in one area also with a remnant population of endangered Patagonian huemul deer (*Hippocamelus bisulcus*).

The distribution, movement behaviour and uncontrolled national and transnational shipments of red deer (Flueck and Smith-Flueck 2006; Flueck 2010*a*) raise concerns over their potential epidemiological role for various diseases such as foot-and-mouth disease (FMD), brucellosis and tuberculosis (Flueck and Smith-Flueck 1993, 2006; Flueck *et al*. 2003; Flueck 2005). Here, we report for the first time on various diseases encountered in red deer in Patagonia and evaluate their potential to have an impact on native ungulates.

Materials and methods

The study area is centred in the ecotone between Andean forests and Patagonian grasslands (40°58′S, 71°12′W), Argentina. The topography is primarily mountainous, with most features formed by glacial and volcanic processes. The study sites are between 900-m and 1800-m elevation and represent grasslands, or ecotones between forests and grasslands (details in Flueck and Smith-Flueck 2011*a*). We evaluated females older than 1 year, shot and collected randomly between 1991 and 2009, and radio-collared deer that died naturally between 2001 and 2009. All individuals were necropsied in the field (Mitchell *et al*. 1976; Wobeser and Spraker 1980). The focus of deer collections varied, relating either to issues of reproduction, development, seasonal body condition, population dynamics, genetics or gross pathology. The examination for the presence of distinct disease entities was thus not equally intense in every collection, and prevalence is indicated only where an adequate number of individuals had been examined for that purpose (Jones *et al*. 1997; Samuel *et al*. 2001; Williams and Barker 2001). The presence of FMD was evaluated by the federal agency SENASA, via detection of antibodies to viral infection-associated antigen. Additionally, in 1994–1995 we collected entire female deer, which were examined exhaustively in the pathology laboratory of the National Institute for Agricultural Technology, INTA. All visceral parasite species reported here were detected during necropsy. Regarding mycobacterial infection, Ziehl-Neelsen staining was used to detect acid-fast organisms. Deer were collected in the following four study sites: Site A (41°00′S, 71°17′W), Site B (40°59′S, 71°11′W), Site C (40°57′S, 71°11′W) and Site D (40°29′S, 70°59′W). Considering possible nutritional deficiencies, the damage and frequency of breakage on antlers collected between 2006 and 2009 were analysed. Damage on antlers was classified as broken tips of tines, tines completely broken off and breakage of the main beam. Cases of campylognathia (facial scoliosis) were recorded from specimens in our collection (*n* = 522) and those from hunters (*n* = 254), and handedness according to hemisphere was analysed using binomial probability tests.

Results

Ectoparasites were not present on gross examination (Site A, *n* = 21; Site C, *n* = 9; Site D, *n* = 43. Flueck *et al*. 1993; Smith-Flueck and Flueck 1998). *Fasciola hepatica* was encountered regularly among deer; at Site A, the prevalence in the population was 50% (*n* = 20) (Flueck *et al*. 1993, 1995; W. T. Flueck, J. M. Smith-Flueck, F. V. Olaechea, unpubl. data), whereas at Site D, it was 9% (*n* = 43) (Smith-Flueck and Flueck 1998). Additional deer examined between 1998 and 2009 at Site A exhibited a prevalence of 13% (*n* = 45). *Taenia ovis krabbei* was identified on the basis of hook characters, size, appearance and anatomical location of a cysticercus. A sylvatic cycle involving red deer appears to have been established (Flueck and Jones 2006). On several occasions, we found taenid larval stages attached to liver, omentum and peritoneum, with the typical gross appearance of *Cysticercus tenuicollis*, which were deposited and identified by the state agency INTA. At Site A, their prevalence was 8% (*n* = 12) (Flueck *et al*. 1993). *Ostertagia* sp. was found at a prevalence of 75%, with two individuals carrying 800 and 900 adult parasites, respectively; *Bunostomum* sp. was found at a prevalence of 25%; and *Dictyocaulus* sp. occurred at 13% prevalence (*n* = 9, Flueck *et al*. 1995; W. T. Flueck, J. M. Smith-Flueck, F. V. Olaechea, unpubl. data). FMD was tested for by SENASA in deer from Site B (*n* = 41) in 1994–1995, to allow export of the tissue as part of a genetic study (Flueck and Smith-Flueck 2011*a*); all samples were negative. Among an additional 393 specimens collected for reproductive and physical-condition studies, the only notable pathological finding was a suspected case of mycobacterial infection from Site D. We submitted fresh tissue from this specimen to INTA, but no cultivation was done. Histological sections were negative for acid-fast organisms; however, a large quantity of macrophages with acidophilic material in the cytoplasm was present. There were substantial multifocal, well demarcated adhesions between the visceral and parietal pleura; congregated, well demarcated and firm granulomatous mediastinal lymph nodes; firm nodules of 5–10-mm thickness practically covering the entire parietal pleura; and additional lesions in the intestinal tract, including well demarcated multifocal and firm nodules of 2–5-mm diameter associated with rumenal lymph tissue, and focal protrusive aggregations of up to 25-mm diameter of well demarcated small firm nodules (1–2 mm) in liver (Fig. 1). The 9-year-old female was lactating, of average build and without other lesions.

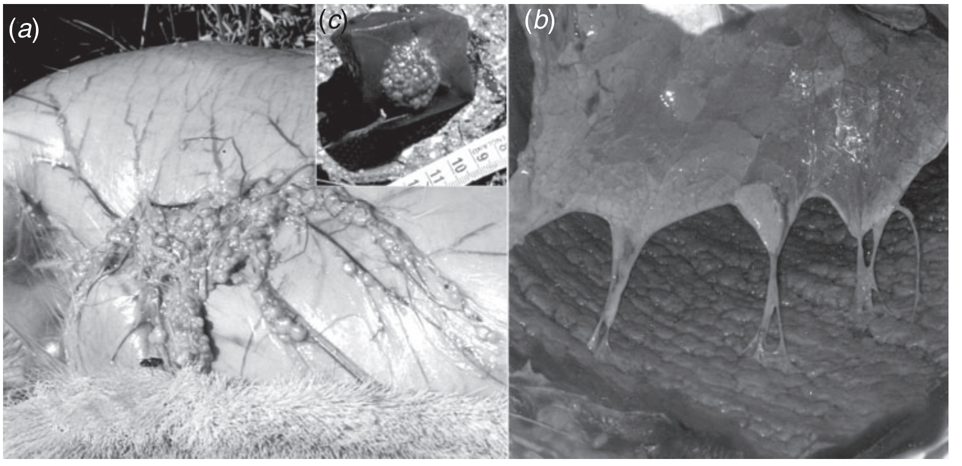

Fig. 1. Female red deer. (*a*) Well demarcated multifocal and firm nodules of ~2–5-mm diameter associated with rumenal lymph tissue. (*b*) Multifocal and well demarcated adhesions between visceral and parietal pleura, and firm nodules of 5–10-mm thickness covering the parietal pleura. (*c*) Focal protrusive aggregation of 25-mm diameter of well demarcated, firm nodules (1–2 mm) diameter in liver.

Broken antlers

Damage was found on 73% of shed antlers ($n = 132$). Antlers with broken tips had on average two broken tips, and 36% of antlers had major breaks of tines and main beam (Fig. 2). Breakages consisted of two main beams only; 10 tines only; three main beams and tips; one main beam, tines and tip; 32 tines and tips; and 50 tips only. An extreme case was a male that died during the rut from fracturing the skull, with antlers remaining solely attached to skin. Not only were two tines and seven tips broken off, but both pedicles with portions of frontal, much of the parietal and craniodorsal portion of occipital bones were broken out such that the animal lost most of the upper brain case (Fig. 2). Additionally, deer and cattle have been observed eating bone or antlers. One ranch reported in 2009 on three free-ranging domestic cows that continued to deteriorate, and when eventually captured for checking, all had bones stuck sideways in the mouth preventing them from foraging.

Campylognathia (facial scoliosis) or bent-nose

Campylognathia affecting principally the maxilla, premaxilla, nasal bone and cranial portion of the mandible were found in two female and five male red deer individuals ($n = 776$). Case 1 was a female ~4 years old, in good condition, average size, reproductively active, and there were no indications of anatomical aberrations in the postcranial skeleton or other gross pathological changes (Fig. 3). Case 2 was a female yearling in good condition, and without indications of anatomical aberrations in the postcranial skeleton or other pathological changes. Although the body size was slightly larger than average, the head length was shorter than average due to the aberrant growth. The other five cases stemmed from males harvested by hunters, with ages between ~4–14 years (Flueck and Smith-Flueck 2011*b*). Of a total of 131 reported cases of campylognathia in cervids (MacNally 1989, 1992*a*, 1992*b*; Horsefield 1993; Prior 1993; Suttie and McMahon 1993; Suttie and Pearce 1994; Campbell 1995; Banwell 1999; the present study), only 12% defy the expected directional asymmetry according to the Coriolis effect (Suttie and McMahon 1993); however, the correlation is significant ($P < 0.001$).

Discussion

The general absence of ectoparasites on gross examination refers foremost to groups such as ticks, fleas and lice. Similarly, wild ruminants such as guanaco living in cold Patagonia are commonly devoid of ectoparasites (Karesh *et al.* 1998), although contact with sheep may lead to cross-contaminations. Infections with *F. hepatica* and *C. tenuicollis*, both cosmopolitan parasites, as well as with the exotic *T. o. krabbei*, are considered to have low pathogenic potential for otherwise healthy cervid hosts. Although it is not possible to differentiate between *T. o. ovis* and *T. o. krabbei* on morphological grounds with absolute certainty, red deer have been reported to be refractory to *T. o. ovis* infection, whereas other potential intermediate hosts such as cattle, goats, pigs and sheep have been shown to be refractory to *T. o. krabbei*. Possible or known definitive hosts in the study area include native felids such as *Puma concolor*, *Felis colocolo*, *F. guigna* and canids such as *Dusicyon griseus*, *D. culpaeus*, and domestic dogs. The adult stage of *C. tenuicollis*, the tapeworm *Taenia hydatigena*, is also found commonly in domestic and wild canids and felids in the region.

Ostertagia sp., *Bunostomum* sp. and *Dictyocaulus* sp. are also considered of low pathogenic potential to otherwise healthy cervid hosts, but the latter two can be a concern when deer are weak for other reasons. These parasites have been noted in Argentine Patagonia in livestock and wildlife, including red deer (Flueck and Jones 2006; Suárez *et al.* 2007; the present study).

In Chile, *Ostertagia* sp., *Capillaria* sp., *Bunostomum* sp., *C. tenuicollis* and *Dictyocaulus* sp. have all been found at low levels in free-ranging exotic fallow and red deer, whereas faecal exams from nine native huemul deer individuals showed only

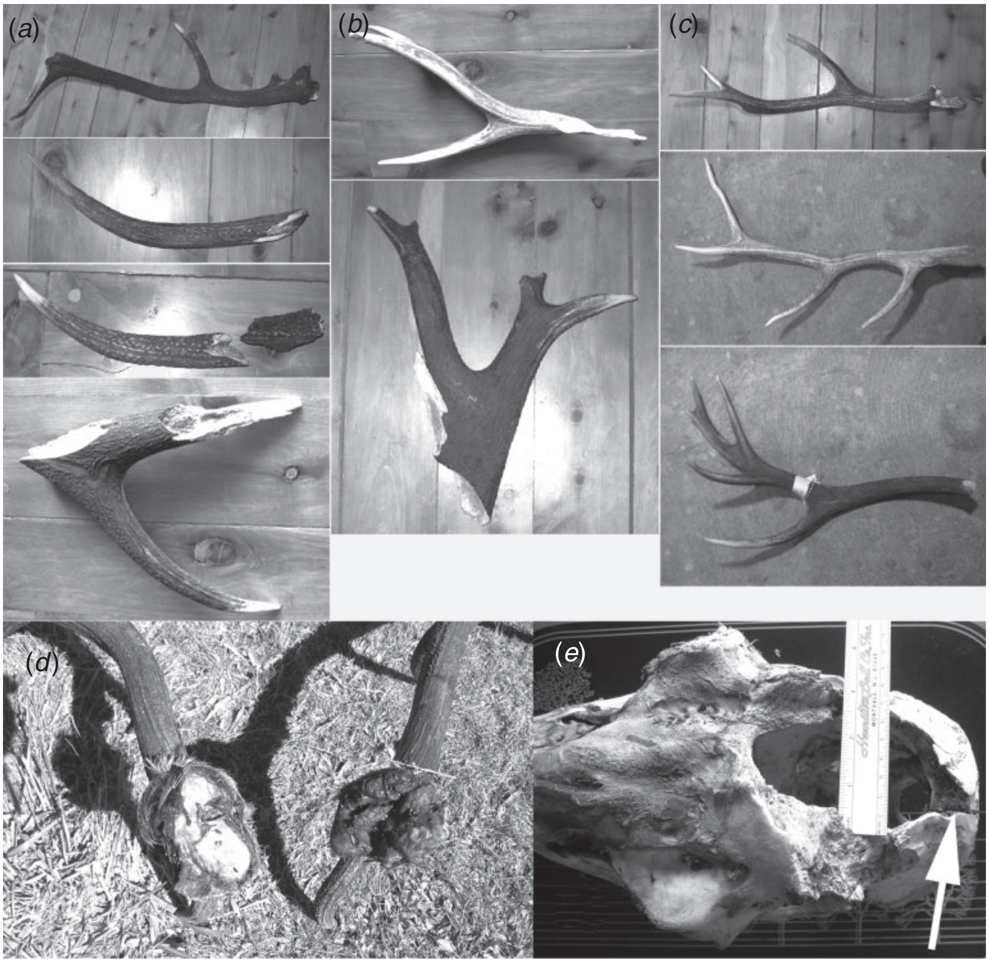

Fig. 2. Antler damage in red deer, including (*a*) broken tines, (*b*) broken crowns and (*c*) broken main beams. Skull fracture, including (*d*) bases of antlers as found and (*e*) dorsal view of cranium, with caudal part of frontals and most of parietal broken out. Note that the occipital is fractured and has the craniodorsal portion broken out (arrow).

very low egg or larval output; and in only three animals *Moniezia* sp. was confirmed and also considered to be harmless to huemul (Rioseco *et al*. 1979). Most of these parasites, considered in general to be non-threatening, are common in livestock and thus occur in most areas with livestock.

Huemul deer are frequently claimed to be highly susceptible to diseases such as *C. tenuicollis*, FMD, coccidiosis, 'parasites', or actinomycosis (Povilitis 1978; Redford and Eisenberg 1992; Simonetti 1995; Wemmer 1998; Lord 2007). According to Simonetti (1995), '*Cysticercus tenuicollis*, when transmitted by livestock is fatal to huemul'. However, the original source did not consider *C. tenuicollis* to have caused death, but rather the deterioration of the female after a premature parturition, aggravated by tight confinement and low variety of food (Texera 1974). Furthermore, in other cervids and ungulates, *C. tenuicollis* has little significance (Leiby and Dyer 1971). The frequently mentioned high susceptibility of huemul to coccidiosis is based on the only existing study on this topic; however, the original source questioned whether coccidiosis was the cause of death, because of many additional problems, again referring to limited space and poor nutrition (Texera 1974). A sheep arriving later to this pen had coccidia, but when the huemul died, it showed many other problems besides coccidia.

The presumptive case of mycobacterial infection would be a concern more for red deer production systems with high densities of animals. The present case stemmed from a high-density population of red deer at ~50 deer/km^2 (W. T. Flueck and J. M. Smith-Flueck, unpubl. data). The disease is widespread in Argentina, particularly related to dairy production, and has been recorded in the province of our presumed case (Perez *et al*. 2002), with a 10% prevalence in one studied Patagonian province (Torres 2011). As a zoonosis, it requires caution by people involved with wild deer. Similar lesions (parietal and pulmonary pleura, rumen, liver) have been described for white-tailed deer (*Odocoileus virginianus*) and red deer infected with *Mycobacterium bovis* (O'Brien *et al*. 2001; Glawischnig *et al*. 2006; Martín-Hernando *et al*. 2010).

FMD tests in deer were all negative, even though there had been a local outbreak in livestock 3 years earlier. Patagonia is declared free of FMD, although there are occasionally focal outbreaks, and northern Argentina has regular recurrences (FBZP 2007). Anecdotal accounts by settlers are cited to

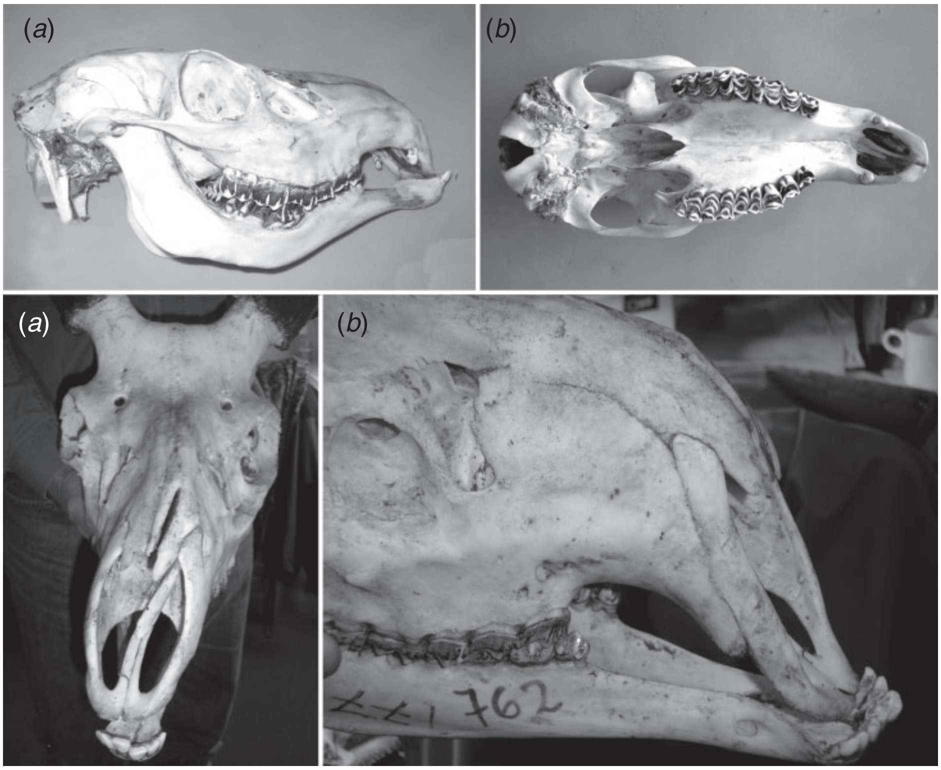

Fig. 3. Campylognathia in red deer affecting principally the maxilla, premaxilla, nasal bone and cranial portion of the mandible. Above, female with (*a*) lateral and (*b*) ventral views of scoliosis; below, male with (*a*) lateral and (*b*) ventral scoliosis.

claim that FMD via livestock was responsible for decimating Patagonian huemul over huge areas 60–70 years ago. In contrast, recent FMD outbreaks in the UK resulted in experimental studies of five cervid species that were all susceptible to FMD. On the basis of natural behaviour of these free-living deer in the UK, they are considered unlikely to be an important factor in the maintenance and transmission of virus during an epidemic of FMD in domestic livestock (Thrusfield and Fletcher 2002; Fletcher 2004). Earlier concerns about FMD spill-over from cattle to deer during an outbreak in 2001 in the UK proved to be unfounded; numerous samples from deer showing lesions suggestive of FMD proved to be negative (Davies 2002). There has been no evidence of wild deer being implicated in this epidemic, despite the fact that the deer population in UK was 10 times greater in 2001 than it was in 1967 (Davies 2002). At normal densities of cervids, FMD is considered a self-limiting disease (Morgan *et al*. 2003). The very low densities of huemul and reactions of other cervids to FMD renders those early anecdotal accounts by settlers doubtful. Additionally, even if FMD would reduce the population, after an outbreak is over and considering the documented annual rate of increase of 21% in Chile for huemul, a population would have recovered by 300% in only 6 years. Thus, claims that FMD decimated huemul populations in the past century are unfounded. Last, a recent review on FMD among several South American wild animal species considered susceptible to this disease found no reports of any previous disease events nor outbreaks in wildlife populations under field conditions (Pinto 2004).

The prevalence of antler breakage reported here was similar to that found in *C. elaphus* in California by Johnson *et al*. (2005), who suggested that it was related to copper (Cu) and/or phosphorus (P) deficiencies (Johnson *et al*. 2007). Moreover, bone and antler chewing in *C. elaphus* was suggested in response to calcium and phosphorus deficiencies in forage plants, and that such inadequacies were related to antler breakage (Bowyer 1983). There are no reports of Cu deficiency in this Andean region; however, P is low in part due to volcanic soils (Thomas *et al*. 1999). Given that the area has been exploited for >100 years without fertiliser replacement, P concentrations might have continued to diminish. The harvest of red deer alone represents an export of ~1.8 kg P/female, whereas removing from the system the antlers shed by a male that is harvested later at an average age of 8 years exports about a total of 7.2 kg of P per animal (Flueck 2009). Removing livestock from the systems exports additional substantial P, and the estimated overall export rate for P compares with rates measured in other extensive production systems which, in contrast, often receive 10–50 kg/ha.year of P as fertiliser to compensate for the losses from biomass exports.

Campylognathia can result from atrophic rhinitis, although restricted to suids (Lutz 1988). Factors such as abnormal fetal position, intra-uterine pressure, mineral deficiencies, or injuries from physical impacts have been suggested (MacNally 1989, 1992*a*), but all cases in cervids were from apparently healthy individuals. Arthrogryposis (inherited, viral or from teratogenic factors) in domestic ruminants is often associated with campylognathia (Bähr *et al*. 2003; de la Concha-Bermejillo 2003). Although wild North American cervids are often seropositive to viral infections causing campylognathia in livestock (Blackmore and Grimstad 1998), we found no reference of seropositive deer exhibiting campylognathia. Furthermore, causative Cache Valley or Potosi viruses have not been reported for southern Argentina (Camara *et al*. 1990). A female deer with facial scoliosis to the left was exported from New Zealand to Canada. There, she produced a daughter that also exhibited campylognathia but to the right, thus suggesting genetic (Suttie and Pearce 1994) or epigenetic inheritance. Nonetheless, there are many confounding variables possibly involved in deer living together and presenting similar pathologies. Genetic inheritance as a primary cause seems unlikely, given that the extensive red deer population in Patagonia (Flueck *et al*. 2003) resulted from 20 initial individuals (Franke 1949), and thus the original frequency would have had to be at least 5% (1 of 20) and is expected to remain so. Since the 1920s, no instances have been reported from this population, and the seven cases found represent <1% of deer revised by us. Thus, the origin of campylognathia in deer appears to be related to a non-inheritable developmental disorder. Primary causes are not known and might include congenital genetic aberrations, teratogenic compounds, infections and other epigenetic factors affecting developmental processes. The pronounced difference in developmental patterns with respect to hemispheres suggests that the disturbed developmental process may be influenced by geophysical factors such as the Coriolis force (see Suttie and McMahon 1993).

Inertial Coriolis forces arise when objects move linearly within a rotating spatial reference frame such as the earth. Any body movement not parallel to the earth axis will be affected by a transient Coriolis force that arises as the movement begins and decays as the movement ceases. For instance, humans subjected to artificial Coriolis forces cannot reach out and hit targets with their finger, until repeated attempts have corrected the responses of the central nervous system and motor compensations (Lackner and DiZio 2000). Similarly, Coriolis forces are constantly acting on arms or legs from limb movements made during voluntary body rotation; although they are not perceived, motor compensations for their presence are made, otherwise the movements would be inaccurate (Lackner and DiZio 2000). Furthermore, Coriolis forces affect early stages of development, such as movements of embryos within the uterus, while the mother herself moves about, causing Coriolis effects that affect innervation patterns of the mammalian vestibular system (Bruce *et al*. 2006). Geophysical forces even have subcellular effects, such as gravity influencing both the plane of bilateral symmetry and the orientation of microtubules in the vegetal pole region of the embryos (Kochav and Eyal-Giladi 1971; Fluck *et al*. 1998). These various systems affected by Coriolis forces all play roles in mammalian ontogeny, yet normal individuals grow symmetrical within the range of geophysical forces encountered on the globe. It is, therefore, conceivable that the networks processing these environmental cues, or the mechanisms responsible for compensation, are malfunctioning and thus result in a preponderance of facial scoliosis in accordance to the earth's rotation.

In conclusion, red deer were found to harbour a few diseases commonly associated with livestock and wildlife, with the only exception of *T. o. krabbei*, which, however, is a parasite of low pathogenic potential. Having been in Argentina for >100 years and in coexistence with livestock, both red deer and livestock play roles in the epidemiology of the various diseases they share. Regarding huemul deer, whereas livestock are commonly sympatric with them (probably 100% of huemul populations), spatial overlap with red deer is exceptionally rare, occurring in <2% of known populations, and is of recent time (Flueck 2010*b*). Even in this latter case, livestock presence is the determining epidemiological factor for disease spill-over, since in the one (of two) population, for each huemul, there were 1.2 red deer, but 25.2 livestock (Pastore and Vila 2003). Thus, for most, if not all, huemul populations, feral and free-ranging livestock plays a key role for spill-over of infectious and parasitic diseases. Research, conservation and management efforts should thus be directed towards finding appropriate solutions, including livestock herd health programs and restriction of free livestock movements, particularly where huemul still occur in protected areas. Livestock, being regularly researched and inspected at slaughter, provide a good proxy for the parasite community and other diseases afflicting sympatric red deer. Although sympatry between red deer and guanaco is common and substantial, including the formation of mixed groups, and has been suggested to affect the epidemiology of shared diseases (Flueck 1996; Flueck *et al*. 2003), we found no other reports expressing sanitary concerns. Uncontrolled importations of wild ungulates are of special concern if they involve cervids, due to 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. Last, mineral disorders, as indicated by the high prevalence of antler breakage, and in relation to extractive production systems, need to be further investigated.

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