

# Vertebrate invaders and their ecological impacts in Chile

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The South American country of Chile has been subjected to relatively few invasions in historic times. In comparison to the ca 610 vertebrate species found in continental Chile, only 24 species (3.9%) have invaded the country. Except for two bird and two or three mammal species that expanded their range and crossed the Andean Ranges from Argentina, the remaining 20 species were all introduced, or aided, by humans. Of the 24 invader species that currently occur in Chile, 11 (46%) were first introduced in central Chile, two (8%) in the northern part of the country, nine (38%) in the southern part, and two (8%) in Juan Fernández Archipelago. For ten (42%) of those species there is no information about their effects on the native flora, vegetation, or fauna. For eight species (33%), the information regarding the effects of the invaders is anecdotal. For six species (25%), there is adequate quantitative documentation available on their effects. Of a total of seven convincingly reported cases, two involve positive effects (increase in the prey base for native predators) and five have negative effects, of which three are on native vegetation and the remaining two on native fauna.

*Keywords:* biological invasions; invaders; vertebrates; biodiversity; South America.

## Introduction

The origin, fate, and putative effects of animal invaders have long fascinated ecologists (De Vos *et al.*, 1956; Elton, 1958; Roots, 1976; Williamson, 1996) and, more recently, historians (Crosby, 1986). Because they are spectacular, the historic invasions (actually, purposeful introductions) and damaging effects of vertebrates in Australia (e.g. Troughton, 1947; Myers, 1970; Kitching and Jones, 1981) and New Zealand (e.g. Wodzicki, 1950; Howard, 1966; Gibbb *et al.*, 1978) have received a great deal of attention. That has not been the case in South America, except for the treatment of Groves and di Castri (1991), which nonetheless concentrates on those invasions occurring in mediterranean-type ecosystems, of which only central Chile possesses any. Furthermore, the analyses of Navas (1987) and Bonino (1995) are restricted to the introduced vertebrates (chiefly mammals) in Argentina.

I here attempt an exhaustive review of vertebrate invasions in the western fringe of South America, as exemplified by the long (ca 4200 km), narrow (177 km on average), and isolated country of Chile (fringed on the west by the Pacific Ocean, on the north by the barren Atacama Desert, on the east by the tall Andean Ranges, and on the south by the continent's terminus). Contrary to general expectations first put forth by Elton (1958; see Case, 1996), this comparatively species-poor country has experienced few invasions in historic times, not all of them successful. In comparison to the ca 610 vertebrate species found in continental Chile, a meager total of 24 species (3.9%) have gained some foothold in the country (Table 1). Except for two bird and two to three mammal species that

**Table 1.** The invaders of continental Chile. Native species (in parentheses) comprise only those present in terrestrial habitats of Chile (i.e. marine turtles, pinnipeds, and cetaceans are not included in the count)

Invader species	Common name	Status <sup>a</sup>	When <sup>b</sup>	Where
Amphibians (42 spp.)				
<i>Xenopus laevis</i>	African clawed frog	Introd.	1973	Central Chile
Reptiles (89 spp.)				
<i>Chelonoidis chilensis</i>	Argentine tortoise	Introd.	n.d.	Central Chile
Birds (380 spp.)				
<i>Bubulcus ibis</i>	Cattle egret	Expan.	1968	Antofagasta
<i>Cairina moschata</i>	Muscovy duck	Introd.	n.d.	Central Chile
<i>Phasianus colchicus</i>	Ring-neck pheasant	Introd.	1886	Coquimbo
<i>Callipepla californica</i>	California quail	Introd.	1864	Limache
<i>Columba livia</i>	Rock pigeon	Introd.	1930s	Central Chile
<i>Molothrus bonariensis</i>	Shiny cowbird	Expan.	1800s	Central Chile
<i>Passer domesticus</i>	House sparrow	Introd.	1904	Central Chile
Mammals (99 spp.)				
<i>Lepus europaeus</i>	European hare	Expan.	1896	Magallanes
<i>Oryctolagus cuniculus</i>	European rabbit	Introd.	1884	Central Chile
<i>Castor canadensis</i>	American beaver	Expan.	1956	T. del Fuego
<i>Ondatra zibethicus</i>	Muskrat	Expan.	1956	T.del Fuego
<i>Rattus norvegicus</i>	Norway rat	Introd.	1800s	Central Chile
<i>Rattus rattus</i>	Black rat	Introd.	1600s	Central Chile
<i>Mus musculus</i>	House mouse	Introd.	1600s	Central Chile
<i>Nasua nasua</i>	Coatimundi	Introd.	1935	J. Fernández
<i>Mustela vison</i>	American mink	Introd.	1987	Aysén
<i>Sus scrofa</i>	Wild boar	Expan.	1960s	Osorno
<i>Cervus elaphus</i>	Red deer	Introd.	1950s	Osorno
<i>Dama dama</i>	Fallow deer	Introd.	1950s	Osorno
<i>Rangifer tarandus</i>	Reindeer	Introd.	1972	Navarino
<i>Capra hircus</i>	Feral goat	Introd.	1574	J. Fernández
<i>Ovis ammon</i>	Mouflon	Introd.	1980s	Osorno

<sup>a</sup> Introd., deliberately introduced to Chile; Expan., naturally expanding its range from Argentina.

<sup>b</sup> n.d., no data.

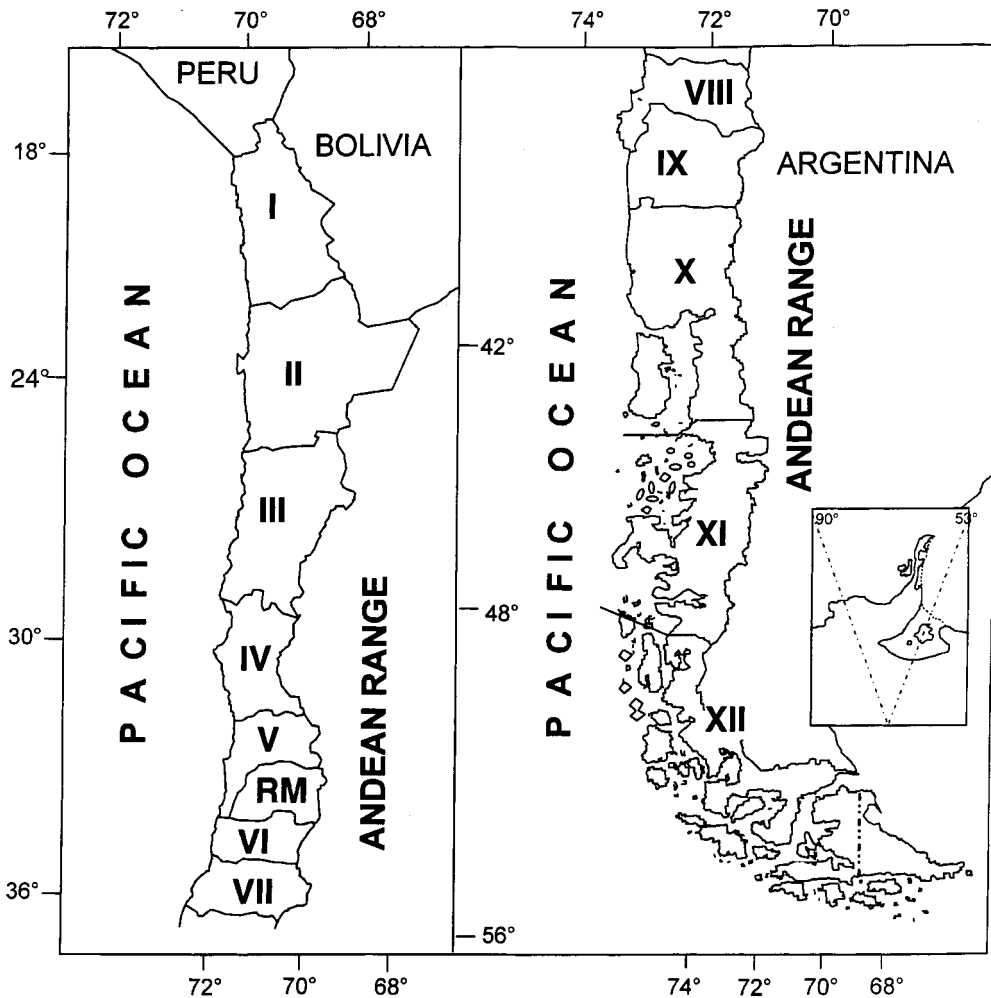
expanded their range and crossed the Andean Ranges from Argentina, the remaining 20 species were all introduced, or aided, by human agents. While some of them have been extremely successful, others cling to an existence near extinction.

Two separate papers have already dealt with the economic impacts of the most prominent of those invaders (Iriarte and Jaksic, 1986; Iriarte *et al.*, 1997). This paper describes all that is known from published records about the origin, fate, footholds, retreats, expansions, and putative effects of vertebrate invaders on Chile's native flora and fauna.

## Methods

I conducted an exhaustive literature review using the extensive reference databases available in Simonetti *et al.* (1995) and Jaksic (1997). Consultation with Chilean experts

aided in finding other literature. The country of Chile is divided into 13 administrative regions. All of them (except for the landlocked Metropolitan Region) extend from the Andean mountains to the Pacific Ocean (Fig. 1). Regions I to III span all of the Atacama Desert, Region IV is a semi-desert, and Regions V to VIII stretch over an area previously dominated by evergreen scrublands, but now occupied by large cities amid agricultural fields and forestry plantations. Regions IX and X were dominated by broad-leaved forests before being burned to open the land for cattle. Regions XI and XII are partly dominated by *Nothofagus* forests and by Patagonian steppe.



**Figure 1.** Map of Chile with its 13 administrative regions (from I to XII plus the Metropolitan Region), latitudes and longitudes, neighbouring countries, and major geographic features. The physiognomy of the regions is described in the Methods section.

## Results and discussion

### *Introduction, establishment, and range expansion*

In Chile there are 42 native species of amphibians (all of them frogs or toads), with one introduced frog, *Xenopus laevis* (Formas, 1995). This frog was introduced to a single lagoon (Carén) near Santiago's international airport in 1973 (Núñez, pers. comm.). Since then, it has spread—likely aided by humans—to other lagoons around and in Santiago, and to the Casablanca Valley (Region V).

There are 89 continental native species of reptiles in the country, and five marine turtles, of which only two are considered as dwellers confined to the Sea of Chile (Veloso *et al.*, 1995). A sixth species is an introduced terrestrial tortoise (*Chelonoidis chilensis*) that, despite its name, is native to Argentina (Cabrera, 1995) and is sold as a pet in stores and in the streets of the capital Santiago. This tortoise has never been found in the wild, although undoubtedly many pets have escaped from their owners. The exact date of its introduction is unknown.

A total of ca 380 bird species exist in Chile, not including some 80 species that have been recorded as accidentals (Araya and Bernal, 1995). Vuilleumier (1991) made a summary review of bird introductions to the central (mediterranean) region of Chile that appears to have received the bulk—if not all—of the invading birds. Five species were introduced: *Cairina moschata*, *Phasianus colchicus*, *Columba livia*, *Passer domesticus* and *Callipepla californica*. Two species expanded their former distributional range from Argentina: *Bubulcus ibis* and *Molothrus bonariensis*.

The cattle egret (*Bubulcus ibis*) was first spotted in Chile at Antofagasta (Region II) in 1968 (Johnson, 1972). This African species reached South America unaided by humans and continues to expand its distributional range. According to Vuilleumier (1991), Chile was the last country in the continent to be invaded by cattle egrets, and according to Araya and Millie (1986) it is now found from Arica (Region I) to Navarino Island (Region XI), wherever there are agricultural fields and pastures. They are most frequently associated with cattle and horses. The Muscovy duck (*Cairina moschata*), an Asian species whose date of introduction is unknown, is essentially a domestic duck, although two feral instances are known (Araya and Millie, 1986): Huencuecho Dam, near Pelarco (Region VII), and Los Quillayes Ranch, near Curicó (Region VII). The ring-necked pheasant (*Phasianus colchicus*), also a species of Asian origin, has been introduced several times and in many places in Chile. The earliest record dates back to 1886 or 1887 for an introduction from England to Coquimbo (Region IV), where the stock initially prospered but finally died out at about the turn of the century (Vuilleumier, 1991, and references therein). Another early record is an introduction made in 1914 from Germany to somewhere in Cautín (Region VIII). Nowadays, the ring-necked pheasant is found in a few areas in the vicinity of Illapel (Region IV), Cautín (Region VIII), and Valdivia (Region X), hardly in feral status (Araya and Millie, 1986).

The introduction of the California quail (*Callipepla californica*), a native of western North America, is particularly curious. According to Swarth (1927) the first introduction was by the Dutch citizen William Groves, who emigrated from San Jose (CA, USA) and brought with him a dozen quails in 1864, which he kept caged in his ranch in Limache (Region V). The quails escaped and became established in the wild. A separate introduction (and not necessarily the second) was effected by the US citizen C.J. Lambert in the vicinity of La Compañía near La Serena (Region IV). Lambert imported quails from San

Francisco (CA, USA) and released them in La Compañía in either 1881 or 1882. Later, US citizen F. E. Booth, who came from San Francisco (CA, USA), made an unusual back-introduction: he bought quails in Santiago's Central Market, sent them by ship, and so a first batch of 134 quails was duly recorded as arriving at San Francisco's Port during the first half of January 1927. Because Swarth's (1927) paper was submitted for publication on 9 February 1927, it is possible that other 'Chilean' quails may have been shipped to California. The exact distributional range of quails in Chile is unknown, but they are found from Atacama (Region II) to Cautín (Region VIII) and also in Robinson Crusoe Island (offshore from Region V); Araya and Millie, 1986). They have been spotted in high numbers even in relatively pristine areas such as La Campana National Park in Region V (MacDonald *et al.*, 1988).

The rock pigeon (*Columba livia*), a Palearctic species, had not been recorded in Chile as late as 1930 (Hellmayr, 1932; Vuilleumier, 1991) but nowadays is found throughout the country, mainly in towns. Only two feral instances are known (Araya and Millie, 1986): one in Robinson Crusoe Island (off the coast of Region V) and the other in the vegas of Chañaral Alto (Region II). The house sparrow (*Passer domesticus*), also a Palearctic species, is said to have been first introduced to South America at Buenos Aires, Argentina, in 1872, and in Chile in 1904 (Hellmayr, 1932; Vuilleumier, 1991), most likely in the vicinity of Santiago. It is found throughout the country and also in Easter Island and the Juan Fernández Archipelago, but only in towns.

The shiny cowbird (*Molothrus bonariensis*), a native of tropical South America and the Caribbean, was either introduced from Argentina in the late 1800s (Reed and Barros, pers. comm., quoted in Hellmayr, 1932) or expanded its distribution from that same country (Vuilleumier, 1991). Cabezas *et al.* (1989) are of the latter opinion, but the issue is yet to be settled. Currently, the shiny cowbird is found from Atacama (Region III) to Aysén (Region XI; Araya and Millie, 1986).

There are 99 native mammals in continental Chile, and 38 species of cetaceans and ten of pinnipeds, all marine (Contreras and Yáñez, 1995). To these 147 native species, 15 introduced species should be added, all in terrestrial or semi-terrestrial habits (Tamayo *et al.*, 1987).

According to Campos (1986) the European hare (*Lepus europaeus*) was introduced somewhere in southern Argentina by a German Consul in 1880. Markham (1971) places the original introduction in the southwestern part of Santa Cruz province (Argentina). Grigera and Rapoport (1983) are even more specific: 36 hares were imported from Germany in 1888 by Mssrs. Engelbert and Woltje Tieljen and released in the vicinity of the town of Cañada de Gomez, province of Santa Fe, Argentina. The European hare was introduced in the area of Última Esperanza of Magallanes (Region XII) in 1896 or 1907, and in the vicinity of Valdivia and Osorno (Region X) in undated years of the 1900s (Grigera and Rapoport, 1983). Currently, European hares are found throughout continental Chile from Copiapó River (Region III) to the continent's terminus, and their greatest abundances are recorded in Regions XI and XII (Grigera and Rapoport, 1983). Observations on its distribution and abundance have been documented by Pine *et al.* (1979), Dietrich (1984) and Johnson *et al.* (1990). The European hare has not yet reached Chiloé Island, Tierra del Fuego Island, or the Juan Fernández Archipelago.

Jaksic and Fuentes (1988, 1991) and Zunino (1989) made thorough and largely similar historical descriptions of the introduction of the European rabbit (*Oryctolagus cuniculus*) in Chile. Briefly, rabbits were not present in Chile during the first half of the 1800s (Gay,

1847), and Philippi (1885) implicitly extends that date toward the late 1800s. Lataste (1892) remarked that the European rabbit was first introduced into Chile in 1884, to the unnamed island that existed in Cauquenes Lagoon (Region VI), from which they escaped when an extended drought established connection of that island to other land. Rabbits do not appear to have increased much in the following years, because they were not mentioned by Albert (1902) in his list of native and introduced mammals present in Chile. According to Castillo (1912), by that date the rabbit had already become an agricultural pest in central Chile, but Osgood (1943) failed to mention this in his monograph, although he did comment on the high rabbit abundance observed in southernmost Chile (Region XII). According to Oliver (1946), the rabbit became a pest during the 1940s in the vicinity of Concepción (coastal area of Region VIII), and similar observations were made by Greer (1965), for the early 1960s in the then-province of Malleco (interior area of Region VIII). Housse (1953) and Ferrière *et al.* (1983) reported subsequent introductions of rabbits in several places in central Chile, and Brescia (1979) reported their introduction to the Juan Fernández Archipelago (off the coast of Region V).

From their release or escape points in central Chile, rabbits expanded their geographic distribution both to the north and south of the country (Péfaur *et al.*, 1968; Péfaur, 1969). According to Fuentes and Campusano (1985), their northernmost limit is the Limarí River (Region IV), but according to Zunino (1989) it is northward, in Quebrada Honda (Region IV). To the south (Zunino, 1989), their limit is in Paillaco (Region X). Rabbits also crossed over the Andean Cordillera out from Chillán (Region VII) toward Argentina (Howard and Amaya, 1975) and have continued their expansion in that country (Bonino and Amaya, 1984; Bonino and Gader, 1987). Extreme aridity in northern Chile and extreme humidity in the southern part of the country apparently constitute the most important barriers to the rabbit expansion; they nonetheless continue increasing in density within those confines (Zunino, 1989).

A separate introduction of European rabbits occurred in Tierra del Fuego Island (Region XII), which was painstakingly detailed by Jaksic and Yáñez (1983). Interestingly, the rabbits involved in this case were different from those in central Chile, which were brought from Spain (Housse, 1953). Those now in Tierra del Fuego were brought from the Falkland (or Malvinas) Islands (claimed by both the UK and Argentina), to which in turn they were introduced from France (Jaksic and Yáñez, 1983). Because rabbits of central Chilean stock crossed the Andes and have steadily moved southward along the eastern side of the Andes, while Fuegian rabbits have moved up northward from the Straits of Magellan, it is likely that these two stocks will come in contact in the near future. This is a phenomenon deserving close scrutiny.

The muskrat (*Ondatra zibethicus*) was first introduced in 1948 (Massoia and Chebez, 1993; Bonino, 1995) and not in 1956 (cf. Markham, 1971) in the northeastern part of Lake Fagnano – in the Argentine side of Tierra del Fuego Island – from where it invaded the Chilean side (Markham, 1971). Massoia and Chebez (1993) provide an amazingly detailed history of this introduction, from the original release of 75 males and 150 females to their spread updated to 1986. Twenty-five pairs of American beaver (*Castor canadensis*) were introduced on the Argentine side of Lake Fagnano in 1946 (Massoia and Chebez, 1993), spreading west and north toward the Chilean side (Markham, 1971). By the mid-1970s the beaver was spotted at Lake Blanco, 110 km SE of Porvenir (Region XII; Pine *et al.*, 1979), and it is now well established in Lakes Lynch and Escondido, and along the basin of River Grande, its northernmost record thus far (ca 53°40'S). Massoia and Chebez (1993) provide

the best detailed history of this introduction. These two invader species seem to be confined to Tierra del Fuego Island and the surroundings across the Beagle Channel (e.g. Navarino, Picton, Lennox, Nueva, and Hoste Islands; cf. Sielfeld and Venegas, 1980; Lizarralde, 1993). No reliable reports exist on their crossing the Straits of Magellan and reaching the mainland (Bonino, 1995; Bustamante, pers. comm.).

The exact date of introduction of black rats (*Rattus rattus*) and of house mice (*Mus musculus*) is unknown, but likely dates go back to the mid-1600s (Campos, 1986). Norway rats (*Rattus norvegicus*) are supposed to be a later arrival in Chile, dated at about the early-1800s (Campos, 1986). Ships of many nations must have carried these rats and mice to the Chilean shores. Norway rats and house mice are closely associated with human habitats, and only the black rat has been trapped far from human dwellings (Pine *et al.*, 1979; Simonetti, 1983).

The coatimundi (*Nasua nasua*) was introduced to Robinson Crusoe Island (off the coast of Region V) in the early 1930s. According to Mann (quoted in Pine *et al.*, 1979), all coatimundis on that island are descended from two pregnant females that escaped captivity around 1935, and the population in 1972 numbered about 4000 individuals. Another version of this introduction (Miller and Rottmann, 1976) states that coatimundis were introduced about 1940, and that the purpose was to control black rats (*Rattus rattus*), which of course they did not. American minks (*Mustela vison*) were first imported from Argentina by two fur establishments in the vicinity of Coyhaique (Region XI) in 1967 and/or 1968 (Servicio Agrícola y Ganadero, 1988). They escaped in unknown numbers, were detected in feral state in 1971, and until 1988 were still confined to Region XI. Since then, American minks have continued expanding their range north through Region X and to Region IX (Rau and Martínez, pers. comm.).

The wild boar (*Sus scrofa*) was introduced into central Argentina in 1906 (Bonino, 1995) and later translocated to Neuquén province, from where it spread into neighbouring Chubut, Rio Negro, and Santa Cruz provinces. At an unknown date, it crossed the Andes at several points along the border with Chile, to Regions X and XI. Interestingly, De Vos *et al.* (1956) did not report the wild boar as having been introduced in South America, but they did report that the red deer (*Cervus elaphus*) was present in Chile. This deer was introduced by ranchers of German descent settled in southern Chile, and it also crossed freely from Argentina, where it had been introduced in about 1906 to central Argentina and later translocated to Neuquén province (Bonino, 1995). It is now found in a feral state from Region VII south to Region XI. The fallow deer (*Dama dama*) was introduced in the 1950s to Region X but has not become feral (Miller and Rottmann, 1976; Campos, 1986). The reindeer (*Rangifer tarandus*) was apparently introduced from the South Georgia Islands (claimed by both Argentina and the UK) to Navarino Island (Region XII) in 1972, but the success of this introduction is unknown (Tamayo *et al.*, 1987). The mouflon (*Ovis ammon*) is said by Rau and Muñoz (1985) to have been introduced in Osorno (Region X). The success of this introduction is also unknown (Rau, pers. comm.). The goat (*Capra hircus*) is a domestic animal throughout Chile, except in the Juan Fernández Archipelago (off the coast of Region V), where it is found in a feral state and is considered a pest (Tamayo *et al.*, 1987). The goat was introduced to all three islands that compose the Juan Fernández Archipelago by the Spanish mariner and explorer of the same name, in 1574. In the early 1970s Mann (quoted in Miller and Rottmann, 1976) estimated that there were about 3000–5000 goats on Alejandro Selkirk Island, fewer than 200 on Robinson Crusoe Island, and about 30 on Santa Clara Island.

*Effects of invaders on native fauna*

No information exists on the possible effects of the introduction of the African clawed frog on sympatric native fauna in central Chile. No reptile has successfully established in the wild and thus no effect is expected (Table 2).

The effects of invading birds on other native species are relatively unknown and worth investigating. The small extent of intrusion in the wild by the cattle egret, Muscovy duck, ring-necked pheasant, and rock pigeon speak against an ecologically relevant effect. If any interaction exists, it may be between the cattle egret, and the native southern lapwing (*Vanellus chilensis*), Buff-necked ibis (*Theristicus caudatus*), and Chimango caracara (*Milvago chimango*), which also feed on invertebrates in agricultural fields and pastures. Although there is some potential for competition for food, none has been reported (Table 2).

**Table 2.** Putative effects of invader species on Chile's endemic fauna and vegetation

Invader species	Putative effects	Evidence <sup>a</sup>
African clawed frog	None known	n.a.
Argentine tortoise	None known	n.a.
Cattle egret	Food competition with native birds	None
Muscovy duck	None known	n.a.
Ring-neck pheasant	None known	n.a.
California quail	Food competition with native birds	None
Rock pigeon	None known	n.a.
Shiny cowbird	Brood parasitism of native birds	Convincing
House sparrow	Food competition with native birds	None
European hare	Food competition with native mammals	None
European hare	Detrimental effects on vegetation	None
European hare	New prey species for native predators	Convincing
European rabbit	Food competition with native mammals	None
European rabbit	Detrimental effects on herbs and shrubs	Convincing
European rabbit	New prey species for native predators	Convincing
American beaver	Detrimental effects on trees	Anecdotal
Muskkrat	Detrimental effects on vegetation	Anecdotal
Norway rat	Loss of crops and stored grain	Anecdotal
Norway rat	Predation on native birds and their eggs	Anecdotal
Black rat	Loss of crops and stored grain	Anecdotal
Black rat	Predation on native birds and their eggs	Anecdotal
House mouse	Loss of crops and stored grain	Anecdotal
Coatimundi	Predation on native birds and their eggs	Convincing
American mink	Predation on native fauna	Anecdotal
Wild boar	Damage to native bulbs	Anecdotal
Red deer	Detrimental effects on trees	Convincing
Fallow deer	Detrimental effects on trees	Anecdotal
Reindeer	None known	n.a.
Feral goat	Detrimental effects on herbs and shrubs	Convincing
Mouflon	None known	n.a.

<sup>a</sup> n.a., none available.

The California quail is often suspected of competing with the Chilean tinamou (*Nothoprocta perdicaria*), with which it shares the same habitat preferences and likely food, but no hard evidence exists on their possible interactions (Table 2). The house sparrow was suspected by Johnson (1967) of having ousted the Rufous-collared sparrow (*Zonotrichia capensis*) and Diuca finch (*Diuca diuca*) from their haunts around towns and forced them to the countryside (Table 2). This claim was doubted by Vuilleumier (1991), and I can attest (pers. obs.) to Rufous-collared sparrows being more common in towns now than they were in the mid-1960s.

Before the introduction or arrival of the shiny cowbird, no such bird existed in Chile. Therefore, a detrimental effect on the reproduction of native birds is to be expected from this invasion (Table 2). The only data available on the possible effect of shiny cowbirds on their parasitized hosts come from a description of the bird nests most often parasitized by this species (Table 3). In addition, I have observed that this brood parasite also takes on eared doves (*Zenaida auriculata*). The proportion of nests parasitized, even for a single species, is yet to be assessed in order to determine how detrimental the effects of the shiny cowbird are to their hosts.

Establishment of the European hare appears to have been beneficial to native fauna, both by increasing the supply of prey to large predators and by decreasing predation pressure on native fauna and livestock. Yáñez *et al.* (1986) reported the puma (*Felis concolor*) diet in Torres del Paine National Park (Region XII) and on neighbouring sheep ranches. In that work, it was shown that predation on European hares (*Lepus europaeus*) was very high, while that on domestic sheep (*Ovis aries*) was very low, contrary to the opinion of local sheep ranchers. Iriarte *et al.* (1991) reported the puma diet in the same park and, again, found that the main prey were native guanacos (*Lama guanicoe*) and European hare; small mammals were scarcely preyed upon. An interesting observation is that from 1982 to 1988 (dates of the respective field studies of Yáñez *et al.* (1986) and of Iriarte *et al.* (1991)), the level of hare consumption remained constant but consumption of guanaco increased from 9 to 29% (from puma faeces) in parallel with a 94% population increase of guanacos during the same period. When guanacos were scarcer, pumas preyed more on birds, chiefly on upland geese (*Chloephaga picta*). On the basis of estimates of field abundance of prey, Iriarte *et al.* (1991) showed that pumas preyed more than expected on hares and less than expected on guanacos. Also, in areas of the park with low

**Table 3.** Nests ( $n = 72$ ) of different Chilean bird species parasitized by Shiny cowbirds (after Johnson, 1967)

Species parasitized	Common name	% Parasitized <sup>a</sup>
<i>Diuca diuca</i>	Common diuca-finch	61
<i>Agelaius thilius</i>	Yellow-winged blackbird	18
<i>Zonotrichia capensis</i>	Rufous-collared sparrow	14
<i>Sturnella loyca</i>	Long-tailed meadowlark	1
<i>Metriopelia melanoptera</i>	Black-winged ground-dove	1
<i>Xolmis pyrope</i>	Fire-eyed diucón	1
<i>Hymenops perspicillata</i>	Spectacled tyrant	1
<i>Passer domesticus</i>	House sparrow	1

<sup>a</sup> Percentages do not add up to 100% because of rounding error.

guanaco density, pumas preyed on hares to a larger extent. These authors noted that hares were introduced in Region XII only 90 years ago, yet had already become the staple prey of pumas there (Table 2).

Establishment of the European hare also appears to have been beneficial to two large native raptor species. Iriarte *et al.* (1990) studied the food habits of two owl species (*Bubo virginianus* and *Tyto alba*) and of two hawks (*Circus cinereus* and *Geranoaetus melanoleucus*) in Torres del Paine National Park (Region XII). They found that the owls were more similar in diet between themselves than with the hawks (as expected from their nocturnal habits), but in turn differed markedly between themselves. A large part of the difference in diet among the four raptors studied was accounted for by the incidence of European hare in their respective diets, an incidence that increased directly with raptor size (Table 2). The dietary differentiation observed among these four raptors was apparently the consequence of their different sizes. It would have been interesting to know what were the food relationships – an important aspect of assemblage structure – of these native raptors before introduction of the European hare, but no data are available.

The establishment and increase of European rabbit populations yields information about how native predators react to the introduction of a new prey species. Jaksic *et al.* (1979) proposed that low predation on European rabbits in central Chile during the early 1970s was a consequence of the lack of behavioural skills on the part of predators to hunt for this relatively recent arrival. The escape response of rabbits is not represented among native prey. Thus, zigzag runs, leaps, and back-tracks may prove bewildering to native predators 'accustomed' to the simple escape response of their staple prey, the native Degu rat (*Octodon degus*), which just dashes straight to the nearest shelter (Yáñez and Jaksic, 1978; Jaksic, 1986). In this light, it is interesting that two research teams detected that in only 15 years, in the same study site of San Carlos de Apoquindo (Metropolitan Region), both the Culpeo fox (*Pseudalopex culpaeus*) and the black-chested eagle (*Geranoaetus melanoleucus*) had increased their consumption of rabbits (Simonetti, 1986; Pavez *et al.*, 1992, respectively; Table 4). These observations give circumstantial support to the hypothesis that behavioural adaptation on the part of predators determined their use of this new prey resource.

**Table 4.** Changes in the consumption of European rabbits (*Oryctolagus cuniculus*) by two native predator species (*Pseudalopex culpaeus* and *Geranoaetus melanoleucus*) in San Carlos de Apoquindo (Metropolitan Region of Chile) over a time span of less than 15 years

Predator	Previous (%) consumption	Later (%) consumption
Fox: <i>Pseudalopex culpaeus</i>	1976	1984
Small mammals	70.0	52.0
European rabbits	19.7	48.0
Other vertebrates	10.3	0.0
Eagle: <i>Geranoaetus melanoleucus</i>	1973–1974	1987–1988
Small mammals	75.9	34.3
European rabbits	18.8	43.9
Other vertebrates	5.3	14.0
Insects	0.0	7.8

No known effects of American beaver, muskrat, or house mouse on native fauna have been reported (Miller and Rottmann, 1976; Table 2). Nevertheless, black rats and Norway rats reportedly prey on bird eggs, nestlings, and even adult native birds (Miller and Rottmann, 1976; Campos, 1986; Table 2). Both the coatimundi and the American mink are known or suspected to prey on native fauna (Table 2). The coatimundi is blamed for having aided the decline of some Juan Fernández birds, specifically pink-footed shearwater (*Puffinus creatopus*) (Miller and Rottmann, 1976) and Juan Fernández firecrown (*Sephanoides fernandensis*) (Colwell, 1989). 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). Reports from Chile are largely similar (Servicio Agrícola y Ganadero, 1988).

Because introduced boar, deer, goats and mouflon are herbivores, their effects on native fauna may be, at best, indirect (Table 2; but see below). Indeed, the only reference (Miller *et al.*, 1983) to a potentially harmful interaction involves presumed competition for food between red deer and Andean huemul (*Hippocamelus bisulcus*), but no evidence is offered to support such a claim.

Colwell (1989) provided a detailed historical and ecological account of the natural history of the two native hummingbird species present in Juan Fernández Archipelago: the island endemic *Sephanoides fernandensis*, and the widespread Chilean hummingbird *Sephanoides galeritus*. The endemic hummingbird has declined in historic time, while the Chilean hummingbird is known to have invaded the Archipelago in the early 1800s and has increased in abundance ever since. The facile explanation that the Chilean hummingbird is the dominant competitor over the endemic one may be disregarded, because the situation is the opposite and the explanation more complex. On the one hand, deforestation by humans and overbrowsing and overgrazing by feral goats (*Capra hircus*), cattle (*Bos taurus*) and European rabbits (*Oryctolagus cuniculus*) have reduced the native sources of nectar for the endemic hummingbird. On the other hand, the introduction first of rats (*Rattus rattus*) and later of coatimundis (*Nasua nasua*) seems to have increased the sources of mortality by predation of the endemic hummingbird, which nests in very exposed sites (a usual trait of insular species that have evolved in the absence of predators). Simultaneously, the introduction and proliferation of blackberry (*Rubus ulmifolius*), whose flowers produce so little nectar that it can be profitably exploited only by the small Chilean hummingbird (*Sephanoides galeritus*), ensures a steady and exclusive food supply to the continental invader, which nonetheless also feeds on the nectar produced by native plants used by the endemic hummingbird (*Sephanoides fernandensis*). Human disturbance, overgrazing, predation, and facilitation of a subordinate competitor all combine to affect the endemic hummingbird. Colwell (1989) issued two recommendations to avoid the extinction of *Sephanoides fernandensis*: eradicate the coatimundis and the blackberries.

#### *Effects of invaders on native vegetation and habitats*

The African clawed frog is carnivorous, and no reptile has successfully established in the wild, thus no effects are expected (Table 2).

Cattle egrets and shiny cowbirds are insectivorous. The Muscovy duck feeds on both terrestrial and aquatic vegetation, but no study has been made of its possible effects. The remaining invaders, ring-necked pheasants, rock pigeons, house sparrows, and California quails, are all granivorous. No study have been conducted on their possible effects on the native seed bank (Table 2).

No quantitative information exists on the effects of European hare on vegetation (though in Argentina it is said to compete with livestock for pasture and to damage grasslands, crops, orchards and forestry plantations) (Bonino, 1995), but there is plenty in the case of the European rabbit (Table 2). Jaksic and Fuentes (1980) showed experimentally that European rabbits play a major role in determining the spatial restriction of native perennial herbs to protected zones under the canopy of shrubs in central Chile. They postulated that the finding of Keely and Johnson (1977), that the mediterranean areas of Chile and California differ in the spatial distribution of herbs, was accounted for by the foraging activities of rabbits rather than by microclimatic effects. According to Jaksic and Fuentes (1980), the herb layers present in Chile and in California must have been much more similar (more ecologically convergent) before the introduction of rabbits in Chile. That rabbits and other small mammals may affect the spatial distribution of the vegetation in the California chaparral was previously shown by Bartholomew (1970, 1971) and Halligan (1974).

When herbs become scarce or disappear, rabbits browse on shrubs and consume their seedlings (Simonetti and Fuentes, 1983). Fuentes *et al.* (1983) showed experimentally that rabbits not only destroy more seedlings than do native small mammals, but that their effect is quicker and more extended spatially. Because rabbits use open microhabitats, they are able to detect and kill seedlings that are out of reach for native small mammals. Fuentes *et al.* (1983) speculated that rabbits may be delaying or arresting the process of secondary succession in the matorral, and that as a long-term consequence, they may be contributing to its progressive clearing (Table 2).

Martínez and Fuentes (1993) compared the ecotones between *Baccharis*-dominated scrub and *Bromus*-dominated grasslands in Chile and California, and showed that the position of the respective ecotones was very stable. They conducted field experiments in central Chile (removed all herbs from ten small plots and measured the rate at which *Baccharis* colonized in comparison to eight control plots). Colonization rates were high in treatments and zero in controls. These results were consistent with those obtained along transects from scrub to grassland, wherein it was evident that shrubs had lower germination rates in open spaces. Under laboratory conditions ( $n = 4$  replicates), they planted *Baccharis* and *Bromus* separately and together, and observed that they inhibited each other. With this evidence, Martínez and Fuentes (1993) proposed that the ecotone in Chile remained stable because grassland and scrub inhibited each other mutually with regard to germination of their respective seeds. This was very different from what happened in the same ecotone in California, where herbs are competitively dominant over shrubs, and where rabbits (*Sylvilagus* spp.) impede their colonization of scrub where lagomorphs seek shelter against their predators. According to Eduardo Fuentes and Leopoldo Fuentes (pers. comm.), the rabbits introduced to Chile (*Oryctolagus cuniculus*) maintain similar activity levels in both scrub and grassland, and thus their role is neutral in comparison to rabbits in California.

Both the American beaver and the muskrat are considered harmful for vegetation (Miller and Rottmann, 1976; Table 2). The first, because in building its dams it destroys *Nothofagus* trees by ringing and inundating them (Bustamante, pers. comm.). The second, because through its tunnelling activities it damages earthen dams and irrigation ditches, causing floods and loss of habitat. The same conclusions have been reached in Argentina (Bonino, 1995). Of course, black rats, house mice, and Norway rats are all considered pests, especially because of their consumption of crops and of stored grain (Miller and

Rottmann, 1976; Campos, 1986; Table 2). Neither the coatimundi nor the American mink is known to affect the vegetation or habitat structure (Table 2).

Little information is published on the effects of red and fallow deer on native vegetation, but the existing accounts coincide in pointing out the heavy damage that they inflict by browsing (Miller and Rottmann, 1976; Ramírez *et al.*, 1981; Eldridge, 1983; Table 2). Similar conclusions have been reached in Argentina (Bonino, 1995). Wild boar is also considered harmful in Chile, especially for native bulbs (Miller and Rottmann, 1976; Table 2). 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). The effects of reindeer and mouflon on the Chilean vegetation are unknown, but reindeer on South Georgia islands are known to have caused major changes in vegetation cover and herb species composition, at least in some grasslands (Leader-Williams *et al.*, 1987, 1989). The effects of feral goats in Chile's Juan Fernández Archipelago are evidently harmful, specially when one considers that the flora is composed chiefly of island endemics (Miller and Rottmann, 1976; Table 2).

#### *Attempts to control invaders*

No attempts have been made to control or eradicate African clawed frogs. No need is perceived to control Argentine tortoises, which have not been found in the wild yet. No attempts have been made to control or eradicate any invader bird species, nor is any need perceived.

Prior to major plantings of trees (mostly *Pinus radiata*), foresters must contract out rabbit control programmes (Pine *et al.*, 1979). Control is effected through poisoned bait, which of course affects non-target, native species. Jaksic and Yáñez (1983) reported the attempts at controlling the rabbit infestation that affected sheep ranching activities in Tierra del Fuego Island (Region XII) during the early 1950s. Sheep ranchers tried to control rabbits first by hunting and trapping, later by poisoning them with cyanide gas (an unwise choice in such a windy place), and then by introducing foxes (*Pseudalopex griseus*) from the mainland. This attempt was rather pathetic, as only 24 young foxes of both sexes were released at Onaisín (65 km east of Porvenir) in 1951. As a last resort, in 1954 sheep ranchers brought the myxoma virus from Brazil, which quickly succeeded in causing the crash of rabbit populations.

Sáiz and Ojeda (1988) reported the population effects of removing rabbits (*Oryctolagus cuniculus*) with snares (a slipknot made of wire and anchored in the ground) on Robinson Crusoe Island, off the coast of Region V. Throughout three consecutive years (1983–1985) capture success was very similar at 18%, 14% and 15% (estimated as number of rabbits captured by unit snare-day). They captured a total of 19 099 rabbits in six removal sites. From 1982 to 1986, removal of rabbits resulted in population decreases in two sites, in population increases in three sites, and in lack of response in another site. Rabbit removals during the breeding season were somewhat more effective than those conducted during the remainder of the year. More than on density, removal effects were evidenced in a decrease in mean weight of the rabbits (from 1343 g in 1982 to 1267 g in 1986 = 6% decrease) and in their mean length (from 453 mm to 426 mm = 6% decrease), as a consequence of the elimination of the largest (older) rabbits. Rabbit removals resulted in spectacular increases in plant biomass (up to five times in dry weight expressed as  $\text{kg ha}^{-1}$ ) in four sites, in a clear reduction in one site, and in lack of response in another. Although with exceptions, those sites where rabbits decreased the most recovered more strongly in plant biomass.

Only black and Norway rats, as well as house mice, are the targets of periodic control measures in Chile. In Tierra del Fuego, during 1971, muskrats became so abundant in the vicinity of Onaisín that a programme to eradicate them was started in 1972. The programme involved trapping muskrats with conibear traps and selling their pelts. For reasons unknown, after their peak abundance in 1971, muskrats declined markedly, so that during the first year of the programme only 200 pelts were purchased. By 1973, muskrat abundance had declined to the point of a population crash (Pine *et al.*, 1979). No attempt has yet been made to control either coatimundis or American mink.

Red deer are culled by sports hunters in deer farms, and their meat is sold in markets and restaurants. No attempt (systematic or otherwise) has been made to eradicate them from the wild. Feral goats in Juan Fernández Archipelago may be hunted legally all year, but their numbers do not seem to have decreased.

#### *Comparison with other regions*

Because of its position, length, and physiography, Chile is hardly comparable to any other country in the world, except perhaps for the same latitudes (17°30' to 56°30') encompassed on the combined western fringe of Mexico, the United States of America, and Canada. Fortunately, because of its geographical location, Chile shares with California (USA), the Mediterranean Basin, southern South Africa, and southern Australia mediterranean-type ecosystems. These are characterized climatically by dry and warm summers and cool and rainy winters, where an evergreen scrub is the dominant vegetation and where the fauna has been considered to be ecologically convergent (i.e. approximately the same ecological roles are played by phylogenetically unrelated species; see di Castri and Mooney, 1973; Mooney, 1977; Thrower and Bradbury, 1977; di Castri *et al.*, 1981). The biological invasions experienced by these mediterranean regions have received in-depth treatment (Groves and di Castri, 1991), which facilitates comparisons. Although some valuable data have not been reported (e.g. the recipient pool of species, successes and failures of invaders), some general conclusions may be drawn from Table 5.

**Table 5.** Vertebrate invaders established in mediterranean-type regions of California, the Mediterranean Basin, South Africa, and Chile (including all of Chile). Number of invader species/total number of species is reported as available

Regions	Birds (%)	Mammals (%)	Source
Mediterranean California	19/284 (6.7)	12/216 (5.6)	Vuilleumier (1991), Lidicker (1991)
Mediterranean Basin	12/347 (3.5)	No data	Blondel (1991)
Mediterranean South Africa	11/no data	8/no data	Brooke and Siegfried (1991), Bigalke and Pepler (1991)
Mediterranean Australia	38/no data	22/no data	Long and Mawson (1991), Redhead <i>et al.</i> (1991)
Mediterranean Chile	7/263 (2.7)	6/80 (7.5)	Vuilleumier (1991), this paper
Lower 48 states of USA	13/553 (2.4)	No data	Case (1996)
All of Australia	17/466 (3.6)	No data	Case (1996)
All of Chile	7/380 (1.8)	15/99 (15.2)	This paper

At least in absolute numbers, birds seem to establish slightly more successfully (numerically speaking) than mammals in mediterranean regions, and Australia ranks first in number of established bird and mammal invaders (Table 5). Few data exist on the relative contribution of invaders to the regional faunas, but they range from 2.7 to 6.7% for birds, and 5.6–7.5% for mammals (Table 5). Comparison of the relatively well-studied mediterranean regions of California and Chile suggests a higher invasibility of the former by birds and of the latter by mammals (Table 5). The regional figures for birds are similar to or exceed those for the whole countries of USA, Australia and Chile (Table 5), thus suggesting that those mediterranean ecosystems are either more prone to receive invaders, more likely to permit invaders to establish, or both.

## Conclusions

Of the 24 invading species that occur in Chile nowadays, 11 (46%) were first introduced in central Chile, two (8%) in the northern part of the country, nine (38%) in the southern part, and two (8%) in Juan Fernández Archipelago. For ten (42%) of those species there is no information about their effects on the native flora, vegetation, or fauna. For eight species (33%), the quality of the information regarding the effects of the invaders is, at best, anecdotal. For only six species (25%) is there adequate quantitative documentation available on their effects. Of a total of seven convincingly reported cases, two involve positive effects (increase in the prey base for native predators) and five have negative effects, of which three are on native vegetation and the remaining two on native fauna.

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