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Review

Invaders without frontiers: cross-border invasions of exotic mammals

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Abstract

We address cross-border mammal invasions between Chilean and Argentine Patagonia, providing a detailed history of the introductions, subsequent spread (and spread rate when documented), and current limits of mammal invasions. The eight species involved are the following: European hare (*Lepus europaeus*), European rabbit (*Oryctolagus cuniculus*), wild boar (*Sus scrofa*), and red deer (*Cervus elaphus*) were all introduced from Europe (Austria, France, Germany, and Spain) to either or both Chilean and Argentine Patagonia. American beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) were introduced from Canada to Argentine Tierra del Fuego Island (shared with Chile). The American mink (*Mustela vison*) apparently was brought from the United States of America to both Chilean and Argentine Patagonia, independently. The native grey fox (*Pseudalopex griseus*) was introduced from Chilean to Argentine Tierra del Fuego. Few spread rates are available: the lowest are <10 km/yr and correspond to American beaver and American mink; intermediate rates are observed in muskrat and rather questionably, in grey fox; the highest rates (10–20 km/yr) are found among European hare and European rabbit. Because of their frequent migration, it is difficult to estimate the natural spread rate for wild boar and red deer. Not all mammal invasions in Chilean and Argentine Patagonia have been methodical advances of species; some involve an overlap of invasion fronts, with advances and retreats, and perhaps with re-invasions to different areas of either country. Because national policies with regard to introduced species may differ between countries sharing porous borders, it seems advisable to coordinate such policies in order to prevent the entry of unwelcome invaders.

Introduction

Human-aided vertebrate introductions have occurred all over the world. Generally small numbers of individuals of a given species have been purposely relocated and introduced to a specific region or country with the hope that they will survive, and eventually thrive and spread unaided to populate a vast region, no matter what the consequences (De Vos et al. 1956; Elton 1958; Roots 1976; Crosby 1986; Williamson 1996). Most concerns about the consequences of vertebrate invasions have emphasized economic losses and ecological impacts (Troughton 1947; Myers 1970; Kitching and Jones 1981, for Australia; Wodzicki 1950; Howard 1966; Gibb et al. 1978, for New Zealand; Jaksic and Yáñez 1983; Jaksic and Fuentes 1991; Jaksic 1998, for Chile). However, during the last decade, invasions have been considered a threat to biodiversity and ecosystem functioning, and an agent of global change that both impoverishes and

homogenizes the world's biota (Chapin et al. 1997; Sala et al. 2000).

Most of the attention to vertebrate invasions has come from certain regional or national concerns (Macdonald et al. 1988 for mediterranean regions; Navas 1987 for Argentina; Bonino 1995 for Argentine Patagonia; Jaksic 1998 for Chile). Borders between countries pose an interesting challenge. Politically, because the country where the initial introduction occurred is not concerned about what happens once a species spills over national borders, passive invasion then becomes the concern of the new host country. Ecologically, because the biotas invaded may differ in their susceptibility or resilience to invasions. Geographically, because landscape geomorphology determines flow corridors and flow barriers, especially when neighbouring countries are separated by tall mountain ranges. Historically, because the account of the introductions, releases, and subsequent invasions may be traced using contemporary archives.

The Patagonian region of South America is a good model system to look at for such border exchanges, and here we address cross-border invasions between Chile and Argentina, with the aim of learning the sources and paths of what we call invaders without frontiers, in this case of exotic mammals. Fortunately, there is a fair number of mammalian invasions that have a reasonably good historical database – even if it has to be dug up from the grey literature – thus permitting unusually detailed analysis of this case.

Chilean Patagonia currently harbours 13 of the 15 mammals that have been introduced to Chile (Jaksic 1998), while 'nearly all mammal species introduced in Argentina are found in semiarid Patagonia' (Bonino 1995), that is, 13 species. In our analysis, we have chosen to disregard those invaders that have not yet crossed the Chile–Argentina border (Fallow deer *Dama dama*, Axis deer *Axis axis* and Reindeer *Rangifer tarandus*), as well as the Norway rat (*Rattus norvergicus*), the black rat (*Rattus rattus*), and the house mouse (*Mus musculus*), which are chiefly restricted to human dwellings. This screening leaves us with eight species that have invaded both Chilean and Argentine Patagonia. We provide a detailed history of the introductions, releases, subsequent spread (and spread rate when documented), and current status of mammal invasions in Patagonia. We describe in general terms the economic and ecological impacts of Patagonian invaders, and consider management and policy concerns in Chile, the country that has most often acted as a host to invaders rather than as an exporter.

Study region and methods

Chile and Argentina are prime examples of countries sharing extensive borders, having in common about 4500 km from latitudes 22° to 54° centered at the continental divide and marked by the highest mountaintops along the Andes Range. Although the Andes seem a formidable barrier for cross-border movement, there are a variety of relatively low mountain passes through out the range. In addition, the Andes taper down steadily from ca. 33° southwards, and virtually disappear as a continuous wall ca. 43° southwards (in Patagonia, passes average 1000 m elevation; Murúa 1995). Chile and Argentina then share extensive areas of Patagonia, without a clear topographical divide, except for a few peaks and the divide of continental waters. In Argentina, Patagonia extends from the Chilean border and south of the Colorado River all the way to the southern tip of Tierra del Fuego Island (Figure 1 in Grigera and Rapoport 1983). In Chile, Patagonia does not have a clear geomorphologic reference to the north, but common usage considers Chilean Patagonia to begin at Palena Province (Region X) and to end at the southern tip of the continent (Cape Horn). As a result of shared biomes, including Patagonian steppe and *Nothofagus* forest, Chile and Argentina share most of their native vertebrate fauna in Patagonia (Vuilleumier 1968, 1972, 1985, 1991; Venegas 1986; Reise and Venegas 1987; Johnson et al. 1990; Kelt 1994), and also most of their exotic mammals (Bonino 1995; Jaksic 1998).

Chile is divided into 13 administrative Regions. All of them (except for the landlocked Metropolitan Region) include the Andes Mountains and the Pacific Ocean (Figure 1 in Jaksic 1998). Chilean Patagonia is contained within the southernmost third of Region X (Palena Province), and Regions XI and XII to the south. Argentina is divided into 23 provinces, of which five are included within Patagonia (Neuquén, Río Negro, Chubut, Santa Cruz, and Tierra del Fuego, arranged from north to south). The geographic coordinates of localities mentioned in this paper may be found in the gazetteers for Chile and Argentina (Instituto Geográfico Militar 1983; Paynter 1985, 1988; and in Appendices 2 and 3).

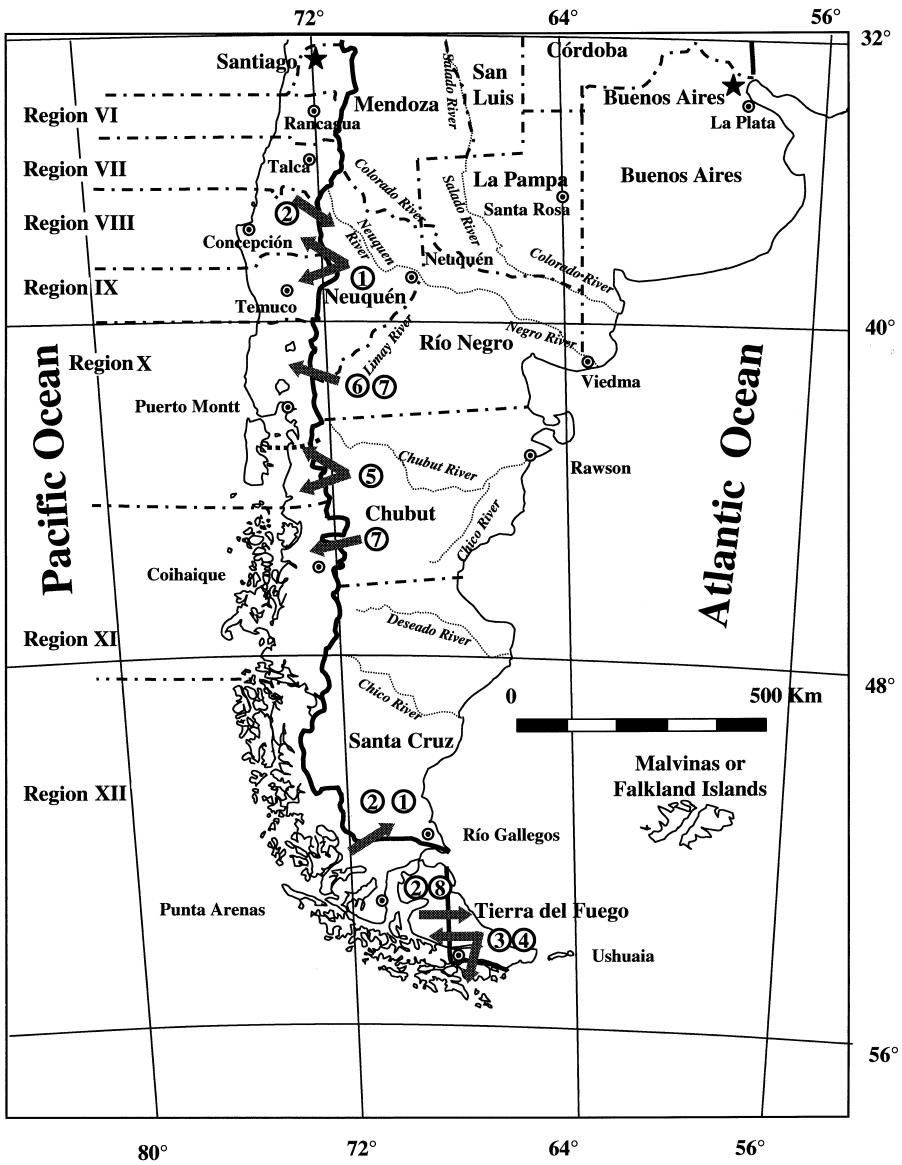

Figure 1. Map of Patagonia, which starts in Chile at the northern border of Palena Province, Region X (dotted line south of Puerto Montt), and in Argentina at the southern shore of the Colorado River, which marks the northern border of Neuquén and Río Negro Provinces. Highlighted are the political divisions (Regions in Chile, Provinces in Argentina), country capitals (stars), regional or provincial capitals (bull's eyes), major rivers, and major invasion paths (arrows) between Chile and Argentina. Codes for invasive species are: (1) European hare, (2) European rabbit, (3) American beaver, (4) muskrat, (5) American mink, (6) wild boar, (7) red deer, and (8) grey fox.

We conducted a literature review using the reference databases available in Simonetti et al. (1995) and Jaksic (1997, 1998) for Chile. We also took advantage of the databanks at the following internet addresses:

- http://www.bio.puc.cl/auco/artic02/carnivor.htm,
- http://www.bio.puc.cl/auco/artic04/micromam.htm,
- http://www.bio.puc.cl/auco/artic05/lagomorf.htm,
- http://www.bio.puc.cl/auco/artic06/mamotros.htm.

In Argentina, the literature is more dispersed, but the following sources were useful for tracing references: Daciuk (1978), Navas (1987), Massoia and Chébez (1993), Bonino (1995), and Grigera (1999).

Consultation with Chilean and Argentine experts aided in finding and retrieving grey literature.

Results

The historical results of our survey are presented in Appendix 1, where the details of species introductions and subsequent movements are described. European hare, European rabbit, wild boar, and red deer were all introduced from Europe (Austria, France, Germany, and Spain) to either or both Chilean and Argentine Patagonia; American beaver and muskrat were both introduced from Canada to Argentine Tierra del Fuego; American mink were apparently brought from the United States of America, to both Chilean and Argentine Patagonia, independently; the native grey fox was introduced from continental Chile to Chilean Tierra del Fuego Island and then it spread to the Argentine side of the island (Table 1, Figure 1). Therefore, seven of the eight invading mammals in Patagonia are alien species, or exotics.

European hare spread over Argentina from within, but it also invaded from the southernmost parts of neighbouring Chile. European rabbit spread separately from within in both central and Patagonian Chile, and then invaded Argentine territory from those two sources. American beaver and muskrat spread over Argentine Tierra del Fuego from within, and invaded the Chilean side of the island as well. American mink and red deer spread over both Argentina and Chile from sources within, but these two species also invaded from Argentina to Chile. Wild boar spread over Argentina from within, and then invaded Chile. Grey fox invaded from the Chilean side of Tierra del Fuego Island to Argentina's side of the island (Table 1, Figure 1).

European rabbit, wild boar, red deer, and American mink crossed the Chilean–Argentine border unimpeded by the Andes Range, likely using $<$1000-m passes. American beaver and perhaps muskrat, negotiated relatively large expanses of water (such as the 7-km-wide Beagle Channel) without much trouble. European hare and grey fox spread over relatively flat and open expanses, but crossed several major rivers in the process. There are few spread rates available: the lowest are $<$10 km/yr and correspond to American beaver and American mink; intermediate rates are observed in muskrat and rather questionably, in grey fox; the highest rates (10–20 km/yr) are found among European hare and European rabbit (Table 1). Because of their frequent migration, it is difficult to estimate the natural spread rate for wild boar and red deer.

Discussion

Geographical patterns of invasion

Not all mammal invasions in Chilean and Argentine Patagonia have been methodical advances of species; some involve an overlap of invasion fronts, with advances and retreats, and perhaps with re-invasions to different areas of either country. The picture that emerges from our review is that of the eight species currently present in both Chilean and Argentine Patagonia, three began their journey in Argentina (American beaver, muskrat, and wild boar), apparently on their own accord, unaided by humans. Two started in Chile (European rabbit and grey fox), also unaided by humans, except for their original release into the wild. The remaining three invaders had a mixed origin (European hare, American mink, and red deer); that is, they were introduced separately to Chile and to Argentina. In addition, these latter three species were apparently often relocated by human agents between Chile and Argentina, and are currently moving back and forth across the two countries on their own accord.

With the exception of American beaver, muskrat, and grey fox, the remaining five species have faced, and negotiated successfully, the barrier posed by the Andes Range, likely using low passes that render that barrier rather porous. American beaver and muskrat do not face altitudinal barriers within their distributional range, but have been able to cross relatively large expanses of water. The only invader that seems to be a prisoner of its success is the grey fox, which is confined to Tierra del Fuego Island and lacks the required swimming abilities.

Economic and ecological impacts of invaders

European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus)* are considered pests throughout Chile and Argentina. However, they are also highly lucrative wildlife commodities. Almost 55,000 tons of hare and rabbit meat were exported from Argentina during a 4-year period in 1976–1979 (Mares and Ojeda 1984; Jackson 1986). This represented over US$ 90 million (25% of the total income from wildlife products exported from Argentina during that period).

Table 1. The best-known introduction events in Chilean and Argentine Patagonia. The primary source is that country or region from which mammals were relocated originally; the secondary source is that restricted region or locality from where introduced mammals started spreading over their host region or country; the current area is the broadest political or geographical region in which introduced mammals dwell currently. The spread rates were obtained from original sources cited in the text.

Species	Primary Source	Secondary Source	Current area	Spread rate km/yr
European hare	Hamburg, Germany (1888)	Cañada de Gómez, Santa Fe Province	Pampas region of Argentina	18.6
European hare	France (1897 or 1898)	Tandil, Buenos Aires Province	Pampas region of Argentina	Unknown
European hare	Germany (1896 or 1907)	Última Esperanza, Region XII	Patagonia of both Argentina & Chile	20
European hare	Unknown, early 1900s	Valdivia and Osorno, Region X	Central & Northern Chile	Unknown
European rabbit	Spain (1884)	Cauquenes Lagoon, Region VI	Central & Southern Chile	Unknown
European rabbit	Chillán, Region VIII of Chile	Neuquén Province	Mendoza & Neuquén Provinces	7–16
European rabbit	Malvinas (Argentina) or Falkland Is. (UK)	Islands in Beagle Channel	Southern Tierra del Fuego (Chile & Argentina)	Unknown
European rabbit	Unknown, 1936	Porvenir, Chilean Tierra del Fuego	Northern Tierra del Fuego (Chile & Argentina)	Unknown
European rabbit	Magallanes, Region XII of Chile, 1970s	Última Esperanza, Region XII	Southwestern Santa Cruz Province	Unknown
American beaver	Canada, 1946	Southeastern Tierra del Fuego (Argentina)	Southwestern & central Tierra del Fuego (Chile)	2.7–6.3
American beaver	Canada, 1946	Southeastern Tierra del Fuego (Argentina)	Navarino Island (Chile)	3.1
Muskrat	Ontario, Canada, 1948	Southeastern Tierra del Fuego (Argentina)	Southwestern & central Tierra del Fuego (Chile)	10.8
Muskrat	Ontario, Canada, 1948	Southeastern Tierra del Fuego (Argentina)	Navarino Island (Chile)	3.9
American mink	USA, 1934–1936	Punta Arenas, Region XII	Did not invade	Not applicable
American mink	Argentina, 1967, 1968 and 1969	Coihaique, Region XII	Puerto Montt, Region X	Not applicable (relocated)
American mink	Unknown, 1930 or 1932, and 1935	Santa Cruz Province	Unknown	Unknown
American mink	Unknown, 1946 and 1968	Cholila, Chubut Province	Cholila & environs, Chile?	5.5–7.7
American mink	Cholila, 1952, 1963?	Lake Futalafquen, Chubut Province	Unknown	Unknown
American mink	Unknown, 1956	Sarmiento, Chubut Province	Sarmiento & environs	Unknown
American mink	Unknown, 1958	La Bolsa, Chubut Province	Unknown	Unknown
American mink	Unknown, 1960s	Río Grande, eastern Tierra del Fuego (Argentina)	Central & northern Tierra del Fuego (Chile)	Unknown
Wild boar	Siberia?, 1904–1906	Ranch San Huberto, La Pampa Province	San Huberto & environs, Collún-co (or Collunco)	Not applicable (relocated)
Wild boar	La Pampa Province, 1917–1922	Collún-co, Neuquén Province	Río Negro Province, & Chile	Unknown
Wild boar	Uruguay, 1924–1926	Ranch Bahía Huemul, Río Negro Province	Río Negro & Chubut Provinces	Unknown
Red deer	Carpathian Mountains, Austria, 1904–1906	Ranch San Huberto, La Pampa Province	San Huberto & environs, Collún-co	Not applicable (relocated)
Red deer	La Pampa Province, 1917–1922	Collún-co, Neuquén Province	Chubut & Río Negro Provinces	Unknown
Red deer	Collún-co, Neuquén Province, 1948	Lake Villarrica, Region IX	Regions IX, X, & XI	Unknown
Red deer	Unknown, 1973	Staten Island, eastern Tierra del Fuego	Only a few are left	Not applicable
Red deer	Germany, 1950s	From Temuco (Region IX) to Puerto Montt (Region X)	Regions IX & X	Unknown
Red deer	Argentina, 1950s	From Regions VII to X	Regions VII to X	Unknown
Grey fox	Magallanes, Region XII of Chile	Onaisín, western Tierra del Fuego (Chile)	Eastern Tierra del Fuego (Argentina)	7.7

Chile exported over four million pelts and skins of hares and rabbits during a 75-year period (1910–1984). This represented (by number) almost 73% of all official Chilean wildlife exports within that period (Iriarte and Jaksic 1986; Iriarte et al. 1997).

The establishment of the European hare in Argentina has resulted in competition with livestock for pasture and in damage to grasslands, crops, orchards, and forestry plantations (Bonino 1995). On the other hand, the European hare appears to have had beneficial effects on the native fauna, both by increasing the supply of prey to large predators, and by decreasing predation pressure on native fauna and on livestock. In Chile, Yáñez et al. (1986) investigated puma (*Felis concolor*) diet in Torres del Paine National Park (Region XII) and on neighbouring sheep ranches, and found that predation on European hares was high, while that on domestic sheep (*Ovis aries*) was low. Iriarte et al. (1991) reported on puma diet in the same Park and found that the main prey were native guanacos (*Lama guanicoe*) and European hare; native small mammals being scarcely preyed upon. Iriarte et al. (1991) also showed that pumas preyed more than expected on hares, due to abundance, and less than expected on guanacos, and that in areas with low guanaco density, pumas preyed on hares to a larger extent. In a separate paper, Iriarte et al. (1990) reported the eating habits of four native raptor species in Torres del Paine National Park and found that both black-chested eagle (*Geranoaetus melanoleucus*) and Magellanic owl (*Bubo magellanicus*) had a high incidence of European hare in their diet. The same two species were reported to depend strongly on hare in Argentine Patagonia (Hiraldo et al. 1995; Donázar et al. 1997, respectively). Similarly, scavenging raptors in Argentine Patagonia seem to depend heavily on the supply of hare carcasses (Travaini et al. 1998). On account of European hare being present in Patagonia for only a century, one is left wondering what were the respective diets and niche relationships between all these predators before hares were introduced (Novaro et al. 2000).

Similar to hares, the establishment and increase of European rabbit populations has at least proved beneficial for the culpeo fox (*Pseudalopex culpaeus*) and the black-chested eagle (*Geranoaetus melanoleucus*) in central Chile (Simonetti 1986; Pavez et al. 1992, respectively). In Argentine Patagonia, the Magellanic owl (*Bubo magellanicus*) is reported to depend strongly on rabbits (Donázar et al. 1997). On the other hand, rabbits have negative impacts on native vegetation. At least in Central Chile, rabbits have been shown to push native perennial herbs to protected zones under the canopy of shrubs (Jaksic and Fuentes 1980). In addition, rabbits browse extensively on shrubs and consume their seedlings (Simonetti and Fuentes 1983). Indeed, Fuentes et al. (1983) showed that rabbits not only destroy more seedlings than do native small mammals, but that their effect is quicker and more extended spatially.

The ecological success of the American beaver (*Castor canadensis*) and of the muskrat (*Ondatra zibethicus*) is surprising, because in both Chilean and Argentine Patagonia there is a native species with a similar niche, the South American nutria (*Myocastor coypus*). This latter species has been introduced to several countries in the Northern Hemisphere with notable success (where it is considered invasive, Lever 1977), but it has not impeded the spread of beavers or muskrats in its own native land. Both the American beaver and the muskrat are considered harmful to the vegetation in Chile (Miller and Rottmann 1976) and in Argentina (Bonino 1995). The first species, because in building its dams destroys trees by ringing them and inundates *Nothofagus* forests (Lizarralde 1993), and also alters the forest's nutrient dynamics (Lizarralde et al. 1996). Skewes and Olave (1999) showed that beavers in Chile's Region XII are seriously damaging over 5400 ha of native Southern beech forest (*Nothofagus pumilio*) by construction of dams and by direct consumption. The muskrat is considered harmful because through its tunnelling activities, it damages earthen dams and irrigation ditches, causing floods and loss of habitat.

The American mink (*Mustela vison*) is considered to be responsible for the decline of the South American river otter (*Lontra provocax*) and of the coypu (*Myocastor coypus*) in Argentina (Pagnoni et al. 1986), but data on the diet and habitat preferences of the two former species in Chile do not seem in line with this view (Medina 1997). Nevertheless, the American mink is considered a pest in Argentina, where it is said to kill native waterfowl, mammals, and fishes, as well as poultry and even newborn lambs (Bonino 1995). The unresolved issue of mink impact in invaded lands is well depicted in the old controversy between English ecologists (Lever 1977, Linn and Chanin 1978a,b).

Wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) are among the most invasive ungulates in both Chile and Argentina. Wild boar is considered harmful in Chile, especially for native bulbs (Miller and Rottmann 1976).

In Argentina, it is considered a pest not only because it uproots and tramples agricultural fields, but also because it '... preys on lambs, goat kids, newly born calves, and probably some small native fauna' (Bonino 1995). Regarding red deer in Chile, there is convincing information pointing out the serious damage that they inflict on native vegetation by browsing (Miller and Rottmann 1976; Ramírez et al. 1981; Eldridge 1983). Similar conclusions have been reached in Argentina (Veblen et al. 1989, 1992; Bonino 1995). In addition, red deer is said to outcompete two native deer species in Chile, the huemul (*Hippocamelus bisulcus*) and the pudu (*Pudu pudu*) (Povilitis 1981; Eldridge 1983).

The impact of grey fox (*Pseudalopex griseus*) on native fauna is currently unknown. It is smaller than its island companion culpeo fox (*P. culpaeus*), their diet overlap is moderate (63%), and they are essentially allopatric in Tierra del Fuego Island (Jaksic and Yáñez 1983; Jaksic et al. 1983). Thus, there is not much reason for expecting an ecological impact of the smaller fox on its larger companion. Massoia and Chébez (1993) believe that this fox may affect rare and endangered birds such as the Ruddy-headed goose (*Chloephaga rubidiceps)* by raiding its nests, but no firm evidence is available.

Control and monitoring of invasive species

Because we are familiar with Chilean, not with Argentine, legislation, we provide below the view from the country that more often acts as a recipient than as a donor of invaders.

In Chile, the governmental control and study of invasive species resides with the Ministry of Agriculture, specifically with the Agriculture and Livestock Service (SAG, in Spanish). Another branch of the same Ministry, the Forest Service (CONAF, in Spanish) is also concerned about invaders, but only if they enter national parks and reserves within the National System of Protected Wildlife Areas (SNASPE, in Spanish). The lion's share of the SAG's task rests with the Department for the Protection of Natural Resources (DEPROREN, in Spanish). SAG, as a whole, has been developing a national programme that includes legislation, research and control programmes. The main aims are: (1) to ban the introduction of potentially invasive species into Chile, even if intended for captive facilities; (2) to prevent the escape of captive individuals; (3) to monitor invasive species populations; (4) to prevent the spread of exotic species to areas where they are not present; (5) to reduce the impact of invaders on native species and their habitats; (6) to promote public education on the impact of invasive species; (7) to assess the potential economic use of invasive species; (8) to set up agreements concerning invasive species with countries that border Chile (Argentina, Bolivia, and Peru).

Toward the achievement of the above goals, the following Chilean legislation is invoked and applied: (1) The Agricultural Protection Act; (2) The Livestock Protection Act; (3) The Fishing Act; (4) The Protected Areas Act; (5) The Wildlife Act. Several of these laws are new, and some specifically include the regulation of species introduction. For instance, the Wildlife Act (Law No. 19,473 of 1996) regulates the import and export of wildlife specimens, including seeds, eggs, spores, or any other biological material capable of propagating in the wild. Therefore, a special permit is needed to import exotic species into Chile, and for their release into the wild. This law also bans the relocation of any native species outside its natural geographic distribution. The penalties for violating this law are a maximum of 3 years in prison, and a fine of up to US$ 10,000. In addition to the country's laws, Chile enforces international agreements such as the Convention on International Trade of Threatened Fauna and Flora (CITES), the Convention on Wetlands (Ramsar), the Convention on Migratory Species (Bonn), and the Convention on Biodiversity (Rio de Janeiro), which regulates the introduction of exotic species in one way or another.

Chilean law involves animal and plant quarantines and strong regulations governing importation. The government has recently appropriated a relatively large budget to improve the control of exotics at international borders and facilities. Most measures are based on an assessment of the risk posed by exotic species and their potential pathways of entry. SAG personnel confiscates from 2000 to 3000 non-native animal specimens every year. The species most commonly confiscated are monkeys (squirrel monkey, common marmoset, capuchin monkey, howler monkey, spider monkey, woolly monkey), parrots (*Amazona* parrots, hyacinth macaw, blue-yellow macaw), land turtles or tortoises, passerine birds, flamingos, and snakes. In order to control the introduction of exotic species into Chilean territory, SAG personnel patrol more than 80 border passes, including marine ports and international airports. In addition, SAG has been developing scientific studies on priority species, and has created a Risk Assessment System for controlling introductions.

Through SAG, the Chilean government has also established joint research and control programmes with Argentina for species such as boar, beaver, rabbits and hares. All information collected is analysed using geographic information systems (GIS) that allow making decisions about the best control methods.

More specifically, during the last decade, SAG has implemented several projects to reduce the impact of introduced species on natural habitats and on native species. Some of the most important invasive species research and control programmes in Chilean Patagonia are: (1) European hare and rabbit population control, Regions XI and XII; (2) wild boar population control in Vicente Pérez Rosales National Park, Region X; (3) mink dispersal control, Regions X and XI (Ruiz et al. 1996); (4) potential of mink fur for use in handcrafts, Region XI; (5) American beaver and muskrat population control in Tierra del Fuego Island, Region XII (Skewes and Olave 1999).

Conclusion

In comparison to neighbouring Argentina, Chile seems to be in a better position to discourage naturally expanding potential invaders on account of the formidable barriers posed by the Atacama Desert to the north, the Pacific Ocean to the west and south, and the Andes Range to the east. However, we have shown here that the Andes Range is rather vulnerable to mammal invasions, and also that when invaders have established in Chile or in Argentina, they have quickly spread throughout the country, leaving behind a trail of suspected or detectable detrimental effects on native flora or fauna.

The permeability of the Andes Range is especially worrisome when one considers potential invaders in waiting on both sides of the divide. In Chile, Fallow deer (*Dama dama*) are just holding their ground and the fate of introduced Reindeer (*Rangifer tarandus*) is unknown (Jaksic 1998), but these two species are successfully established in the wild in Argentine Patagonia (Bonino 1995). In Argentina, Axis deer (*Axis axis*) and Antelope (*Antilope cervicapra*) seem to be so successfully established that from 1976 to 1979, a total of 56,000 kg of meat from these deer was exported (Ojeda and Mares 1982; Mares and Ojeda 1984). An eye should also be kept on two other potentially invasive deer: the Corzo deer and the Black buck. In 1990, 54 Corzo deer (*Capreolus capreolus*) were introduced from Austria to the surroundings of Osorno city (Chile's Region X). Presently, the population consists of over 500 individuals and the Chilean Government has requested several studies to analyse the potential impact of Corzo deer on native species. Another ungulate introduced to Chile for hunting purposes is the Black buck (*Antilope cervicapra*), which is already widespread in seven Argentine Provinces close to the Chilean border.

Because national policies with regard to introduced species may differ between countries sharing porous borders, as exemplified here by Chile – Iriarte and Jaksic (1986), Iriarte et al. (1997), and Argentina – Ojeda and Mares (1982), Bonino (1995), it seems advisable to coordinate such policies in order to prevent the entry of unwelcome invaders.

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Appendix 1. Historical account of the eight species analysed in the text

1. *European hare* (Lepus europaeus)

Daciuk (1978) and Grigera and Rapoport (1983) provide coincident and detailed accounts of the introduction of hare into Argentina: 36 hares were imported from Hamburg, Germany, in 1888 by Mrs Engelbert and Woltje Tieljen (then German Consul in Rosario) and were released at La Hansa Ranch (property of Mr Nelson Tilgen), near the town of Cañada de Gómez, Santa Fe Province. Navas (1987) provides a similar account but states that only four pairs of hare were released. According to Grigera and Rapoport (1983), a separate introduction was effected from France in 1897, by Mr Emilio Delpech to a ranch near Tandil, Buenos Aires Province. But according to Daciuk (1978), those French hares were imported by Mr Sulpicio Gómez in 1897, and when the stock failed to take hold, another batch was brought the following year, 1898. Navas (1987) states that those hare were either from France or Austria, and that a later (undated) introduction was effected at ranch Las Isletas, San Luis Province. In

two newsletters issued by agricultural societies of Argentina, it was reported that by 1897, hare had already reached the status of pests from Cañada de Gómez to the vicinity of Córdoba city (Daciuk 1978). Nine hares of unknown origin were also released in 1930 somewhere in Santa Cruz Province. The number of hare increased rapidly, and by 1907 they were declared a pest in central Argentina by the federal government. Simpson (1936) found that in the area of Lake Colhué-Huapi, hares were abundant and so he wrote in his journal (27 October 1930) that 'European hares were introduced into Patagonia a few years ago by some very misguided souls and now have overrun the country, threatening to do in the native and more valuable fauna.' The European hare currently occupies most if not all of Argentina (at least 2,700,000 km^2 according to Amaya 1981), with the only exception being Tierra del Fuego Island (Navas 1987). Considering Cañada de Gómez as the main point of dispersal, Grigera and Rapoport (1983) estimated a dispersal rate of 18.6 km/yr. Nevertheless, these authors considered that the spread of hare in Patagonia originated from a different introduction, in southernmost Chile.

Hares were imported to Chile from Germany in 1896 and were introduced into the area of Última Esperanza Province, Magallanes (Region XII). Some settlers in the region believed that it was later, in 1907. Howard (1969) suggested that the site of release was at the headwaters of the Gallegos River (Argentina), and Markham (1971) that is was in southwestern Santa Cruz Province, Argentina. Taking 1896 as the year of the dispersal of hare in Patagonia (both Chilean and Argentine), the spread then occurred at a rate of 20 km/yr (Grigera and Rapoport 1983), disregarding any human agency. Also in Chile, hares were released in the vicinity of Valdivia and Osorno cities (Region X) in undated years of the 1900s (Grigera and Rapoport 1983). Housse (1953) reported that in 1921, two pairs of hare were introduced to the largest island in Aculeo Lagoon, to the south of Santiago (Metropolitan Region), and that within a few weeks they swam across the 500-m stretch that separates the island from the mainland. Oliver (1946) stated that hare appeared in the Concepción metropolitan area (Region VIII) on an unknown date, but that starting in 1926 they had become recognised agricultural pests. Greer (1965) indicates that hare arrived from Argentina into Malleco Province (Region IX) sometime before 1928, but does not clarify if the animals crossed the border freely or were introduced from Argentina. Housse (1953) points out that hare crossed the Andes on their own in 1931, fleeing a drought in Argentina, and that they used the Diguillín River Valley (southeast of Chillán city, Region VIII) to spread into Chile. According to the same author, hare reached southwest to Purén town in 1933, having covered 120 km in fewer than 3 years. This is an unrealistically fast spread and speaks in favour of humans having transported hare intentionally over extended distances before releasing them.

Currently, European hares are found throughout the continental Chile from the Copiapó River (Region III) to the continent's terminus, and their greatest abundances are recorded in Regions XI and XII (Iriarte et al. 1997). Nowadays, it is considered common in Última Esperanza and Magallanes Provinces (Venegas and Sielfeld 1998). Interestingly, the hare has not crossed the Strait of Magellan east to Tierra del Fuego (Goodall 1979; Pine et al. 1979; Amaya 1981; Massoia and Chébez 1993; Bonino 1995). Although Pine et al. (1978) listed hares as present on Observatorio Island (Año Nuevo Is.), and Massoia and Chébez (1993) are convinced that they were mistaken for European rabbits (*Oryctolagus cuniculus*). Miscellaneous observations on hare distribution and abundance in Chile have been documented by Pine et al. (1979), Dietrich (1984), and Johnson et al. (1990). Regarding hare abundance in Chile, Dietrich (1984) extrapolated from night-counts in Purranque town, near Osorno city (Region X) during May 1982, to 0.3 hare/ha and discussed that this figure was very low in comparison with Europe. Johnson and Franklin (1994) conducted walk-transect censuses from 1987 to 1989 in Torres del Paine National Park (Region XII) and estimated 0.248 hare/ha in low-quality habitats, and 0.866/ha in high-quality habitats.

2. *European rabbit* (Oryctolagus cuniculus)

Jaksic and Fuentes (1991) and Zunino (1989) made thorough and largely coincidental historical descriptions of the introduction of the European rabbit into Chile. Their findings were summarised by Jaksic (1998). There were roughly two geographical areas where rabbits were released, central and southernmost Chile. According to Lataste (1892), rabbits were first introduced from Spain into central Chile in 1884, to the unnamed island that existed in Cauquenes Lagoon (Chile's Region VI), from which they escaped when an extended drought enabled the connection of that island to solid ground. These 'northern' rabbits expanded their geographic distribution both to the north and south of the country. According to Zunino (1989), their northernmost distributional boundary is Quebrada Honda Bay (Region III), and their southernmost one is Paillaco town (Region X).

A cross-boundary invasion occurred when 'northern' rabbits crossed over the Andean Cordillera from Chillán city (Region VIII) toward Argentina. Howard (1969) reported that rabbits had apparently entered northwestern Neuquén Province at about 36°80′ W between 1945 and 1950. They apparently took advantage of the relatively low passes (<1800 m elevation) that provide fairly good rabbit habitat during summer in terms of forage availability and protective shrubs. Rabbits were first spotted at the headwaters of the Neuquén River, a tributary of the Negro River. Howard and Amaya (1975) surveyed the area in 1969 and noted that rabbits occupied 31,000 km^2 having spread north to the neighbouring Mendoza Province. In 1972, rabbits had spread an additional 3000 km^2 to the north, south and east of their former range. They had crossed the Colorado River to the north, and the Neuquén and Agrio Rivers to the south. Since their crossing of the Andes, rabbits averaged 16 km/yr until 1969, but including their later expansion until 1972, this average reduced to 8 km/yr. Bonino and Amaya (1984) pursued the study further during 1975 and 1978. In 1975, the northern expansion of rabbits had not proceeded beyond the limit of 1972; it was rather slow to the east, and faster southwards. In 1978, the situation was similar to that described for 1975: apparently rabbits were not able to cross the Colorado River to the north and east, but were proceeding southward toward the Aluminé River, a tributary of the Limay River. Up until 1978, the area of expansion of rabbits was 45,000 km^2. Bonino and Amaya (1984) estimated rabbit density at 83–114 individuals/ha (sic) in suitable habitats. Bonino and Gader (1987) updated all previous information to 1982 and 1986. They commented that there was no further advance toward the south, but that from 1982 to 1986 rabbits had advanced southeastwards by 40 km (10 km/yr). Toward the east, the advance was similar: 40 km in 4 years. Toward the north, rabbits surpassed the Grande and Malargüe Rivers, and are now approaching the Salado River. In this latter case, rabbits have advanced 100 km from 1972 to 1986 (14 yr), that is 7 km/yr. According to Bonino and Gader (1987), rabbits in continental Argentina already occupied 50,000 km^2.

A separate introduction of rabbits occurred on Argentine Tierra del Fuego Island, which was detailed by Jaksic and Yáñez (1983) and by Massoia and Chébez (1993). These 'southern' rabbits were brought around 1880 by Mr Thomas Bridges from the Malvinas (or Falkland) Islands, which in turn were brought from France (Jaksic and Yáñez 1983). These rabbits were introduced to a number of islands on the Beagle Channel, from where they spread throughout southern Tierra del Fuego. Rabbits were also introduced to San Juan de Salvador Bay at the end of the XIX century (Payró 1898, in Schiavini et al. 1999) and in 1902 were released on Observatorio Island (Schiavini et al. 1999). They were also transported during the 1950s to several islands near Ushuaia by the Argentine Navy. Even as late as 1973, rabbits were introduced to Staten Island (Massoia and Chébez 1973). Amaya and Bonino (1980) reported densities of 54–69 rabbits/ha in suitable habitats.

Yet another introduction was made on Chilean Tierra del Fuego Island (Region XII) by a sheep rancher at Santa Ana Point, near Porvenir town, across the Strait of Magellan from Punta Arenas city. Two pairs of rabbits set free in 1936 originated the largest ever irruption of rabbits on Tierra del Fuego Island, spreading to all the northern (steppe) confines of the island and reaching its peak during 1950–1953 (Jaksic and Yáñez 1983). Arentsen (1953) estimated that rabbits averaged 30 individuals/ha during that period and were spread over 1 million ha, with a range from 12/ha to 50/ha (Godoy 1963). This same author indicates that in 1953 rabbits had already reached Argentine Tierra del Fuego, spread from the Chilean border north to Cape Espíritu Santo, east to San Sebastián Bay, and south to beyond Río Grande city. By December of 1953, a density of 5.5 rabbits/ha was estimated to be spread over 550,000 ha. Decisive control by sheep ranchers later pushed rabbits to the south of the Grande River, thus reducing their occupancy of Argentine Tierra del Fuego to 12,000 km^2, with densities ranging 39–70 rabbits/ha (Bonino and Amaya 1984).

How rabbits crossed – or were transported across – the Strait of Magellan to the mainland is unknown (Vargas 1998). Osgood (1943) documents that he saw small numbers of rabbits in the vicinity of Punta Arenas city during December 1939 and February 1940. Johnson et al. (1990) indicate that rabbits were introduced in the 1970s to continental Chilean Patagonia, but they refer to Ferriere et al. (1983), where no such claim is made. Johnson et al. (1990) pointed out that rabbits are found within a few kilometres of Torres del Paine National Park (Region XII). Perhaps rabbits migrated north from around Punta Arenas city, Magallanes Province. Or, as suggested by Vargas (1998), they escaped from captivity at Colonia Isabel Riquelme (a village to the south of Puerto Natales city), Última Esperanza Province, sometime before 1980. Whatever their origin in this latter province, they were estimated to number from 10 to 117 rabbits/ha in different sites (Latorre 1987). Today, rabbits are considered common in continental Chilean Patagonia (Última Esperanza and Magallanes Provinces) and quite reduced to near eradication from Chilean Tierra del Fuego (Venegas and Sielfeld 1998). Bonino and Gader (1987) noted that rabbits were appearing in El Turbio village (southwestern Santa Cruz Province, Argentina) and that they were arriving from the Puerto Natales region in Chile.

3. *American beaver* (Castor canadensis)

American beaver was first introduced on the Argentine side of Lake Fagnano, shared by Chile and Argentina on Tierra del Fuego Island in November 1946 (Massoia and Chébez 1993, not 1944 as stated by Goodall 1979, not 1948 as stated by Navas 1987, and not 1956 as stated by Markham 1971). Twenty-five mating pairs of beavers were introduced by the Secretary of the Navy of Argentina in the northeastern part of Fagnano Lake (or Cami), around the Claro River (Godoy 1963). These beavers were flown in from somewhere in Canada (Daciuk 1978). By November 1947, tracks of adult beavers were already joined by those of juveniles (Massoia and Chébez 1993). In 1963, beavers had already spread to several rivers draining into Fagnano Lake, and their hunting or trapping was prohibited by the government (Godoy 1963). Hunting was authorised starting in 1981 (Lizarralde 1993). Following a northwestern course along the Claro River, beaver reached Yehuin (Jhuin) Lake by the mid-1960s (Daciuk 1978). Until 1993, beavers were distributed from the Carmen Silva (or Chico) River in the north, and south to the Beagle Channel shoreline, encompassing a geographical range of about 20,000 km^2, almost all of Argentine Tierra del Fuego. They occupied 91% of all streams in the 53 watersheds within Argentine Tierra del Fuego (Lizarralde 1993).

Markham (1971) established the first published record of beavers on the Chilean side of Tierra del Fuego, specifically in Lynch and Blanco Lakes (to the west of Fagnano Lake), and along the basin of the Grande River. According to Skewes and Olave (1999), beaver first appeared in Chilean Tierra del Fuego on the western part of Fagnano Lake in 1964. They were subsequently sighted from 1972 to 1974 in Timaukel village, in 1974 in the Moneta and Chico Rivers, in 1979 in San Sebastián village, in 1986 in the China Creek River, in 1987 in the Calafate River, in 1990 in the Oro River, in 1995–1996 in Puerto Nuevo village, and in 1996 in the Altos de Boquerón Hills and the Cordón Baquedano Hills. In January 2001, DRM spotted a beaver dam in the Calafate River (at 52°43′35″ S; 68°54′05″ W). Because no trees are available in that steppe area, the dam was built with branches of the shrub 'romerillo' (*Chiliotrichum diffusum*), together with some discarded pieces of woodplank (old apple boxes). From this spot, the Calafate River stretches for some 10 km before reaching the southern shore of the Magellan Strait at a locality called Lomas Bay. Skewes and Olave (1999) calculated that from their release point on eastern Fagnano Lake to their appearance on western Fagnano Lake, the beaver took 18 years to cover 70 km (3.9 km/yr), and took 26 years to reach Cameron village, 150 km to the west (5.8 km/yr). To span the distance from Cameron village north to Onaisín village (40 km), the beaver took 15 years (2.7 km/yr), and from Onaisín village north to the head of the Oscar River (50 km), they took 8 years (6.3 km/yr). Thus, beavers appeared to be following a northwest-bound path of colonisation within Chilean Tierra del Fuego.

Nevertheless, Sielfeld and Venegas (1980) reported that beaver arrived in 1962 and colonised most watercourses on Navarino Island (south of the Beagle Channel, in Chilean territory) and also on Dumas Peninsula on Hoste Island. These beavers had reached across the Beagle Channel (ca. 7 km wide), from Argentina to Chile, on their own accord, unaided by human introductions. Indeed, beaver had been observed by Argentine Navy tactic frogmen (Massoia and Chébez 1993), swimming across the Beagle Channel toward Gable Island (Argentina) and then toward Navarino Island (Chile). Therefore, 'Argentine' beavers have also been spreading southward. Skewes and Olave (1999) calculated that from their release point on eastern Fagnano Lake, beavers took 18 years to reach Navarino Island, 55 km to the south (3.1 km/yr).

Massoia and Chébez (1993) report that by then there were some 6000 beaver colonies in Argentine Tierra del Fuego, affecting a forest area of about 5200 ha. Lizarralde (1993) estimates that there are about 25,000 beavers in that same area. Skewes and Olave (1990) estimate that there are about 41,000 beavers in Chilean Tierra del Fuego and close to 20,000 on Navarino Island, seriously damaging more than 5400 ha of southern beach forest. Previously, Sielfeld and Venegas (1980) estimated the presence of 8400 to 13,000 beavers on the 2000 km^2 Navarino Island (4.2–6.7 individuals per km^2). In Chilean Tierra del Fuego, Skewes and Olave (1990) estimated the presence of 0.15, 0.64, and 1.91 colonies/km of stream in the northern, central and southern parts of the island, respectively. They also estimated 1.1 colonies/km of stream on Navarino Island. In Argentine Tierra del Fuego, Lizarralde (1993) estimated 0.2–5.8 colonies/km of stream. This latter figure is higher than those reported in New Brunswick, Canada (1.25 colonies/km of stream) and in Wyoming, USA (0.9 colonies/km; Lizarralde 1993).

The beaver today seems to be confined to Tierra del Fuego Island and surroundings across the Beagle Channel (e.g. Navarino, Picton, Lennox, Nueva, and Hoste Islands; cf. Sielfeld and Venegas 1980; Lizarralde 1993). Its northernmost limit in Tierra del Fuego has already surpassed the boundary between the southern beech forest and the Patagonian steppe (Lizarralde 1993; Jaksic 1998; Skewes and Olave 1999). It now extends all the way up to an imaginary line stretching from the Oro River to San Sebastián village (Chile) and to the Carmen Silva or Chico River (Argentina). In the south, beavers were able to swim either north from Navarino Island or west from Tierra del Fuego, to Dawson Island, where they arrived ca. 1990 (Skewes and Olave 1999). Thus far, beaver have not crossed north of the Strait of Magellan and reached the mainland. However, the fact that a few individuals were killed in Parrillar Lagoon, close to Punta Arenas city, indicates that some illegal attempts at introduction have already been made (Venegas and Sielfeld 1998; Skewes and Olave 1999).

4. *Muskrat* (Ondatra zibethicus)

The muskrat was first introduced in 1948 (Massoia and Chébez 1993; Bonino 1995) and not in 1944 (Goodall 1979), nor in 1956 (Markham 1971) in the surroundings of Yehuin (Jhuin) Lake – on the Argentine side of Tierra del Fuego Island – from where it invaded the Chilean side (Markham 1971). Massoia and Chébez (1993) provide a detailed account of this introduction, specifically about the original release of 75 males and 150 females. Muskrats were brought from Port Rowan, Ontario, Canada, by the Secretary of the Argentine Navy. They were released in small groups during April 1948 at several lakes, including Yehuin and Colorado, rivers including Olivia and Bonpland, and many lagoons (Massoia and Chébez 1993). By 1954, muskrats were declared vermin and elimination by all means was permitted (Daciuk 1978). Specimens were captured during 1981–1982 in southern parts of Tierra del Fuego, including Ushuaia city, Bridges Island, and Gable Island, located in the Beagle Channel (Massoia and Chébez 1993).

According to Markham (1971), from their points of release, muskrats dispersed toward the north and the south of the Chilean side of Tierra del Fuego. To the north, they were observed in May 1971 at Onaisín village, and had also been seen at San Sebastián village (Pine et al. 1979). On January 2001, DRM found evidence of muskrat activity and actually spotted one individual at the lagoons created by beaver dams at the Calafate River (see account of American beaver, above). To the south, muskrat presence was first reported by Rosenmann (1961) on Navarino Island, who noted that they were quite abundant on the island in January 1960 and commented that they had arrived 5 or 6 years before (1954 or 1955) from across the Beagle Channel (ca. 7 km wide). Sielfeld (1977) observed muskrats on Hoste Island, to the south of Navarino Island. Up to now, the muskrat seems to be fully confined to Tierra del Fuego and surrounding islands. It has not reached the mainland (Venegas and Sielfeld 1998).

Using the same calculation basis as Skewes and Olave (1999) for beaver, it may be estimated that muskrat took 24 years to advance from eastern Fagnano Lake to its western fringe, and then to Cameron village and to Onaisín village, a distance of 260 km. That is a spread rate of 10.8 km/yr. By the same token, muskrat may have taken 14 years to reach Navarino Island (Chile), 55 km to the south (3.9 km/yr). Muskrat in central Europe have been estimated to spread at a rate of 10.9 km/yr before eradication campaigns, and at 5.1 km/yr when control measures have been in effect (van den Bosch et al. 1992, Williamson 1996). Therefore, the spread of muskrat within Tierra del Fuego is in line with figures from central Europe.

5. *American mink* (Mustela vison)

According to Lariviere (1999), 'The current distribution of *M. vison* in South America is unknown.' However, we seem to know enough about its distribution in the southern cone of the continent. The first imports of American mink to Chile were made by Mr Edmundo Pisano during 1934 and 1936. An unknown number of mink were imported to Punta Arenas city (Region XII) from somewhere in the USA Mink were apparently kept and pelts were sold at Mr Pisano's establishment until 1950, when he terminated this business. He sacrificed part of the stock and sold the remainder to another establishment (unknown owner and location), which in turn went under in 1970. During 1968 and 1970, Mr Hernán Pisano and partners (relationship to Mr Edmundo Pisano is unknown), started a new mink-raising farm in Punta Arenas city, but it failed. No further attempts at introduction seem to have been made in this region and no minks have been seen in the wild since (Sandoval 1994).

In the neighbouring Region XI (to the north), the first imports of American mink were effected in 1967. González and Lagos Inc. imported, from somewhere in Argentina, two batches of 110 live mink each to the neighbourhood of Coihaique city. During 1968, the same enterprise imported another batch of 720 mink, followed by a third one of 60 mink in 1969. In 1973, Pavez Castillo Bros & and Co. imported 100 live mink to Coihaique city from Mar del Plata city and from Sarmiento city, both in Argentina. Due to negative economic returns, these two enterprises ceased their mink-raising activities, but not before selling part of the stock as pelts and releasing the rest into the wild (Sandoval 1994).

Up north in Region X, the same González and Lagos Inc. from Coihaique city seem to be responsible for selling mink during the 1970s to prospective raisers from Puerto Montt city. Here, mink-raising again failed to live up to economic expectations, and part were sold as pelts and part were released. Some of those released mink may have reached Puyehue and Vicente Pérez Rosales National Parks (both in the Region X), causing CONAF (Chile's National Forestry Corporation) to hire experts in 1995 to control mink in those national parks (Ruiz et al. 1996). Navas (1987) raises the intriguing possibility that those mink may be descendants of an early introduction effected

in 1940 at Lake Todos Los Santos, but he does not cite the source of his information. Murúa (1995) indicates that mink have been detected around Valdivia city, and Medina (1997) states that the species is now widely distributed between latitudes 39° and 46°15′ S.

Further north in Chile, in 1957, Mr Bernardo Schmutzer in Los Angeles city (Region VIII) and Mr Sergio Hirmas in Longaví town (Region VII) started new mink-raising farms, but they failed (Bidegain 1963). In 1975, Mr Sergio Calonge started yet another farm in Los Angeles city (Region VIII), which failed as all preceding ones (Sandoval 1994). The reason for failure in these two cases was pure economics: costs exceeded returns. Currently, no mink are found in the wild in Region VIII.

Feral mink now in Chile were not only released from farms in Regions XII, XI, and X; they also entered as escapees from farms in Argentina. According to Daciuk (1978), the first attempt at mink introduction into Argentina occurred in 1930 in Santa Cruz Province, but it failed. Although according to Pagnoni et al. (1986), the first import of American mink was made in 1932, but it did not prosper (García Matta 1982). It did succeed in 1935, when García Matta established the first successful mink-raising farm in Argentina. No follow-up to this introduction seems to have been undertaken, unlike in Chubut Province (see below).

In Argentina, the first mink farm was established in 1946 near Cholila town (northern Chubut Province) by Mr R. Errasti, and it was in operation until 1974. The second one was established in 1952 by Mr Braeze in the northern arm of Futalafquen Lake (Chubut Province), and it lasted until 1963. Another farm was set up in Cholila town again in 1968, by Mrs S. Torres and Mrs J. Nicoletti. This farm collapsed, with part of the stock released into the wild and part sold to Mr U. Denicola, who set up his operation on an unknown date (1968?) near Futalafquen Lake, and which lasted until 1971. In Sarmiento city (southern Chubut Province), there was a farm from 1956 to 1975, from which mink also escaped (Pagnoni et al. 1986). In La Bolsa (Lago Rivadavia) town, by the shores of Rivadavia Lake, there was a farm from 1958 to 1979 as well. Overall, in 1960–1961, there were 55 mink farms spread over ten Argentine Provinces, including the then Territory of Tierra del Fuego (Daciuk 1978). Nevertheless, the major exporters of feral mink seem to be the provinces of Chubut and Río Negro (Bonino 1995).

The spread of released mink in Chubut Province was analysed by Pagnoni et al. (1986) and by Navas (1987). Mink spread from Cholila Valley east to the valley of the Chubut River, and southwest to the valleys of Futaleufú, Carrenleufú and Pico. On the other hand, mink spread from Sarmiento city toward Musters Lake and Colhue Huapi Lake, and west to the valley of the Senguerr River and to the Simpson River, extending to Fontana Lake and La Plata Lake. By 1973, mink were detected as far north as Los Alerces National Park, Chubut Province (Foerster 1973), and later in Nahuel Huapi Lake, Río Negro Province (Chehébar 1983). According to Pagnoni et al. (1986), mink may have found their way west to Chile crossing the headway of the Futaleufú, Palena, and Cisnes Rivers by 1986. Within Chubut Province, the rate of dispersal of mink was estimated at 7.7 km/yr on steppes and at 5.5 km/yr in forest habitats (Pagnoni et al. 1986, Navas 1987).

On the Argentine side of Tierra del Fuego, American mink were raised on farms located in Río Grande city, and some of them reportedly escaped into the wild during the 1960s. That some of them established into feral status was attested by Massoia and Chébez (1993), who recorded a sighting in the Grande River. More dubious records indicate that mink have been observed in Policarpo Bay (Mitre Pensinsula, on the westernmost tip of Tierra del Fuego Island). Venegas and Sielfeld (1998) reported that the mink is present but not common in the central and northern parts of Chilean Tierra del Fuego. Very recently (Martínez 2001), a press release reported that mink from Tierra del Fuego had swam across the Beagle Channel (ca. 7 km wide) and reached Navarino Island.

6. *Wild boar* (Sus scrofa)

The first boar were introduced from Europe by Mr Pedro Luro, owner of the ranch San Huberto near Santa Rosa town, La Pampa Province, sometime during 1904–1906. These boar were kept in an 800-ha enclosure, but some of them managed to escape into the wild shortly thereafter (Daciuk 1978). Navas (1987) disagrees with this account only in stating that the enclosure was 200 ha. Some boar from ranch San Huberto were relocated to Collún-co (Collunco) Ranch, Neuquén Province, by its administrator Mr Roberto Hohmann sometime between 1917 and 1922 (Daciuk 1978). These boar were released or escaped and spread to Lanín and Nahuel Huapi National Parks (Río Negro Province), and also across the Andes to Chile. A third introduction was made by the owner of Bahía Huemul Ranch, Río Negro Province, sometime during 1924 or 1926 (Daciuk 1978). The owner imported a few boar from ranch La Barra de San Juán, Uruguay. In 1931, a pair of adults and their piglets escaped into the wild and subsequently spread to Nahuel Huapi National Park, Río Negro Province, and also to Los Alerces National Park, Chubut Province, over 300 km away from their escape point. Daciuk (1978) expected that these boar would soon move south to Santa Cruz Province and that they would not stop their advance until reaching the northern shores of the Strait of Magellan. Navas (1987) stated that boar had invaded southern San Luis Province, southern Córdoba Province, southwestern Santa Fe Province, most of La Pampa Province, northern and southwestern Río Negro Province, southwestern Neuquén Province, and western Chubut Province. He expected that they would soon reach Lake Buenos Aires in northwestern Santa Cruz Province. In addition, Navas (1987) stated that a new (undated) introduction of boar had been effected in the Colón department, Entre Río Province. Daciuk (1978), citing Ángel Cabrera, states that all boar introduced into Argentina derive from Siberian stock. Curiously, De Vos et al. (1956) did not list wild boar as present in South America.

Given that wild boar crossed to Chile sometime during the late 1920s or early 1930s, it is puzzling that there are so few records of its occurrence in Chile. Pine et al. (1979) give the following confirmed records: Villarrica National Park, just across the Argentina border; Palena town, in Region X; and the Cisnes River, 80 km east of Puerto Cisnes town, in Region XI. Murúa (1995) reports that boar are present in the forest of the Andean area around Panguipulli Lake (Region X), and that they are scarce. The wild boar has not reached Region XII (Markham 1971; Venegas and Sielfeld 1998), nor Tierra del Fuego (Goodall 1979; Massoia and Chébez 1993).

7. *Red deer* (Cervus elaphus)

In Argentina, the first red deer were introduced by Mr Pedro Luro to ranch San Huberto, La Pampa Province, sometime during 1904–1906 (same as the first wild boar). Ortíz (1991, citing Wollenhaupt 1983) specifies that the exact date was 1904 (not 1902, as in Petrides 1975), and that deer came from the Carpathian Mountains in the then

Austro-Hungarian Empire. Navas (1987) points out that these deer were from two stocks, one from the Hungarian Carpathian Mountains and the other from the Austrian side. These introduced deer were kept in an 800-ha enclosure, but they managed to escape into the wild and soon expanded to the Atreuco, Guatreche, Toay, and Ultracán departments (Daciuk 1978). Some deer (together with some boar) from Ranch San Huberto were relocated to Collún-có (Collunco) Ranch, near Junín de los Andes town, Neuquén Province, by Mr Roberto Hohmann sometime between 1917 and 1922 (the latter date, according to Navas 1987). These deer numbered 8000 individuals in 1951 and 12,000 in 1960 (Navas 1987). From here, the deer naturally expanded their distribution southwards to Nahuel Huapi National Park, Río Negro Province, and eventually they reached Fontana and La Plata Lakes, Chubut Province. From 1902 to 1911, Mr Aarón Anchorena introduced a few deer to Victoria Island, within Nahuel Huapi National Park (Navas 1987), which by 1959–1960 numbered about 800 individuals (Daciuk 1978). Veblen et al. (1989) report that red deer were introduced to Nahuel Huapi National Park as early as 1911 and definitely by 1936. In addition, Veblen et al. (1992) report that red deer have also colonised the eastern two thirds of Lanín National Park, from Collunco Ranch. Since the first introduction in 1904–1906, red deer have been frequently introduced into several parts of Argentina (Bonino 1995). One such introduction occurred in April or May of 1973, when 11 individuals were introduced to Staten Island, off the southwestern tip of Tierra del Fuego (Daciuk 1978). According to Goodall (1979) and to Navas (1987), there were eight, and this reference is quoted by Massoia and Chébez (1993), who nonetheless provide plenty of additional details. Two of these deer (or their descendants) were spotted as late as December 1982, but did not seem to be doing well on the island (Massoia and Chébez 1993).

According to De Vos et al. (1956), red deer were imported to Chile for aesthetic and game purposes from a German zoo and released on several estates between Temuco city (Region IX) and Puerto Montt city (Region X), including an island in Ranco Lake, near Valdivia city (Region X). According to Ortíz (1991, citing Wollenhaupt 1983), eleven red deer were first introduced from Germany to Chile in 1928, and placed in a fenced area on a farm somewhere in Region IX. A second introduction involved the import in 1948 of eight deer from Collunco Ranch (Neuquén Province, Argentina), which were placed on a farm on the northern side of Villarrica Lake (Region IX). A third and final – thus far – introduction occurred sometime between 1952 and 1953, when calves were imported from somewhere in Argentina and placed on four unspecified farms and an island within Region X. Descendants were later relocated to other areas within Region X, and also to the Region XI. Ortíz (1991) considers that this group of introduced deer were the origin of most of the feral deer currently in Chile, except for those that crossed in large numbers from Argentina (Ortíz 1991). Migrating deer likely used low Andean passes to move from: (a) Lanín National Park in Argentina to Chile's Villarrica National Park (Region IX); (b) Nahuel Huapi National Park in Argentina to Chile's Ranco Lake (Region X); and (c) the surroundings of Fontana and La Plata Lakes in Argentina to Chile's Mañihuales village (Region XI) (Figures 4.1 and 4.2 in Ortíz 1991).

Specific locality records in Chile involve a sighting at the Claro River, 60 km east of Molina town (Region VII) and sightings by locals near La Laja Lagoon (Region VIII), but most other information is rather vague (Pine et al. 1979): Red deer are reportedly found in isolated mountainous locations in Ñuble Province (Region VIII), Temuco city (Region IX), and Aysén Province (Region XI); an antler was picked up at the headway of the Ñireguao River (Region XI). Ramírez et al. (1981) mention that red deer arrived from Argentina into southern Chile around 1950, that local farmers made voluntary introductions, and that a donation of fine game specimens arrived from Germany. Pine et al. (1979) point out that apart from releases within Chile, red deer have been expanding their range into Chile from Argentina. Eldridge (1983) dates red deer introductions during the 1950s (which is only partially correct, judging from Ortíz 1991), noting that red deer also crossed on their own accord from Argentina. Eldridge (1983) states that an unknown number of red deer were released during 1954 and 1956 on a 135-ha island in Rupanco Lake (40°53′ S, 72°25′ W), near Osorno city, which during 1974 and 1976 numbered 80 individuals. Ortíz (1991) estimates that there are about 4200 free-ranging deer spread over 340,000 ha in Regions IX and XI (which combined yield a total of 20 million ha).

8. *Grey fox* (Pseudalopex griseus)

This species is native to both Chile and Argentina, but is included here because it is an introduced exotic on Tierra del Fuego Island. Twenty-four young foxes of both sexes were captured in continental Magallanes Province and released at Onaisín village (65 km east of Porvenir town), Chilean Tierra del Fuego in 1951 (Pine et al. 1979). This species did not occur naturally on this island (Osgood 1943, Massoia and Chébez 1993), and they were introduced in an attempt to control the rabbit (*Oryctolagus cuniculus*) infestation that affected the sheep ranching activities in Tierra del Fuego (Jaksic and Yáñez 1983). This attempt was rather limited because of the small number of foxes involved, and as a last resort, sheep ranchers brought the myxoma virus from Brazil in 1954, which quickly succeeded in causing the crash of rabbit populations. Currently, grey foxes are considered common in Última Esperanza, Magallanes, and Tierra del Fuego Provinces in Chile (Venegas and Sielfeld 1998). Goodall (1979) commented that this fox is restricted to the northern part of Tierra del Fuego Island. Nevertheless, Massoia and Chébez (1993) reported that grey foxes were very common in Estancia Carmen during January 1986, and that they collected the crania of 15 specimens, together with one from a culpeo fox (*P. culpaeus*). According to Goodall (1979), Estancia Carmen is located between Yehuin and Fagnano Lakes, 72 km south of Río Grande city. If grey fox are assumed to have followed roads to spread from Onaisín village to Río Grande city (158 km), and to Estancia Carmen (72 km), and took 30 years to reach there, they would have spread at a rate of 7.7 km/yr, which is a very conservative estimate. Massoia and Chébez (1993) indicate that unconfirmed sources report the presence of this fox on the shores of the Beagle Channel. Even more puzzling is the mention made by Olrog and Lucero (1981), that the grey fox was introduced to the Malvinas (Falkland) Islands, a statement repeated by Chébez (1994).

Appendix 2. Gazetteer of Chilean places cited in the text

Aculeo Lagoon (33°50′ S; 70°54′ W). Altos de Boquerón Hills (53°18′ S; 69°49′ W). Beagle Channel (54°56′ S; 67°30′ W). Blanco Lake (54°03′ S; 69°02′ W). Calafate River (52°37′ S; 68°52′ W). Cameron village (53°37′ S; 69°38′ W). Cauquenes Lagoon (34°17′ S; 70°43′ W). Chico River (53°31′ S; 68°52′ W). Chillán city (36°34′ S; 72°06′ W). China Creek River (53°09′ S;

69°07′ W). Coihaique city (45°33′ S; 72°06′ W). Colonia Isabel Riquelme (ca. 51°45′ S; 72°15′ W). Concepción city (36°47′ S; 73°04′ W). Cordón Baquedano Hills (53°18′ S; 69°55′ W). Dawson Island (54°00′ S; 70°45′ W). Diguillín River (36°50′ S; 72°11′ W). Dumas Peninsula (55°04′ S; 68°37′ W). Espíritu Santo Cape (52°40′ S; 68°16′ W). Hoste Island (55°15′ S; 68°52′ W). La Laja Lagoon (37°17′ S; 71°19′ W). Lennox Island (55°18′ S; 66°56′ W). Lomas Bay (52°38′ S; 68°04′ W). Longaví town (35°55′ S; 71°41′ W). Los Angeles city (37°23′ S; 72°21′ W). Lynch Lake (53°58′ S; 69°09′ W). Mañihuales village (45°11′ S; 72°10′ W). Molina town (35°06′ S; 71°16′ W). Navarino Island (55°05′ S; 67°37′ W). Nueva Island (55°15′ S; 66°33′ W). Onaisín (Caleta Josefina) village (53°23′ S; 69°17′ W). Oro River (53°03′ S; 69°52′ W). Osorno city (40°34′ S; 73°08′ W). Paillaco town (40°02′ S; 72°52′ W). Palena town (43°35′ S; 71°47′ W). Panguipulli Lake (39°41′ S; 72°13′ W). Parrillar Lagoon (53°25′ S; 71°17′ W). Picton Island (55°03′ S; 66°53′ W). Porvenir town (53°17′ S; 70°19′ W). Puerto Cisnes town (44°43′ S; 72°43′ W). Puerto Montt city (41°30′ S; 72°50′ W). Puerto Natales city (51°45′ S; 72°15′ W). Puerto Nuevo village (53°20′ S; 69°31′ W). Punta Arenas city (53°08′ S; 70°55′ W). Purén town (37°59′ S; 73°06′ W). Purranque town (40°53′ S; 73°09′ W). Puyehue National Park (40°42′ S; 72°18′ W). Quebrada Honda Bay (28°47′ S; 71°24′ W). Ranco Lake (40°11′ S; 72°22′ W). Rupanco Lake (40°46′ S, 72°30′ W). San Sebastián village (53°19′ S; 68°38′ W). Santa Ana Point (53°37′ S; 70°55′ W). Strait of Magellan (53°52′ S; 71°15′ W). Temuco city (38°41′ S; 72°35′ W). Tierra del Fuego Island (54°37′ S; 69°00′ W). Timaukel village (54°01′ S; 68°52′ W). Torres del Paine National Park (51°00′ S; 72°48′ W). Valdivia city (39°48′ S; 73°14′ W). Vicente Pérez Rosales National Park (41°08′ S; 72°23′ W). Villarrica Lake (39°13′ S; 72°06′ W). Villarrica National Park (39°20′ S; 71°58′ W).

Appendix 3. Gazetteer of Argentine places cited in the text

Bridges Island (54°52′ S; 68°17′ W). Cañada de Gómez town (33°00′ S; 61°30′ W). Cholila town (42°31′ S; 71°27′ W). Colhue Huapi Lake (45°30′ S; 68°48′ W). Collún-có (Collunco) (39°59′ S; 71°11′ W). Colorado Lake (51°45′ S; 70°39′ W). Córdoba city (31°24′ S; 64°11′ W). El Turbio village (51°42′ S; 72°00′ W). Fagnano (Cami) Lake (54°38′ S; 68°00′ W). Fontana Lake (44°56′ S; 71°30′ W). Futalafquen Lake (42°48′ S; 71°41′ W). Gable Island (54°53′ S; 67°29′ W). La Bolsa (Lago Rivadavia) town (42°34′ S; 71°35′ W). La Plata Lake (44°50′ S; 71°52′ W). Lanín National Park (39°55′ S; 71°25′ W). Los Alerces National Park (42°50′ S; 71°50′ W). Malvinas (Falkland) Islands (52°00′ S; 59°00′ W). Mar del Plata city (38°00′ S; 57°33′ W). Mitre Pensinsula (54°48′ S; 65°40′ W). Moneta River (53°47′ S; 68°15′ W). Musters Lake (45°27′ S; 69°13′ W). Nahuel Huapi Lake (40°58′ S; 71°30′ W). Nahuel Huapi National Park (40°54′ S; 71°34′ W). Observatorio (Año Nuevo) Island (54°39′ S; 64°08′ W). Policarpo Bay (54°38′ S; 65°31′ W). Bahía Huemul (40°55′ S; 71°30′ W). Río Grande city (53°47′ S; 67°42′ W). Rivadavia Lake (42°37′ S; 71°41′ W). San Juan de Salvador Bay (54°44′ S; 63°51′ W). San Sebastián Bay (53°12′ S; 68°20′ W). Sarmiento (Colonia Sarmiento) city (45°34′ S; 69°05′ W). Staten Island (54°47′ S; 64°15′ W). Tandil town (37°15′ S; 59°10′ W). Ushuaia city (54°48′ S; 68°18′ W). Victoria Island (40°56′ S; 71°33′ W). Yehuin (Jhuin) Lake (54°25′ S; 67°41′ W).

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