

The exotic mammals of Argentina

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Abstract Exotic mammals in South America represent about 20% of world mammal introductions. The aim of our paper is to provide a global assessment of the exotic mammals of Argentina, their pathways, impacts, and a synthesis of their attributes as potential invasive species. We reviewed and compiled data from a diversity of sources and databases on alien mammals occurring in feral state exclusively. We recorded 18 species of exotic mammals for Argentina. The majority of introductions occurred between the 18th and 19th centuries and their ports of entry were located in temperate ecosystems, between 34° and 55° SL. Most of their entry pathways were associated with human activities (e.g. sport hunting, food and fur industry). The exotic mammals occupy ecoregions similar to their original distributions, but most of them have experienced a range expansion to novel habitats. The fauna of exotic mammals of Argentina represents a good opportunity to understand the dynamics of the invasion process as they represent a diversity of ecological groups and environmental contexts.

Keywords Biological invasions · Ecoregions · Introduced mammals · South America · Traits of invasiveness

Introduction

Biological invasions are a hot topic today. The scientific community has identified that biological invasions, climate change and habitat fragmentation are among the leading threats to the maintenance of global biodiversity (Vitousek et al. 1996). Disruptive effects on native species, affecting ecological processes, altering natural systems (i.e. nutrient and water cycles), human health and countries economy are examples of this threat (Mooney et al. 2005 and references therein). Thus, an enormous amount of scientific publications, books, projects, organizations and web sites are devoted to the study, dissemination, and management of introduced species (Drake et al. 1989; Lockwood and McKinney 2001; Cox 2004; Simberloff 2004; Sax et al. 2005; Settele et al. 2005; Cadotte et al. 2006a, b; GISP: The Global Invasive Species Programme).

Among the first steps of the invasion process are the transport, establishment and spread of species. Each of these steps can be analyzed through several approaches at different biological levels of organization (Sakai et al. 2001). In this respect, biological invasions are like natural experiments that offer excellent opportunities for research, such as attributes of invading species, basic processes in population and community ecology, and the structure and function of ecosystems (Ehrlich 1989; Williamson 1996; Sakai et al. 2001; Brown and Sax 2004; Cox 2004; Sax et al. 2005; Vazquez 2006).

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Several attributes were suggested for the success of invasive species (Ehrlich 1989; Williamson 1996; Rejmanek and Richardson 1996). These traits are not only intrinsic to the species (i.e. reproductive rate, body mass, abundance, size of native range, and so on) but also to the habitat they invade (i.e. vacant niches, climatic matching, diversity of resources, and so on). However, generalizations of traits of invaders are difficult to evaluate because either there are too many exceptions for them to be useful (Williamson 1996) or they are based on retrospective explanations for past invasions, correlation and classification rather than experimentation (Mack et al. 2000 and references therein).

Regarding mammals, most of introductions were in Europe and America (Kraus 2003). North and South America account for 93 and 37 introductions respectively, which represent 13.9% and 18.5% of worldwide introductions (Long 2003). Of the 37 introductions in South America, only 25 were established successfully as feral populations (Long 2003), and most of them (76%, excluding domestics) occupied the southern cone of Argentina and Chile.

The status of exotic mammals has been well documented for Chile (Jaksic 1998; Jaksic et al. 2002; Iriarte et al. 2005). However, this information has remained scattered for Argentina, and mostly reported in local publications and grey literature (Amaya 1978; Amaya and Bonino 1981; Jackson 1988; Lizarralde 1993; Bonino 1986; Lizarralde and Escobar 2000; Vazquez and Aragon 2002; Bonino and Soriguer 2004).

The aim of this paper is to provide an overall assessment of the exotic mammal fauna of Argentina, with references to their pathways, attributes and ecological roles.

Methodology

We conducted an exhaustive literature search from a diversity of sources including general standard books (Lever 1985; Long 2003), scientific and non-scientific (grey literature) articles, reliable internet databases: GISD's (Global Invasive Species Database, IUCN/SSC, 2007); IABIN (Inter-American Biodiversity Information Network, 2007) and personal communications with experts. Data were compiled for alien mammals occurring in feral state

exclusively (i.e. cows and other domestic mammals were excluded as there is basically no information about feral populations). We synthesized the ecological characteristics of invaders and invaded habitats respectively (e.g. dispersal capacity, reproductive capacity, etc). Most of these attributes have already been used as surrogates for invasive capacity (Ehrlich 1989; Williamson 1996). Native geographic ranges of introduced species were extracted from Long (2003) and characterization of native and invaded habitats was determined with Bailey's ecoregions (1989).

Results

Feral populations of 18 species of exotic mammals occur in Argentina (see Species account). This represents about 5% of Argentina's terrestrial native mammals (Barquez et al. 2006). The majority of introductions occurred in temperate ecosystems, between 34° and 55° SL (Fig. 1), into ecoregions that match their original distributions. Most species are from Eurasia, and recorded dates of introductions are mainly from the second and first half of the 19th and 20th centuries. Pathways for invaders were associated with human activities (i.e. sport hunting, food and fur industry, and for ornamental purposes) and hitchhiker species (i.e. old world mice and rats through ships). Nearly all of the introductions ended in accidental escapes or intentional release into the wild.

Species account and impacts

A summarized account of species, their potential impacts and attributes of invasiveness are shown in Tables 1 and 2.

Old world rats

A small fraction of alien mammals were unintentionally transported by humans (i.e. ships from Europe between 1600 and 1800). The first black rats in South America arrived at Peru in the ships of early explorers in 1544 (Lever 1985). These "hitchhiker" species are the brown rat, *Rattus norvegicus*, black rat, *Rattus rattus*, and house mice, *Mus musculus*.

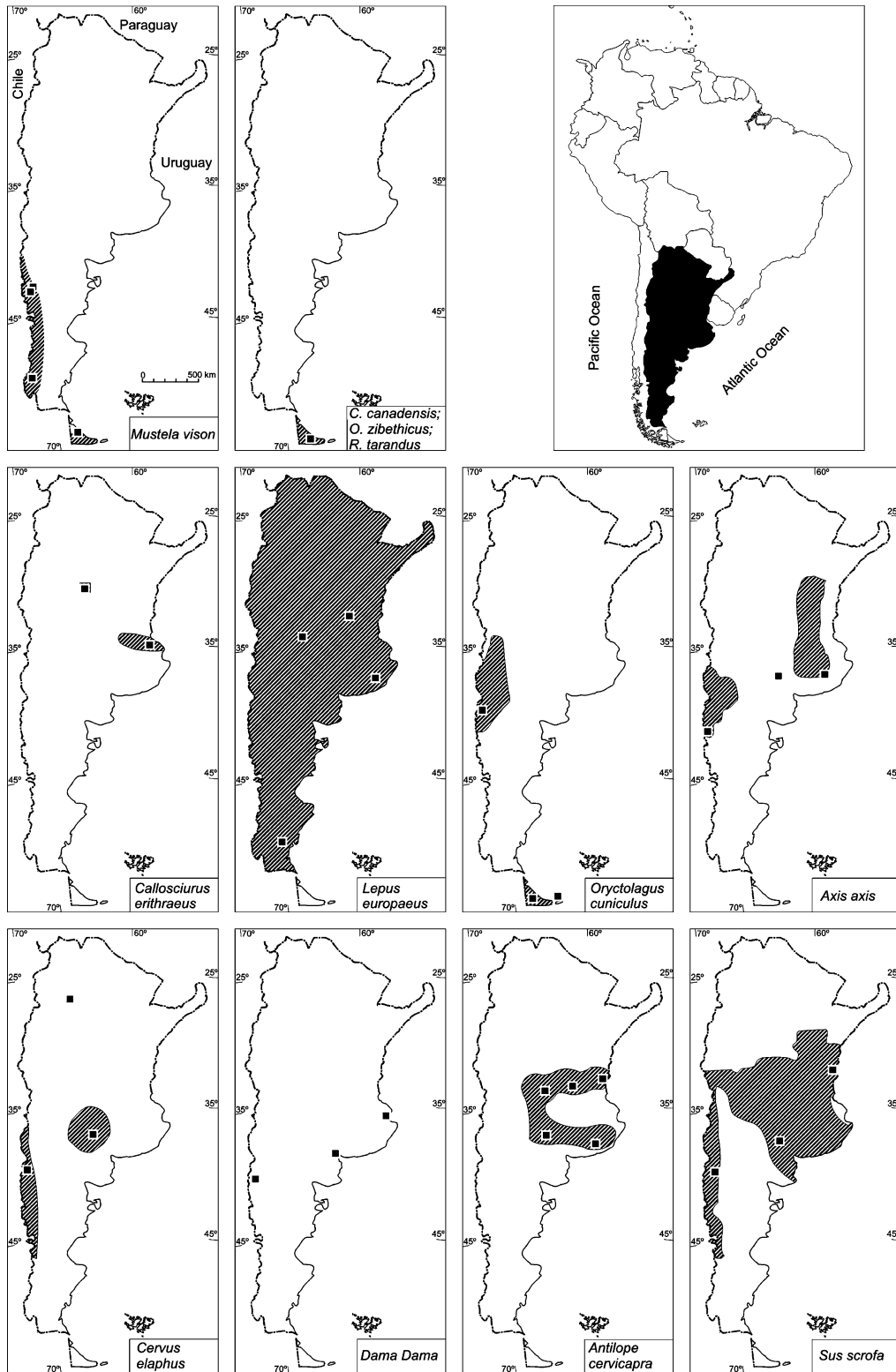


Fig. 1 Port of entry (localities) of invasive mammals in Argentina and current distribution

Table 1 Invasive species, ecological equivalent, and impacts

Species	Ecological equivalent	Impacts
<i>Mustela vison</i>	River otter, <i>Lutra provocax</i> , marine otter, <i>Lutra felina</i> , common weasel <i>Galictis cuja</i> (Carnívora)	Potential competition with native carnivores and species displacement
<i>Castor canadensis</i>	Coipo, <i>Myocastor coipus</i> (Rodentia)	Hydrologic structure of rivers alteration; deforestation of <i>Nothofagus</i> species; dam construction
<i>Ondatra zibethicus</i>	Coipo, <i>Myocastor coipus</i> (Rodentia)	River banks alteration and sedimentation affect water quality
<i>Callosciurus erythraeus</i>	None in the area of occurrence	Negative effect over fruit tree plantations and tree bark
<i>Rattus norvegicus</i>	Native rodents	Host to several diseases
<i>Rattus rattus</i>	Native rodents	Host to several diseases
<i>Mus musculus</i>	Native rodents	Host to several diseases; interaction with native rodents
<i>Lepus europaeus</i>	Patagonian hare <i>Dolichotis patagonum</i> , plains viscacha, <i>Lagostomus maximus</i> (Rodentia) and tapeti <i>Sylvilagus brasiliensis</i> (Lagomorpha)	Impact on natural regeneration of native forest; potential competition with native herbivores
<i>Oryctolagus cuniculus</i>	<i>Dolichotis patagonum</i> , <i>Lagostomus maximus</i> , <i>Sylvilagus brasiliensis</i>	Vegetation damages; potential competition with native herbivores
<i>Axis axis</i>	Guanaco, <i>Lama guanicoe</i> , huemul, <i>Hippocamelus bisulcus</i> , pudu, <i>Pudu puda</i> (Artiodactyla)	Impact on natural regeneration of the native forest, competitive displacement of native deer
<i>Cervus elaphus</i>	None in the area of occurrence	Impact on natural regeneration of the native forest; competitive displacement of native deer
<i>Dama dama</i>	Guanaco, <i>Lama guanicoe</i> , huemul <i>Hippocamelus bisulcus</i> , pudu <i>Pudu puda</i> (Artiodactyla)	Impact on natural regeneration of the native forest; competitive displacement of native deer
<i>Rangifer tarandus</i>	None in the area of occurrence	Unknown
<i>Capra hircus</i>	Brocket deer spp, <i>Mazama</i> , guanaco, <i>Lama guanicoe</i> , vicuña, <i>Vicugna vicugna</i> (Artiodactyla)	Impact on natural regeneration of the native vegetation; overgrazing
<i>Antilope cervicapra</i>	None in the area of occurrence	Unknown
<i>Sus scrofa</i>	None in the area of occurrence, but potentially the collared peccary, <i>Tayassu tajacu</i> (Artiodactyla)	Impact on natural vegetation and soil
<i>Equus asinus</i>	Guanaco, <i>Lama guanicoe</i> (Artiodactyla)	Potential competition with native herbivores; potential damage to cacti
<i>Equus caballus</i>	Native Birds (<i>Vanellus chilensis</i> , <i>Anthus</i> spp.)	Impacts over nesting birds of grassland, overgrazing

These species expanded their ranges in conjunction with human settlements and currently occur all over the country. Rats are considered pests to human populations as they are hosts of a plethora of diseases (i.e. Trichinosis, Typhus, Rat Bite Fever and bubonic plague) (Nowak 1999). They are responsible for destruction of crops and food stores (Barnett 1963), predators of avian species that nest on the ground, and cause competitive displacement of native small rodent species.

American mink (Mustela vison)

The American mink was introduced for fur farming in many parts of Santa Cruz and established successfully during the 1930s and 1940s (Lizarralde and Escobar 2000), and by 1959 almost 60 breeding ranches were active in Argentina. At present it is distributed from the south of Neuquén to the center of Santa Cruz and Tierra del Fuego (Lizarralde and Escobar 2000). There is a potential competition for

Table 2 Attributes of “good invaders”, explanations, examples and references

Attributes of “good invaders”	Explanation	Species
Broad diet	Able to feed on different items	Old world rats; <i>L. europaeus</i> ; <i>O. cuniculus</i> ; <i>C. hircus</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
Large body mass	Advantages for competition, dispersal, etc.	<i>C. elaphus</i> ; <i>R. tarandus</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
Associated with Homo sapiens	<i>H. sapiens</i> assist some species deliberately or unintentionally	Old world rats; <i>L. europaeus</i> ; <i>O. cuniculus</i> ; <i>C. hircus</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
High dispersal capacity	Advantage to colonize new environments	<i>M. vison</i> ; <i>C. canadensis</i> ; <i>O. zibethicus</i> ; <i>C. erythraeus</i> ; <i>R. norvegicus</i> ; <i>R. rattus</i> ; <i>M. musculus</i> ; <i>L. europaeus</i> ; <i>O. cuniculus</i> ; <i>C. elaphus</i> ; <i>D. dama</i> ; <i>R. tarandus</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
Habitat generalism	Type of habitat is not a limiting factor	<i>L. europaeus</i> ; <i>O. Cuniculus</i> ; <i>A. axis</i> ; <i>C. elaphus</i> ; <i>D. dama</i> ; <i>R. tarandus</i> ; <i>C. hircus</i> ; <i>A. cervicapra</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
Short generation time/high reproductive capacity	Advantage to fast population increase and colonization	<i>M. vison</i> ; <i>C. canadensis</i> ; <i>O. zibethicus</i> Old world rats; <i>L. europaeus</i> ; <i>O. cuniculus</i> ; <i>C. hircus</i> ; <i>S. scrofa</i>
Large native range/many native ecoregions	Able to function in a wide range of physical conditions	<i>M. vison</i> ; <i>C. canadensis</i> ; <i>O. zibethicus</i> ; <i>R. norvegicus</i> ; <i>L. europaeus</i> ; <i>C. elaphus</i> ; <i>R. tarandus</i> ; <i>S. scrofa</i>
No ecological counterpart	Species distinct from any of those in the community may be at an advantage. Theory of vacant niche	<i>C. canadensis</i> ; <i>O. zibethicus</i> ; <i>C. elaphus</i> ; <i>R. tarandus</i> ; <i>C. hircus</i> ; <i>A. cervicapra</i> ; <i>S. scrofa</i> ; <i>E. assinus</i> ; <i>E. caballus</i>
Old data introductions	More time for acclimatization	Old world rats; <i>L. europaeus</i> ; <i>S. scrofa</i> ; among others
Climatic matching	Sets of species seem to be limited by climate	<i>L. europaeus</i> ; <i>S. scrofa</i> ; <i>O. cuniculus</i>
Much genetic variability	Ensures rapid expansion in the new habitat	No data for invasive species of Argentina

food resources and space with native ecological equivalents such as the river otter “huillín”, (*Lutra provocax*), the marine otter, (*Lutra felina*) and the common weasel (*Galictis cuja*) (Medina 1997; Previtali et al. 1998; Aued et al. 2003; Delibes et al. 2003).

Beaver (*Castor canadensis*)

The beaver was introduced between 1945 and 1946 into Tierra del Fuego. Twenty-five pairs were released to the north of Fagnano and Claro Rivers in Isla Grande, Tierra del Fuego, by the Army (Lizarralde 1993; Massoia and Chebez 1993). Fur industry was the main objective of this introduction. In 1950 they crossed the channels and invaded Chile (Anderson et al. 2006). The beaver is considered a keystone species or one of the most important natural agents of habitat alteration, and an ecosystem engineer (Paine 1966; Anderson et al. 2006). Examples of this are the modification of the hydrologic structure of streams and rivers, through the cutting of trees,

dam construction, changes in water composition and nutrient dynamics (higher concentration of C, P and N) (Daciuk 1978; Naiman et al. 1988; Lizarralde et al. 1996, 2004). The beaver has an important impact on the *Nothofagus* forest ecosystem as it generates watercourse expansion, modifies the structure and dynamics of the riparian zone and produces deforestation of species such as *Nothofagus pumilio*, *N. betuloides*, *N. antarctica*, *Drymis winteri* (Fagaceae), replacing forest with grasslands (Lizarralde et al. 1996). The density of their colonies is very high (0.2–5.8 colonies/km²) compared to North America (0.08–1.4 colonies/km²) (Lizarralde 1993; Briones et al. 2001). The estimated population in Tierra del Fuego is between 35,000 and 50,000 (Lizarralde et al. 2004). Beavers affect forests and change plant richness and abundance of the herbaceous layer. However, part of this increase in richness is due to creation of disturbed habitats and dispersal corridors (invasion pathways) for invasion of exotic plants. Overall, beaver activities are causing long-term alterations by almost eliminating *Nothofagus forest* regeneration, and threatening the pristine character of

the sub-Antarctic ecosystem (Anderson et al. 2006). 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.

Muskrat (Ondatra zibethicus)

Most of Tierra del Fuego watercourses are inhabited by muskrats (Massoia and Chebez 1993; Bonino 1995; Lizarralde and Escobar 2000). Their digging activities alter the stability of river banks, causing bank erosion, sediment alteration and negative impact on water quality which can result in algae blooms (Massoia and Chebez 1993; Bonino 1995, 2005; Lizarralde and Escobar 2000).

Red bellied beautiful squirrel (Callosciurus erythraeus)

The red squirrel is one of the latest invaders recorded in Argentina (Aprile and Chicco 1999). Originally, ten individuals were imported from Belgium and introduced as ornamental species in 1970 in a ranch at the locality of Villa Flandria, Buenos Aires (Aprile and Chicco 1999). In 1973 some individuals escaped and established as feral populations in the surrounding areas (Recarey 1990). Currently this squirrel is expanding through cropping areas into northern Buenos Aires and in La Cumbrecita, Córdoba (Aprile and Chicco 1999; Guichon et al. 2005). The major impact is to fruit tree plantations (nuts, citrics, plums and pears), with damage to tree barks (Setoguchi 1990). Possibly red squirrels could feed on native passerine birds eggs, as already seen in Japan (Azuma 1998).

European hare (Lepus europaeus)

Hare expanded so fast that was declared pest by the federal government in 1907, by that time it was also present in Córdoba and Buenos Aires. Finally, it spread across the country (Grigera and Rapoport 1983; Jaksic et al. 2002). Several potential counterparts are some of the native medium sized herbivores

(*Dolichotis patagonum*, *Lagostomus maximus* and *Sylvilagus brasiliensis*) (Bonino 1986; Bonino et al. 1997). The presence of the hare favors predator (foxes and puma) expansion (Ramilo 2000). General impacts are mainly grassland decrease and negative impact over agriculture and regeneration of the native forest (Amaya 1978; Ramilo 2000), competition with domestic livestock, damages to fruit, seeds and forest crops, etc. Considering the high abundance, great dispersion ability and occupation of the same habitats as the middle host of *Fasciola hepatica*, *Lepus* is considered a threat to cattle in the Patagonian area (Kleiman et al. 2004). Commercial hunting of European hares for meat exports is important in Argentina. Approximately 6 million hares are shot in the wild annually (Jackson 1988). Between 1976 and 1979 Argentina exported to Europe about 14 million kg of hare meat per year (Mares and Ojeda 1984).

European rabbit (Oryctolagus cuniculus)

Rabbits were introduced to different islands on the Beagle channel from where they spread to the south of Tierra del Fuego. The first introduction was from Malvinas Islands in 1880. By 1936 they occupied all Tierra del Fuego showing a high propagation rate (Howard and Amaya 1975; Bonino and Gader 1987). Another introduction was from Chile in 1945. Rabbits expanded their geographic distribution by crossing over the Andean Cordillera toward Argentina (Howard and Amaya 1975). They entered Neuquén in 1945 (Jaksic and Yáñez 1983; Bonino and Amaya 1984; Bonino and Gader 1987; Jaksic et al. 2002) and by 1969 expanded north to Mendoza. By 1972 they expanded 3000 km to the north, south and east. During 1986 they crossed the Malargue and Grande rivers and were proximate to the Salado River (Bonino and Soriguer 2004). The rabbit was declared pest in Argentina during the 1950s and was controlled with the mixomatosis virus, a method already used in New Zealand and Australia (Jaksic and Yáñez 1983). The present distribution of the European rabbit includes Tierra del Fuego, Malvinas Islands, southwest of Santa Cruz, Neuquén, and southwest of Mendoza (Amaya and Bonino 1981; Clarke and Amaya 1986). High densities of rabbits as observed in Argentina caused fodder reduction and disruption

of native forest regeneration by seedling consumption (Lizarralde and Escobar 2000). In Tierra del Fuego National park, rabbits reduce plant growth and inhibit regeneration, affecting the development of grasslands (Lizarralde and Escobar 2000). The European rabbit and cattle alter the structure and functioning of the matorral sclerophyllous forest ecosystems of central Chile. Thus, the central valley has been replaced by savannas of *Acacia caven*, an exotic legume, whereas the “matorral or Mediterranean scrubland” remains on dry slopes as isolated clumps. Introduced European rabbits prevent the re-colonization of clearings by matorral on the slopes and push native herbs to protected microhabitats (i.e. under the canopy of shrubs) (Jaksic and Fuentes 1980; Simonetti and Fuentes 1983; Holmgren 2002). The loss of woodlands is likely to have resulted in reduced carbon storage capacity, nutrient recycling, and in increased erosion and climatic aridity within the region (Holmgren 2002).

Axis deer (Axis axis)

The first introductions were to La Pampa in 1906, as game hunting and ornamentation (Lever 1985). In 1930 Axis deer were introduced to Buenos Aires (Navas 1987) and later on to Isla Victoria in Bariloche, Santa Fe, Neuquén and Río Negro (Petrides 1975). Wild populations of axis deer are also present in El Palmar National Park, Entre Rios but no general impacts have been reported so far (Crespo 1982; Balabucic and Cichero 1994).

Fallow deer (Dama dama)

It was introduced in the pampas region and southwestern Argentina at the end of the 18th century (Lever 1985). During 1930 Fallow deer were released to the surrounding areas of Sierra de la Ventana, Bahía Blanca, Buenos Aires. In 1972 deer populations reached about 5600 animals. In 1930 they were introduced to Neuquén and Río Negro (Lever 1985; Navas 1987; Bonino 1995). Impacts of the fallow deer are habitat modification, effects over tree composition, structure and regeneration, and competitive displacement of native species of deer (Veblen et al. 1989; Jaksic 1998).

Reindeer (Rangifer tarandus)

It was introduced in South Georgia Island in 1909, and brought to Tierra del Fuego in 1948, however, no impact has been recorded so far (Lever 1985; Lizarralde and Escobar 2000).

Red deer (Cervus elaphus)

It was introduced to La Pampa in 1904 (Godoy 1963; Daciuk 1978). The first introduction in the Patagonian region was between 1917 and 1922 in Neuquén (Daciuk 1978; Lever 1985). In 1940 red deer were common in western Neuquén and north of Río Negro. Deer expanded from Río Negro to the northern Chubut, Buenos Aires, Bariloche, San Martín de los Andes and Junín de los Andes (Lever 1985; Flueck et al. 1995). Red deer cause negative effects over the native flora (Flueck et al. 2003), alteration of forest growth patterns and composition (Veblen et al. 1989) and negative effects over Ciprés, Maqui and Maitén. They also disrupt forest regeneration (Bonino 1995) and impact over the endemic pudu deer, *Pudu pudu* and Andean huemul, *Hippocamelus bisulcus* (Lever 1985). Diet overlap with *Lama guanicoe* and *Hippocamelus bisulcus* has been mentioned (Bahamonde et al. 1986; Galende et al. 2005). Recent observations suggest that red deer populations are expanding their occupation ranges into the Patagonian shrub steppe habitat (Richard Sage pers. comm.).

Wild boar (Sus scrofa)

It was introduced between 1904 and 1917 in La Pampa and Neuquén (Daciuk 1978; Bonino 1995). The current distribution in Argentina includes several National parks (Los Alerces, Lago Puelo, Nahuel Huapi, Lihue-Calel, Sierra de las Quijadas and El Palmar; El Leoncito Reserve). The wild boar has been reported as having a detrimental impact on livestock, on agricultural activities, and on the environment in several places (Bratton 1975). It is responsible for legume seed predation (Campos and Ojeda 1997). Alteration of plant community structure and composition, tree bark damages (i.e. *Prosopis*, *Geoffroea*), soil property alteration and modifications of nutrient dynamics are some of the potential

impacts of this species (Cuevas et al. 2006). Probably boars also facilitate expansion of exotic plant species (i.e. *Salsola kali*, etc.) generate a negative effect on ground-nesting bird species (i.e. *Athene cunicularia*, *Eudromia elegans*) and could consume eggs of lizards (*Tupinambis meriane*) and turtles (*Chelonidis chilensis*). Wild boars host several diseases (e.g. porcine fever, trichinosis, etc), and sheep and goat offspring are among its prey items (Herrero and Fernandez De Luco 2003).

Goat (*Capra hircus*)

It was introduced in 1856 to Isla de los Estados (Lizarralde and Escobar 2000; Deferrari pers. comm., 2005). Wild populations are present in Tierra del Fuego, but goats are raised as livestock all over Argentina. Major impacts are predominantly overgrazing, negative pressure over herb and shrub communities, modification of flora abundance and composition (Jaksic 1998). Goats have high potential for deforestation and land degradation (Álvarez-Romero and Medellín 2005).

Antelope/blackbuck (*Antilope cervicapra*)

Blackbucks were introduced in La Pampa in 1906 (Lever 1985). During 1912 more releases were made in Santa Fe, Cordoba and Buenos Aires. Currently blackbucks are distributed in the Pampean region, Chaco, Buenos Aires, Santa Fe, Entre Ríos (National Park El Palmar), San Luis and Córdoba. They are especially numerous in the east of the country (Lever 1985).

Donkey (*Equus assinus*)

It was introduced as a pack animal from Asia, but the dates and history of introduction are unknown (Parera 2002). Feral populations are present in reserve areas of San Juan (Ischigualasto), La Rioja (Talampaya) and Salta (Los Cardones). Impacts are unknown but potential damage on the bark of native cacti (*Trichocereus terscheckii*) was suggested (Acebes et al. 2006).

Horse (*Equus caballus*)

It was introduced during the XVI century by Spanish colonizers to Buenos Aires. There were many subsequent introduction events, ending in unintentional escapes to the wild (Long 2003). There are feral populations of horses in the cordillera and precordilleran areas of Chubut, Santa Cruz, Mendoza and San Juan provinces. Also there are feral horses in protected areas as Tornquist state park (Buenos Aires), and Los Glaciares national park. Negative impacts on birds nesting in grasslands were reported (Zalba and Cozzani 2004).

Discussion

We provide the first global assessment of the distribution and ecological generalities of the exotic mammals of Argentina, which, together with earlier contributions (Jaksic 1998; Jaksic et al. 2002; Vazquez 2002), broadens our understanding of the biological invasions in the South American southern cone.

The highest density of exotic mammals in South America is found in the temperate ecoregions. At a smaller scale, in the region of Cabo de Hornos, species richness of exotics is higher than that of natives (Rozzi and Sherriffs 2003).

Ecological attributes of invasive species, in addition to ecological characteristics of the habitats to be invaded, were mentioned by several authors (Ehrlich 1989; Williamson 1996; Rejmanek and Richardson 1996) as potential predictors of successful invasions. Most of the invasive mammals of Argentina exhibit some of these attributes (Table 2). The species encompassing most of these traits are *Sus scrofa*, *Cervus elaphus*, *Capra hircus*, *Lepus europaeus* and the old world rats (*Rattus* and *Mus*). Furthermore, six of the invader mammals occurring in Argentina are among the 100 worst invasive species of the world (Lowe 2000).

Most of alien mammals display good climatic matching (i.e. occupy ecoregions similar to their native ranges), and some species have experienced a range expansion to new habitat types (e.g. hare, rabbit, wild boar). The wild boar, *Sus scrofa*, is a broad niche species (after Vazquez's criteria 2006; ISSG), with most of the attributes of a successful

invader. The invaded ecoregions in Argentina not only match its native Eurasian distribution, but some of its populations expand their ranges to novel habitats, as for example its recent colonization into the temperate central Monte Desert (Cuevas et al. 2006). Exceptions to this range expansion correspond to narrow niche specialists in their use of habitat and food resources, such as the beaver, muskrat, red squirrel and the reindeer, either because of recent establishment (*Callosciurus*) or because of geographic barriers such as the Beagle Channel separating Tierra del Fuego from the continental land (e.g. *Castor*, *Ondatra*). Moreover, some of the alien species still remain as small populations with restricted distributional ranges, despite they were repetitively introduced (or inoculated). This is the case of the fallow deer (*Dama dama*) with a long history of introductions in more than 40 countries (Long 2003). Some of these restricted ranges might be due to other biological or ecosystem constraints but it is difficult to assure with the scant data at hand.

Recently, Fridley et al. (2007) listed some of the aspects which contribute to contradictory results regarding the ecology of invasive species and the relationship between native and exotic species richness (i.e. the so called invasion paradox). Among these factors, which we extend to the broader issue of predictability of invasions, is the nature of research (observational versus experimental), interacting with different scales and methodological views. To this we should add critical factors such as propagule size, number of inoculations (or introduction events), and year of introductions, some of them rarely available and making predictability of invasions rather ambiguous. Despite these difficulties, we agree with Cadotte et al. (2006a, b) that even though a species-by-species prediction is not possible, there is potential for the emergence of trends and generalities through macroecological approaches and phylogenetic information for large regional databases.

In conclusion, the fauna of exotic mammals of Argentina represents a diversity of ecological groups which offers an enormous opportunity for research. Our synthesis pinpoints several interesting topics to be explored, such as the ecological role of keystone species/ecosystem engineers (e.g. wild boar, beaver), coexistence and interactions among potential ecological counterparts (e.g. native and exotic medium sized herbivores), rates of dispersal of recent invaders

(e.g. squirrel), their role in plant and animal communities, seed dispersal and seed predation, among others.

Biological invasions are of scientific and practical interest as they could inform us about the evolution of traits, how communities are assembled, and ways to prevent invasions (Mack et al. 2000). As long as we approach their study with appropriate scientific methodologies our contribution to the understanding and management of invasive species will be enormously beneficial.

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