SAREM Series A
Mammalogical Research
Investigaciones Mastozoológicas

VOLUME 3

INTRODUCED INVASIVE MAMMALS OF ARGENTINA

MAMÍFEROS INTRODUCIDOS INVASORES DE ARGENTINA

Alejandro E. J. Valenzuela, **Christopher B. Anderson**, **Sebastián A. Ballari** and **Ricardo A. Ojeda**, EDITORS

The Argentine Society for the Study of Mammals (Sociedad Argentina para el Estudio de los Mamíferos – SAREM) was created in 1983, and currently has about 300 members from several countries. SAREM is an interdisciplinary society of natural sciences professionals whose main goals are the promotion of scientific and technical research, the consolidation of national collections and research centers, and the publication and diffusion of research on living and/or extinct mammals. SAREM has organized scientific meetings for mammal researchers since 1994, publishes the journals *Mastozoología Neotropical* and *Notas sobre Mamíferos Sudamericanos*, and has edited books on the systematics, distribution and conservation of the mammals of southern South America, including *Libro Rojo de los mamíferos amenazados de la Argentina* (first ed. 2000, second ed. 2012) and *Mamíferos de Argentina. Sistemática y distribución* (2006), as well as contributing to the *Libro Rojo de los mamíferos y aves amenazados de la Argentina* (currently out of print).

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Introduced Invasive Mammals of Argentina

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SAREM Series A
Mammalogical Research
Investigaciones Mastozoológicas

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Introduced Invasive Mammals of Argentina / Alejandro Valenzuela … [*et al.*]. – 1ª ed. – Mendoza : Sociedad Argentina para Estudio de los Mamíferos SAREM, 2023.
Memoria USB, PDF

ISBN 978-987-98497-9-8

1. Mamífero. 2. Animales Exóticos. I. Valenzuela, Alejandro.
CDD 599.0982

Cover collage: Gabriela F. Ruellan

Cover photo credits: Kev on Pixabay (European hare) | Dorota Kudyba (dogs and horses) | Ruediger50 on Pixabay (water buffalo) | Sergio Anselmino (American mink) | Gabriela Ortega (cow hide) | efPercy05 on Pixabay (goat) | suksao on Freepik (chital) | Guillermo Deferrari (muskrat) | J. Cristóbal Pizarro (North American beaver damage) | Peter Chou (Pallas's squirrel) | Public Domain Pictures (red and fallow deer antlers) | marco on Pixabay (wild boar)

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Introduced invasive species are a major driver of local to global environmental change, including important negative impacts on biodiversity, ecosystem processes, economies, health and other social values. At the same time, however, different social actors can hold diverse representations of these species, particularly of introduced invasive mammals (IIMs). Such divergent values and perceptions can lead to conflicts regarding the management of IIMs, but also invite researchers and managers to be reflexive regarding their own work at a more fundamental level. Therefore, it is key that we advance towards a holistic understanding of IIMs and develop strategies to manage them based on solid technical information and plural perspectives regarding their multiple values. Despite a rich history of initiatives in Argentina to study and manage IIMs, until now there has not been an opportunity to assess the state-of-the-art knowledge in our country. This book seeks to provide rigorous, relevant and legitimate information to support research, policymaking and management decisions regarding IIMs in Argentina. With this objective in mind, the book presents a series of chapters selected to highlight priority topics concerning the conceptualization and implementation of IIM research and management. Then, fact sheets are provided for the different IIMs found in Argentina. Finally, beyond the realm of academic inquiry, the timing of this publication is ideal to re-enforce policy and decision-making, such as the recently approved National Invasive Exotic Species Strategy, which seeks to implement actions and enhance institutional capacities related to invasive species management in Argentina, and the Convention on Biological Diversity's new Global Biodiversity Framework, which also addresses biological invasions as part of broader efforts to attain the 2050 Vision for Living in Harmony with Nature.

Dr. Alejandro E.J. Valenzuela
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Foreword

Biological invasions by introduced species are one of the great changes rapidly transforming the globe today, with innumerable impacts on economics, human health, ecosystem services, and biodiversity. Mammals are among the most impactful of invasive species, transmitting diseases to humans, livestock, and native animals, trampling native grasslands, voraciously devouring vegetation from groundcover to saplings of forest trees, fouling water, causing erosion, and preying on and outcompeting native animals. They were among the first species humans introduced worldwide and in Argentina, both deliberately (*e.g.*, livestock) and inadvertently (*e.g.*, rats and mice). They have been introduced for sport (*e.g.*, deer, boar) and companionship (*e.g.*, cats, dogs), or simply as attractive ornamentals (*e.g.*, squirrels). Some that are meant to be kept in captivity, such as cats, dogs, and squirrels, escape and establish feral populations.

Argentina looms large in the history of biological invasions by introduced mammals. The earliest permanent European settlers of Buenos Aires in 1580 discovered huge herds of feral horses already on the pampas, and soon after, Vázquez de Espinoza described feral horses in Tucumán that were "in such numbers that they cover the face of the earth…". Many sheep were in Tucumán as well at that time, and of course later sheep were enormously numerous in Patagonia, effecting huge changes in the vegetation and driving land degradation and desertification to this day. When Charles Darwin visited the La Plata region in 1832 during the voyage of the Beagle, he reported that "…countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less-frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills."

Approximately 40 mammals have been introduced to South America, of which 25–30 have established populations; most of these are in the Southern Cone. In Argentina, I count 23 successfully introduced mammal species, including feral cats, dogs, and cows. Many, such as rats, rabbits, boar, and goats, are widely distributed around the world. By contrast, the hairy armadillo has been introduced nowhere else but from the mainland of Patagonia to Tierra del Fuego Island. Strikingly, except for the rats and house mouse, all these mammals were brought to Argentina deliberately; this is very different from, say, introduced insects. A few of these invasive mammals, like the squirrel, were not intended to be released, but I hesitate to term such invaders truly "accidental," because the people who brought them should have realized that escapes or later releases were almost inevitable. Of course, almost all of these mammals were introduced before the late twentieth century, which was when most scientists and the public began to recognize the extent and importance of impacts of introduced species. However, the squirrel and armadillo introductions were recent enough that potential impacts should have been foreseen. Things could be worse, of course—mammals deliberately brought to Argentina that either were released, but did not establish persistent populations or have not yet escaped from hunting preserves include reindeer, silver fox, mule deer, African buffalo, white-tailed deer, Père David's deer, thar, barbary sheep, wisent, mouflon, chamois, and ibex.

The technology of eradicating introduced invasive mammals has made enormous strides in the last thirty years—at least 31 mammal species have been eradicated from islands worldwide, including relatively large islands like South Georgia. Both Norway and ship rats have been eradicated hundreds of times, and house mice about 100 times. Most large mammals, such as deer and horses, are technologically easier eradication targets—many can simply be tracked and shot, for instance. However, mammals more than any other introduced species pose the complication that many people—especially hunters—simply do not want to eradicate them, and many animal welfare advocates, even those recognizing the damage some invaders cause, object to eradicating them by the only currently feasible means—killing them, humanely if possible. Even rat eradication has been impeded on animal rights/animal welfare grounds, and free-ranging dog and cat populations frequently are seen more as animal welfare issues than as conservation problems to broad sectors of some societies. In Argentina, the problem of implementing feasible eradication programs for invasive mammals is epitomized by the rather schizophrenic attitude taken by the National Parks Administration (Administración de Parques Nacionales–APN) towards red deer. The APN's conservation imperative is supported by the section of Law #22,351 that forbids propagating introduced animals, yet red deer, known to damage native species and ecosystems, are managed in Lanín National Park to foster ongoing hunting, and even to improve the size and quality of the deer for better hunting trophies. Additionally, there is often inconsistent and inadequate funding for managing and eradicating invasive mammals in protected areas, almost always constituting a supervening impediment even when a rational and effective goal is stated.

Argentine scientists have participated heavily in the rapid growth of modern invasion science since its inception in the 1980s, and they and overseas colleagues have conducted substantial research on the biology and impacts of many of the introduced invasive mammals in Argentina, as well as other invasive species. Some of the threats posed by these mammals have even become widely known to the general public in Argentina and beyond—the spread of the beaver from Tierra del Fuego to the mainland has been an international news story. *Introduced Invasive Mammals of Argentina* is therefore an exciting and timely addition to the literature on invasions in southern South America for both the Argentine public (and its political representatives and environmental managers) and scientists worldwide. The many authors assembled for this book explore how these biological invasions happened in the first place, how they spread, what they do to biodiversity, ecosystems, and human enterprises, what has been done about them so far, what can be done about them now, and what might be done with them in the future. The editors and authors are to be congratulated for an excellent exposition of the Argentine part of a growing global phenomenon.

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1 INTRODUCED AND INVASIVE MAMMALS: CONCEPTUAL AND HISTORICAL PERSPECTIVES FOR ARGENTINA

MAMÍFEROS INTRODUCIDOS E INVASORES: UNA PERSPECTIVA CONCEPTUAL E HISTÓRICA PARA ARGENTINA

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Abstract. Species that experience range expansions, high population growth and negative social or ecological impacts in a non-native location due to human actions are defined as both introduced and invasive. In particular, introduced invasive mammals (IIM) are more harmful than other vertebrates, and their social-cultural interactions are especially strong. IIMs in the Americas represent about 20% of mammal introductions worldwide, and their high species richness is concentrated in South America's Southern Cone. The aim of this chapter is to provide an overview of the state-of-the-art on IIMs in Argentina. We present the main concepts and applications of the biological invasion process, the major contributions of IIM studies in Argentina, and perspectives for future research. By viewing biological invasions as a multi-stage process with major drivers and a series of sequential steps, IIMs can be used as a relevant model and opportunity to promote a scientific agenda encompassing a diversity of topics and dimensions. Such a fundamental research program, coupled with strategic and integrated planning with governmental agencies, could provide the groundwork for aiding in the prevention of biotic homogenization and biodiversity loss in Argentina.

Resumen. Las invasiones biológicas facilitadas por los seres humanos constituyen uno de los aspectos más relevantes del cambio global. La propagación de especies invasoras ocurrió a lo largo de la historia, principalmente durante los siglos XIX y XX. La expansión del comercio, los desplazamientos humanos y el movimiento de continente a continente realizado por diferentes medios de transporte produjeron la dispersión y el aumento drástico de nuevas especies en diferentes regiones del planeta, con consecuencias ambientales inesperadas.

Muchas especies no nativas proporcionan beneficios y son componentes omnipresentes e integrales de la economía global. Especies utilizadas en la agricultura, la silvicultura, la piscicultura y otras actividades productivas de utilidad para el humano son no nativas. Sin embargo, los costos negativos de las especies no nativas surgen cuando estas alcanzan el estatus de introducidas, se naturalizan e invaden un nuevo ambiente. Las especies introducidas invasoras son definidas como toda especie introducida por el ser humano que se ha dispersado y establecido fuera de su área de distribución natural y constituye una amenaza para la biodiversidad (Convenio sobre la Diversidad Biológica,

CDB, 1992). Dichas especies en general son oportunistas y fácilmente adaptables a nuevos hábitats, lo que les permite aumentar sus números rápidamente, convirtiéndose en componentes dominantes en las comunidades invadidas; resultan además la causa principal de extinción, retracción y reestructuración de las poblaciones biológicas. Los daños y perjuicios ambientales producidos por las especies invasoras involucran costos económicos importantes para diversas actividades humanas, incluyendo además situaciones de riesgo para la salud, lo que las lleva a ser consideradas análogas a los desastres naturales.

Entendiendo que las especies introducidas invasoras en general, y los Mamíferos Introducidos Invasores (MII) en particular, son un fenómeno mundial con gran relevancia a escala local, el objetivo del presente capítulo es proporcionar una visión global del estado del arte en la investigación sobre MII en Argentina. En las dos primeras secciones introducimos aspectos conceptuales claves de las invasiones biológicas, proceso de invasión y teoría de nicho aplicada a las invasiones. En las dos últimas secciones abordamos y analizamos la historia y el contexto de las investigaciones de MII en Argentina.

Fundamentalmente, el éxito de las especies invasoras es resultado de la conjunción de factores: 1) intrínsecos de la especie (tasa de reproducción, masa corporal, abundancia, tamaño del área de distribución natural) y 2) extrínsecos, o del hábitat que invaden (disponibilidad de nichos vacantes y recursos alimenticios, clima, entre otros). Sin embargo, no es posible establecer generalizaciones que permitan caracterizar la invasión de una especie, ya que este proceso varía de región a región y de ecosistema a ecosistema.

En particular, los mamíferos son uno de los grupos de invasores biológicos más exitosos y sus interacciones socioculturales son especialmente fuertes. Los MII en América representan alrededor del 20% de las introducciones de mamíferos en todo el mundo, y su mayor densidad se concentra en América del Sur. De un total de 37 especies citadas, el 76% (excluyendo las especies domésticas) ocuparon el cono sur de Argentina y Chile. La mayoría de las introducciones de mamíferos fueron hechas deliberadamente por el ser humano para posibilitar su caza deportiva, realizar actividades de explotación económica o confinar los animales en explotaciones privadas, rurales, criaderos, parques o zoológicos donde constituyeron poblaciones asilvestradas. En ausencia de regulaciones específicas, estas introducciones ocasionaron perjuicios de amplio impacto por la expansión de varias especies, en ciertos casos incontrolables, como el jabalí (*Sus scrofa*). La tendencia en la investigación de MII en Argentina entre los años 1978 y 2021 se enfocó principalmente en abordajes biológicos y ecológicos, así como de impacto ambiental. Menor importancia presentan las aproximaciones en investigación aplicada, mostrando que aún existen importantes vacíos, tanto en estudios de impactos económicos, sociales y culturales como de desarrollo de políticas de manejo.

La comunidad científica ha identificado a las invasiones biológicas como un fenómeno de disrupción y amenaza al mantenimiento de la biodiversidad. Algunos autores también consideran a las especies invasoras como organismos modelo que podrían proporcionar una comprensión más general de la naturaleza y de problemas aplicados, como la extinción, funcionamiento de ecosistemas y respuestas al cambio climático. Más aún, las invasiones biológicas abarcan una amplia gama de dimensiones de investigación que va desde los aspectos biológicos-ecológicos a consideraciones socio-económicas, análisis de riesgos y desarrollo de políticas.

Al estudiar las invasiones biológicas como un proceso multifacético con grandes impulsores y una serie de pasos secuenciales, los MII ofrecen un modelo único y una oportunidad para una agenda de investigación que engloba una gran diversidad de temas y dimensiones. Tal programa de investigación fundamental, junto con la planificación estratégica e integrada con organismos gubernamentales, agencias estatales en varios niveles y diferentes sectores sociales, políticos y económicos, debe proporcionar las bases para prevenir la homogeneización biótica y la pérdida de biodiversidad en los principales ecosistemas de Argentina.

Introduction

> "…Few countries have undergone more remarkable changes, since the year 1535, when the first colonist of La Plata landed with seventy-two horses. The countless herds of horses, cattle, and sheep, not only have altered the whole aspect of the vegetation, but they have almost banished the guanaco, deer and ostrich. Numberless other changes must likewise have taken place; the wild pig in some parts probably replaces the peccari; packs of wild dogs may be heard howling on the wooded banks of the less-frequented streams; and the common cat, altered into a large and fierce animal, inhabits rocky hills." (Darwin, 1833).

Species that experience rapid range expansions into a non-native location via human actions are defined as being both introduced and invasive (Lockwood *et al.*, 2007). These species also provoke changes in ecological, economic, and social systems as a result of their new interactions in the recipient environment (Simberloff *et al.*, 2013; Blackburn *et al.*, 2014). The impact upon the new region is context-dependent and is contingent on both the identity of the invader (*i.e.*, on its biological traits) and the recipient community or ecosystem (*i.e.*, on the biological traits of resident species) (Valéry *et al.*, 2008). Typically, ecologists also have identified biological invasions as an ecological disturbance and a threat to biodiversity (Vitousek *et al.*, 1996).

However, non-native and even invasive species also can provide benefits to some stakeholders and conceptually are a source of opportunities to understand fundamental ecological and evolutionary processes of ecosystems (Sax *et al.*, 2007). The benefits from some non-native species are pervasive and integral components of our global economy. For example, fiber-producing crops, such as cotton, are often grown outside of their native range to great advantage, and livestock, such as sheep, that produce food and material for clothing; these benefits are typically received from managed species (Sax *et al.*, 2007). The negative costs of introduced species usually come from those that have become naturalized and invasive; that is, those which have established self-sustaining populations in the absence of human assistance and expanded their range across the recipient environment. These invasive species have caused or contributed to the extinction of many native species, as exemplified by rats and cats introduced onto islands (Blackburn *et al.*, 2005; Medina *et al.*, 2011; Harper and Bunbury, 2015 and references therein). Thus, biological invasions can generate enormous environmental damage and have been considered analogous to natural disasters (Ricciardi *et al.*, 2011).

Globally, the list of human-introduced species increases, as does the number of those that become invasive and have significant ecological, economic, and cultural effects (Mooney and Hobbs, 2000). Therefore, biological invasions are actually socio-ecological phenomena because humans are involved as both a driver and recipient in the entire invasive process: they serve as vectors for introductions (accidental or intentional), suffer the consequences, and possess the capacity to act and make decisions for managing these species (García Llorente *et al.*, 2008) (see Anderson and Pizarro, this volume). Environmental decision-makers and scholars recognize the need to integrate the social dimension into biological invasions research and extend it beyond the fields of biology and ecology, encompassing sociological, political and economic aspects of the problem that must be understood to develop effective policies and management solutions (Van Wilgen *et al.*, 2014; Estévez *et al.*, 2015; Schiavini *et al.*, 2016).

In this context, introduced invasive mammals (IIMs) stand out for being more invasive than other vertebrates, and their social-cultural interactions are especially stronger (Jeschke, 2008; Ballari *et al.*, 2016). IIMs in the Americas represent about 20% of mammal introductions worldwide, and their high species richness is concentrated in South America's Southern Cone (Novillo and Ojeda, 2008; Ballari *et al.*, 2016). The aim of this chapter is to provide an overview of the state-of-the-art on IIMs in Argentina. In the **first section,** we introduce key concepts of the biological invasion process, using IIM examples in Argentina. The **second section** discusses niche theory applied to biological invasions and some case studies for the country. In the **third section,** we examine the main contributions of IIM research in Argentina. Finally, we propose IIMs as a research model to better understand ecological processes (*e.g.*, niche, competition, disturbance dynamics, etc.) and as a tool for the conservation and management of biodiversity.

Invasion process of introduced invasive mammals in Argentina

A "biological invasion" is the end product of a multi-staged process (Lockwood *et al.*, 2007), which is not necessarily linear. Each stage includes a series of barriers or ecological filters, and species must pass these to advance to the next stage in the invasion process (Richardson *et al.*, 2000; Colautti and MacIsaac, 2004). At the same time, each stage is associated with a term that indicates the degree of progress: introduction, naturalization/establishment, expansion, and invasion. Here, we use the term IIMs to refer to introduced mammals that have passed the stages of establishment and expansion in Argentina (*i.e.*, are or are becoming "invasive").

The terminology, definitions and stage numbers of the biological invasion process vary among authors (Valéry *et al.*, 2008; Blackburn *et al.*, 2011), generating different interpretations and some confusion regarding concepts and theory (Colautti and MacIsaac, 2004). In this contribution, we follow the neutral theoretical framework suggested by Colautti and MacIsaac (2004) with seven distinct stages, attempting to avoid preconceived terms and imprecisions (Fig. 1). The model begins with a "Stage 0," defined by the potential invading propagules resident in a main donor region (previous to primary dispersal stage). If these propagules go through the primary dispersal filter, into the transport vector, they pass to "Stage I". If they survive the transport vector and release filter, they pass to "Stage II." Those propagules that become established and proliferate, survive in the new environment and go through the reproduction filter in a novel region pass to "Stage III." Finally, there are four categories of established species, based on two filters: local dispersal, and environment and community suitability. Thus, local dispersal of individuals (*i.e.*, propagule pressure) determines which Stage III species (localized, but rare) reach "Stage IVa" (widespread, but rare), or which "Stage IVb" species (localized, but dominant) reach "Stage V" (widespread and dominant). Also, environment and community suitability filters determine if species at stage III reach stage IVb, or which stage IVa species go on to Stage V (Fig. 1). Three factors affect the probability that a potential invader will pass through each filter: propagule pressure (PP); environmental requirements of the potential invader (physico-chemical) (ER), and community interactions (CI).

The IIMs in Argentina exhibit intrinsic (*i.e.*, high dispersal capacity, high reproductive capacity, broad diet, habitat generalists) and extrinsic attributes (*i.e.*, vacant niches, natural enemy release, diversity of resources, climate matching), as well as factors associated with human activity (*i.e.*, game hunting or commercial purposes, transport vectors and pathways, propagule pressure), that can explain successful invasions. For example, the Pallas's

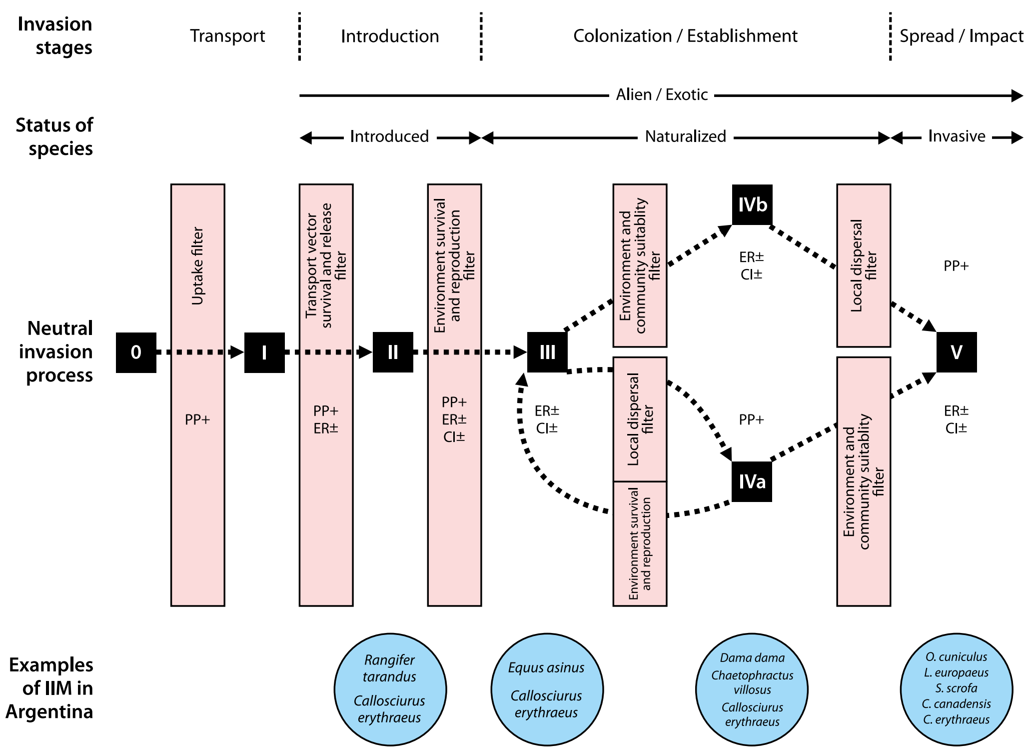

Figure 1. The biological invasion process defined using a proposed neutral theoretical framework (modified from Colautti and MacIsaac, 2004), merging the stages in the process with commonly used terms and the status of species (Catford *et al.*, 2009). In the lower portion of the figure, several introduced invasive mammals are categorized based on their status in different parts of Argentina. For example, Pallas's squirrel (*Callosciurus erythraeus*) was introduced to two sites in the city of Buenos Aires (**Stage II**). Pallas's squirrel have established, but localized populations in Salto (Buenos Aires province) (**Stage III**). Pallas's squirrel is localized and dominant (**Stage IVb**) in Arrecifes (Buenos Aires province), as well as the hairy armadillo (*Chaetophractus villosus*) in Tierra del Fuego's main island (**Stage IVa**). Pallas's squirrel is widespread and dominant in Luján (Buenos Aires province) (**Stage V**).

squirrel (*Callosciurus erythraeus*) was able to successfully colonize a broad area, starting with 10 initial individuals that have kept expanding to become one of the country's main foci of invasion (Aprile and Chicco, 1999; Benitez *et al.*, 2013). Furthermore, given their charismatic appeal, these squirrels are transported and released by people, which provides new invasion points due to translocation events (Guichón *et al.*, 2015). This case also allows us to establish different stages of the invasion process for different squirrel focal points (see Fig. 1). Thus, the Pallas's squirrel shows high invasive potential in Argentina, due to its charismatic appeal combined with high reproductive potential, the probability of establishment from a few founding individuals, its ability cope with modified environments and a lack of natural enemies (see also Guichón *et al.*, this volume; Gozzi *et al.*, this volume). For its part, the American mink (*Neogale vison*) is another successful invader in Argentina, introduced for fur farming and subsequently establishing itself in the wild (Fasola and Valenzuela, 2014). The American mink shows remarkable ecological adaptability, as a carnivore with a generalist and opportunistic diet, a high reproductive rate, particular reproductive features (*e.g.*, delayed implantation), and high genetic variability that allows it to inhabit a wide range of habitats (Valenzuela *et al.*, 2016; Malerba *et al.*, 2018).

In particular, the niche requirements of an introduced species can be used as predictors of potential invasion risk in areas of introduction and establishment (Qiao *et al.*, 2017). Environmental factors (biotic and abiotic) in the native range would pre-adapt populations for similar habitat types in the invaded range (*i.e.*, habitat suitability) (Lee, 2011). For example, many IIMs occupy ecoregions similar to their native ranges, which provide good climate niche matching, but some species have even experienced range expansions to completely new habitat types (Novillo and Ojeda, 2008; Ojeda *et al.*, 2010), which are discussed in the next section.

Niche theory applications for invasive species

A given species can persist under a limited set of habitat conditions. Therefore, a habitat's biotic and abiotic factors are relevant for enabling an organism to survive and reproduce, determining its environmental niche (Hutchinson, 1959) (Fig. 2). Niche differentiation between native and recipient ranges may result from changes in either the fundamental niche of the species (*i.e.*, the requirements of a species to maintain a positive population growth rate, disregarding biotic interactions) or the realized niche (*i.e.*, the fundamental niche constrained by biotic interactions) (Broennimann *et al.*, 2007).

The distinction between realized and fundamental niches is important for describing and understanding niche dynamics—expansion, contraction or shift of a species' niche- (Pearman *et al.*, 2008). Thus, when propagules are transported to a novel range, there could be a match between their realized niche and at least one habitat in the area of introduction (*i.e.*, habitat compatibility) to enable their survival at initial stages of invasion (Steinmaus, 2011). In other words, a proportion of the native niche should be overlapping the introduced niche (*i.e.*, niche stability) (Guisan *et al.*, 2014) (Fig. 2). The challenges imposed by abiotic and biotic factors in novel ranges could induce a rapid evolutionary response and introduced species would undergo niche shifts (Lee, 2011). Thus, introduced species

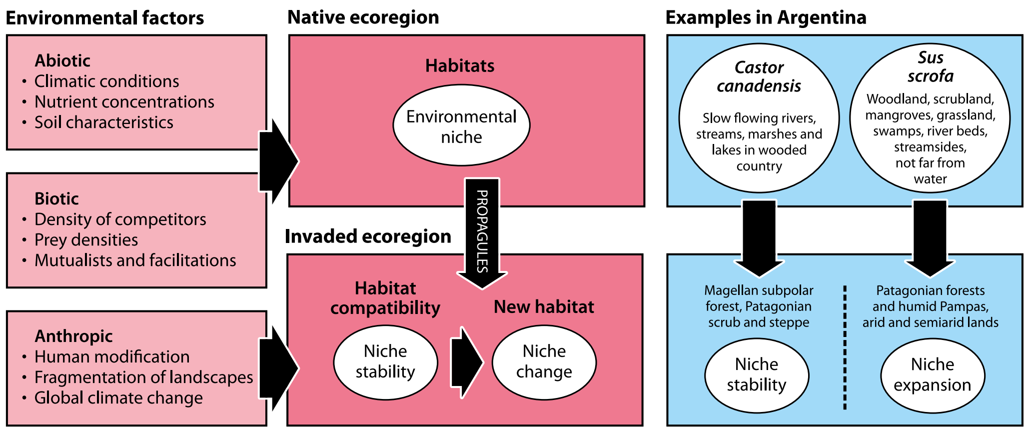

Figure 2. Representation of native and invaded ecoregions showing environmental factors that determine environmental niche (**left**); changes in the niche (stable, changed or expanded) (**center**) and possible examples with introduced invasive mammals in Argentina (**right**).

experience changes in their ecological processes in a new geographic range. For example, release from natural enemies in the new environment could influence their environmental niche (Pearman *et al.*, 2008). In this sense, niche shift may be a factor in mediating the establishment and expansion success of the organism introduced into a novel environment (Broennimann *et al.*, 2007).

Nevertheless, ecological and evolutionary theory suggests that niche conservatism ought to be more common than niche shifts (Qiao *et al.*, 2017). Niche shifts confound the idea of fundamental niche with aspects of condition availability across real-world landscapes. Thus, the use of new environments by invasive species in the invaded range may require conditions that are unavailable or inaccessible in the native range (Fig. 2). For example, the wild boar (*Sus scrofa*) occupies a broad range of habitats in Argentina, from the Patagonian forests and humid pampas to arid and semiarid regions (Cuevas *et al.*, 2013a). In the temperate Monte Desert, wild boar could be invading a new environment, therefore experiencing a niche expansion (Ojeda *et al.*, 2010) (Fig. 2). On the other hand, the North American beaver (*Castor canadensis*) inhabits slow-flowing rivers, streams, marshes and lakes in wooded country in North America, from Alaska south to northern Mexico (Long, 2003). In Tierra del Fuego, it occupies ecosystems, such as the Magellanic subpolar forest and Patagonian scrub and steppe, limited mainly by hydrological resources (Wallem *et al.*, 2007) (Fig. 2). Another good example is the establishment of the European rabbit (*Oryctolagus cuniculus*) in central Chile, where the climate matches that of its native range (Mediterranean-type climate). When the rabbit population expanded towards Argentina (Neuquén and Mendoza provinces), it initially established in two different environments: one to the west where a rainy Mediterranean climate prevails and another one to the east with semiarid Mediterranean characteristics. Therefore, the principal invaded distribution in Argentina also shows a climate regime similar to that of the native range (Bobadilla *et al.*, 2021). This is reflected in the good match between native and invaded ecoregions and partially explains the successful establishment of this IIM.

In summary, niche dynamics occur during the biological invasion process as a result of differences in the realized niche (*i.e.*, where the biotic interactions are important) or adaptation to new conditions (*i.e.*, where rapid evolutionary responses are important) (Broennimann *et al.*, 2007; Steinmaus, 2011). In this way, extrinsic factors (*e.g.*, transport vectors and release filter, local dispersal filter; see Fig. 1) impose challenges and opportunities for invading species, while intrinsic properties of organisms and populations (*i.e.*, body size, locomotion, reproductive rate, population size, habitat and trophic ecology) dictate their response to extrinsic factors via mechanisms like phenotypic plasticity or evolutionary adaptation (Lee, 2011).

Historical context of IIM research in Argentina

Like in many other regions, biological invasions pose a serious threat to biodiversity in South America, where 41 out of the 100 most invasive species in the world are already established (Speziale *et al.*, 2012; Ballari *et al.*, 2016). In this way, the publication trend on biological invasions at the regional level has been shown to correlate with or even exceed that seen at the global level, and Argentina is the Latin American and Caribbean country with the most ISI-indexed publications on this subject (Pauchard *et al.*, 2011). The same trend is shown for research on IIMs where the number of studies published in South America has increased exponentially since the beginning of the 21st century, and Argentina has shown a marked increase, especially between 2006 and 2010 (Fig. 3). Despite this, Speziale *et al.* (2012) showed that research trends in non-native species are not of major concern for South American countries. This could reflect a low level of social interest due to historical and recent socio-cultural particularities. For example, South American societies are often dominated by more recent immigrants or a rural to urban transformation could suffer "generational amnesia," meaning urban residents are not aware of the past biological environmental conditions (Speziale *et al.*, 2012). Overall, an historical understanding of species introductions demonstrates how they have been driven largely by human social practices that have existed and, in some cases, still exist, whereby native species are either less known or less valued than those brought from other parts of the world to "improve" local ecosystems (Anderson and Valenzuela, 2014; Archibald *et al.*, 2020; Anderson and Pizarro, this volume). Particularly, introduced mammals are associated with human activities and the principal reasons why they were brought to southern South America were hunting, livestock, fur trade, pets, aesthetic purposes and so on (Long, 2003; Ballari *et al.*, 2016).

In Argentina, the first assessments of introduced mammals occurred before the 1980s with the contribution of Daciuk (1978), who studied the Araucana sub-region. This author provided the first data on the introduction of red deer (*Cervus elaphus*) into Chubut province and reindeer (*Rangifer tarandus*) to Tierra del Fuego Island and South Georgia Island. Nowadays, there are no reindeer on Tierra del Fuego, and they have been eradicated from some sectors of South Georgia Island (Adalbjornsson, 2018). Some years later, Jackson (1985) documented the status, population trends and expansion of the blackbuck (*Antilope cervicapra*) across some regions of the country. Since 1990, with the consolidation of invasion biology as a subdiscipline of ecology, research on the IIMs in Argentina has begun to

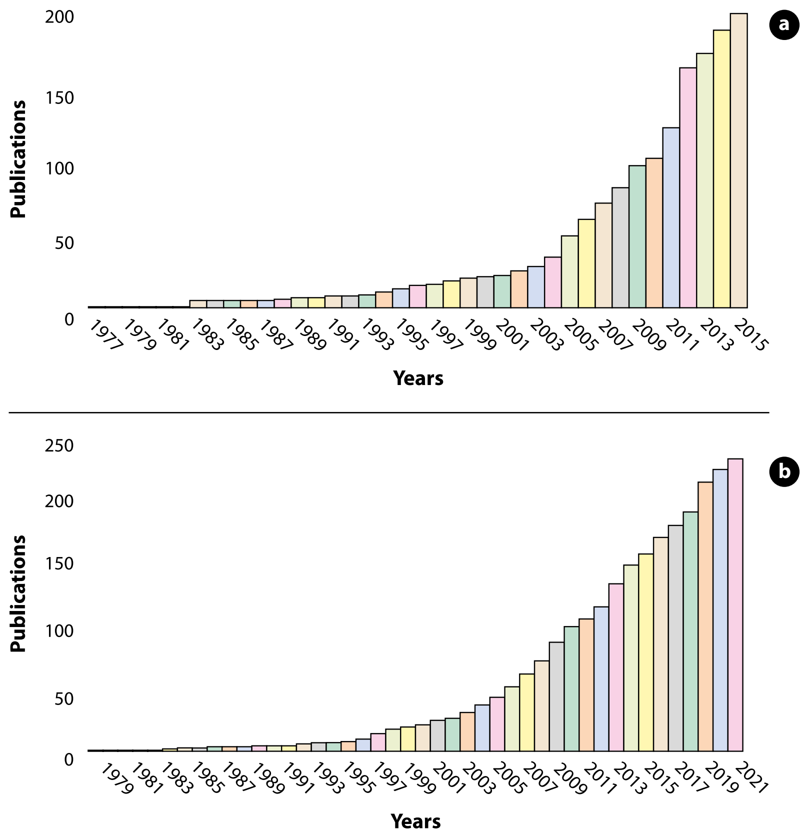

Figure 3. a. Number of papers published on introduced invasive mammals in South America, represented cumulatively between 1977 and 2014 (Ballari *et al*., 2016); **b.** Number of scientific publications on introduced invasive mammals in Argentina graphed cumulatively between 1977 and 2021 (reviews not included).

flourish, starting with seminal studies of the impact of North American beavers in Tierra del Fuego (Lizarralde, 1993) and the diet and habitat use of the American mink in Patagonia (Previtali *et al*., 1998).

A synthesis of IIM research in Argentina is presented in Table 1, where we have considered 1) the type of study carried out: biological and ecological, of impacts (inside protected areas or in unprotected areas) or management, and 2) the taxa studied. We found 248 IIM studies published in Argentina between 1978–2021. Forty-one percent (n=102) of the studies have been focused on the biology and ecology of the mammal species, principally on their habitat and diet (18%) and dispersal and population (16%). To a lesser extent, 33% (n=82) of the studies have been focused on the impacts, where the most evaluated environment consequences are inside protected areas (19%). The most studies in unprotected areas were about zoonotic diseases (13%), and only two studies quantify economic impacts. Only 8% of publications have been focused on applied research. Of these studies, only 2% were on social and education topics, while the 6% were about policy development and management. Finally, a category of "other," including reviews and inventories, represented 18% of the total (Table 1).

Table 1. Summary of the principal literature on introduced invasive mammals in Argentina, identifying the characteristics of each publication. For this analysis, feral domestic mammals, such as horses, dogs, cats and livestock, are not included.

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Chaetophractus villosus	Abba *et al.,* 2005[1] Poljak *et al.,* 2007[2] Abba *et al.,* 2014[2] Cabello *et al.,* 2017[1] Gallo *et al.,* 2020[2] Poljak *et al.,*2020[4]				Valenzuela *et al.*, 2014 Ezquiaga *et al.*, 2016 Gallo *et al.*, 2019
Lycalopex gymnocercus	Funes *et al.,* 2006[3] APN, 2007[2] Gómez *et al.,* 2010[1]				Jaksic *et al.*, 2002 Zanini *et al.*, 2006 Valenzuela *et al.*, 2014 Luengos Vidal *et al.*, 2019
Neogale vison	Previtali *et al.,* 1998[1] Gómez *et al.,* 2010[1] Fasola *et al.,* 2011[2] Valenzuela *et al.,* 2013a[1] Valenzuela *et al.,* 2013b[1] Guichón *et al.,* 2016[2] Fasola and Roesler, 2018[1] Malerba *et al.,* 2018[3] Failla and Fasola, 2019[2]	Peris *et al.*, 2009[5] Fasola *et al.*, 2009[6] Roesler *et al.*, 2012[5]		Fasola and Valenzuela, 2014 Fasola and Roesler, 2016	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Valenzuela *et al.*, 2014 Valenzuela *et al.*, 2019
Sus scrofa	Merino and Carpinetti, 2003[2] Pescador *et al.*, 2009[2] Cuevas *et al.*, 2010[1] Cuevas *et al.*, 2013a[1] Cuevas *et al.*, 2013b[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Nuñez *et al.*, 2013[1] Ballari *et al.*, 2015b[1] Gantchoff and Belant, 2015[1] Guichón *et al.*, 2016[2] Soteras *et al.*, 2017[1] Caruso *et al.*, 2018[1] Sagua *et al.*, 2018[4] Acosta *et al.*, 2019[4] Ballari *et al.*, 2019c[1] Panebianco *et al.*, 2019[1]	Campos and Ojeda, 1997[5] Vázquez, 2002[6] Meier and Merino, 2007[5] Pérez Carusi *et al.*, 2009[5] Cohen *et al.*, 2010[6] Sanguinetti and Kitzberger, 2010[5] Barrios-García and Ballari, 2012[5] Cuevas *et al.*, 2012[5] Barrios-García and Simberloff, 2013[5] Barrios-García *et al.*, 2014[5] Winter *et al.*, 2019[6] Ballari *et al.*, 2020[5] Cuevas *et al.*, 2020[5] Bercê *et al.*, 2021[5]		Ballari *et al.*, 2015a Gürtler *et al.*, 2018 Gürtler and Cohen, 2021 Nicosia *et al.*, 2021	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Valenzuela *et al.*, 2014 Ballari and Barrios-García, 2014 Cuevas *et al.*, 2016 Sanguinetti and Pastore, 2016 Ballari *et al.*, 2019a

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Dama dama	Frisina and Frisina, 1997[1] Relva and Caldiz, 1998[1] Flueck, 2010[2] Barrios-García *et al.*, 2012[1] Ballari *et al.*, 2019c[1]	Veblen *et al.*, 1989[5] Veblen *et al.*, 1992[5] Vázquez, 2002[6] Simberloff *et al.*, 2003[5] Nuñez *et al.*, 2008[5] Relva *et al.*, 2009[5] Relva *et al.*, 2010[5] Relva and Nuñez, 2014[5] Relva *et al.*, 2014[5]			Daciuk, 1978 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Barrios-García *et al.*, 2019
Axis axis	Burgueño *et al.*, 2021[1]	Relva and Veblen, 1998[3]		Gürtler *et al.*, 2018 Gürtler and Cohen, 2021 Nicosia *et al.*, 2021	Daciuk, 1978 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Fracassi *et al.*, 2010 Tellarini *et al.*, 2019
Cervus elaphus	Bahamonde *et al.*, 1986[1] Relva and Caldiz, 1998[1] Flueck *et al.*, 1999[1] Flueck, 2001[2] Flueck *et al.*, 2003[2] Flueck, 2004[3] Flueck *et al.*, 2005[2] Ortiz and Bonino, 2007[1] Soler *et al.*, 2007[4] Aller *et al.*, 2009[4] Flueck, 2010[2] Flueck and Smith-Flueck, 2011[4] Barrios-García *et al.*, 2012[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Nuñez *et al.*, 2013[1] Guichón *et al.*, 2016[2] Ballari *et al.*, 2019c[1]	Veblen *et al.*, 1989[5] Veblen *et al.*, 1992[5] Relva and Veblen, 1998[5] Relva and Sancholuz, 2000[6] Vázquez, 2002[6] Simberloff *et al.*, 2003[5] Flueck and Jones, 2006[6] Meier and Merino, 2007[5] Nuñez *et al.*, 2008[5] Relva *et al.*, 2009[5] Relva *et al.*, 2010[5] Flueck and Smith-Flueck, 2012[6] Relva and Nuñez, 2014[5] Relva *et al.*, 2014[5] Reissig *et al.*, 2016[6] Charro *et al.*, 2018[6] Reissig *et al.*, 2018[6]		Sanguinetti *et al.*, 2014	Daciuk, 1978 Jaksic *et al.*, 2002 Novillo and Ojeda, 2008 Merino *et al.*, 2009 Relva and Sanguinetti, 2016 Relva *et al.*, 2019
Antilope cervicapra	Jackson, 1985[1] Frisina and Frisina, 1997[1] Carpinetti, 2001[2]				Novillo and Ojeda, 2008 Merino *et al.*, 2009 Ballari *et al.*, 2019b

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Callosciurus erythraeus	Guichón *et al.*, 2005[2] Guichón and Doncaster, 2008[2] Bridgman *et al.*, 2012[2] Benitez *et al.*, 2013[2] Gabrielli *et al.*, 2014[4] Guichón *et al.*, 2015[2] Coniglione and Zalba, 2018[2] Zarco *et al.*, 2018[1] Guichón *et al.*, 2020[2]	Gozzi *et al.*, 2013a[6] Gozzi *et al.*, 2013b[6] Gozzi *et al.*, 2014[6] Messetta *et al.*, 2015[6] Bobadilla *et al.*, 2016[6] Pedreira *et al.*, 2017[7] Gozzi *et al.*, 2020[6] Pedreira *et al.*, 2020[7]	Borgnia *et al.*, 2013	Benitez *et al.*, 2010 ENEEI, 2016	Aprile and Chicco, 1999 Fasola *et al.*, 2005 Novillo and Ojeda, 2008 Cassini and Guichón, 2009 Guichón *et al.*, 2019
Castor canadensis	Lizarralde, 1993[2] Lizarralde *et al.*, 2004[2] Lizarralde *et al.*, 2008[4] Fasanella *et al.*, 2010[4] Pietrek and González-Roglich, 2015[1] Davis *et al.*, 2016[1] Pietrek *et al.*, 2016[1] Pietrek *et al.*, 2017[2] Eltall *et al.*, 2019[2] Feldman *et al.*, 2020[1] Huertas Herrera *et al.*, 2020[2]	Lizarralde *et al.*, 1996[5] Vázquez, 2002[6] Martínez Pastur *et al.*, 2006[6] Anderson and Rosemond, 2010[5] Wallem *et al.*, 2010[6] Simanonk *et al.*, 2011[6] Ulloa *et al.*, 2012[5] Anderson *et al.*, 2014[5] Henn *et al.*, 2014[6] Henn *et al.*, 2016[5] Westbrook *et al.*, 2017[5] García and Rodríguez, 2018[6] Francomano *et al.*, 2021[6]	Estévez *et al.*, 2014 Santo *et al.*, 2015 Anderson *et al.*, 2017 Santo *et al.*, 2017	Sanguinetti *et al.*, 2014 Anderson *et al.*, 2015 ENEEI, 2016 Schiavini *et al.*, 2016 Jusim *et al.*, 2020 Pastur *et al.*, 2021	Daciuk, 1978 Jaksic *et al.*, 2002 Coronato *et al.*, 2003 Wallem *et al.*, 2007 Anderson *et al.*, 2009 Pietrek and Fasola, 2014 Valenzuela *et al.*, 2014 Anderson *et al.*, 2019
Ondatra zibethicus	Deferrari *et al.*, 1996[2] Deferrari, 2011[1]	Vázquez, 2002[6] Deferrari, 2006[5]			Daciuk, 1978 Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Deferrari, 2019
Mus musculus	Miño *et al.*, 2007[1] León *et al.*, 2007[2] Gómez *et al.*, 2008[2] Guidobono *et al.*, 2009[3] Cavia *et al.*, 2009[1] Vadell *et al.*, 2010[4] León *et al.*, 2013[1]	Larrieu *et al.*, 2004[5] Aristegui *et al.*, 2015[6] Fitte and Kosoy, 2021[6]			Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Cavia *et al.*, 2019a
Rattus rattus, R. norvegicus	Gómez Villafañe and Busch, 2007[1] Gómez Villafañe *et al.*, 2008[2] Cavia *et al.*, 2009[1] Vadell *et al.*, 2010[4]	Cueto *et al.*, 2008[5] Shepherd and Ditgen, 2012[5], 2013[5] Gómez Villafañe *et al.*, 2013[6] Alonso *et al.*, 2019[6] Fitte and Kosoy, 2021[6]			Novillo and Ojeda, 2008 Valenzuela *et al.*, 2014 Cavia *et al.*, 2019b Cavia *et al.*, 2019c

Table 1. (Continued).

Species	Biology and ecology	Impact	Social perception and education	Policy development and management	*Other
Lepus europaeus	Grigera and Rapoport, 1983[2] Bonino and Montenegro, 1997[4] Campos *et al.*, 2001[1] Puig *et al.*, 2007[1] Nabte *et al.*, 2009[2] Bonino *et al.*, 2010[2] Galende and Raffaele, 2008[1] Galende and Raffaele, 2013[1] Gantchoff *et al.*, 2013[1] Lantschner *et al.*, 2013[1] Gantchoff and Belant, 2015[1] Puig *et al.*, 2015[1] Puig *et al.*, 2017[1]	Bonino *et al.*, 1997[5] Vázquez, 2002[6] Delibes *et al.*, 2003[5] Kleiman *et al.*, 2004[6] Puig *et al.*, 2006[5] Kufner *et al.*, 2008[5] Raffaele *et al.*, 2011[5] Palacios *et al.*, 2012[5] Zanón Martínez *et al.*, 2012[5] Reus *et al.*, 2013[5] Scioscia *et al.*, 2013[6] Puig *et al.*, 2014[5] Barbar *et al.*, 2018[5] Barbar and Lambertucci, 2019[6] Aguirre *et al.*, 2021[6]			Daciuk, 1978 Hiraldo *et al.*, 1995 Donázar *et al.*, 1997 Novaro *et al.*, 2000 Jaksic *et al.*, 2002 Donadio *et al.*, 2005 Monserrat *et al.*, 2005 Campos *et al.*, 2008 Merino *et al.*, 2009 Monteverde *et al.*, 2019
Oryctolagus cuniculus	Howard and Amaya, 1975[2] Bonino and Soriguer, 2004[2] Bonino and Borrelli, 2006[1] Bonino and Soriguer, 2008[4] Galende and Raffaele, 2008[1] Bonino and Soriguer, 2009[2] Nabte *et al.*, 2009[2] Cuevas *et al.*, 2011[2] Laspina *et al.*, 2013[1] Galende, 2014[2] Guichón *et al.*, 2016[2] Udrizar Sauthier, 2017[2]	Vázquez, 2002[6] Delibes *et al.*, 2003[5] Veblen *et al.*, 2004[6] Bonino, 2006[6] Barbar and Lambertucci, 2019[6] Bobadilla *et al.*, 2020[5]			Daciuk, 1978 Hiraldo *et al.*, 1995 Donázar *et al.*, 1997 Jaksic *et al.*, 2002 Aparicio *et al.*, 2004 Donadio *et al.*, 2005 Aparicio *et al.*, 2006 Bonino and Donadio, 2010 Valenzuela *et al.*, 2014 Cuevas *et al.*, 2019

*Includes reviews, inventories and general topics.

Type of research is noted using numbered superscripts (1–7) for Biology and ecology ([1]Habitat and diet, [2]Population and dispersal, [3]Behavior, [4]Reproduction and genetics); Impacts: Environmental impacts ([5]Protected areas / [6]Non-protected areas) and [7]Economic impacts.

Among the 248 publications, the most-studied orders were Cetartiodactyla (37%), Rodentia (32%), Lagomorpha (20%), and Carnivora (8%), followed by Cingulata (3%). The most-studied species were the red deer (13%), wild boar (13%), North American beaver (13%), European hare (*Lepus europaeus*) (12%), European rabbit (9%), and Pallas's squirrel (8%).

IIM research highlights per taxonomic order

Cingulata. A particular example is the large hairy armadillo (*Chaetophractus villosus*), endemic to southern South America, but introduced and invasive on Tierra del Fuego's main island since about 20 years ago (Poljak *et al.*, 2007).

Carnivora. There are studies on American mink related to its diet and habitat use (Valenzuela *et al.*, 2013a,b). However, several relevant issues, such as population trends, behavior and genetics, have not been well addressed. Within this group, the grey fox (*Lycalopex gymnocercus*) is another example of a native species from the South American mainland, but that has been introduced and become invasive to Tierra del Fuego Island (Ojeda *et al.*, 2016).

Cetartiodactyla. The red deer has been rather well studied, but this is not the case for the blackbuck. Some studies on fallow deer (*Dama dama*) have been associated with red deer on Argentina's Patagonian steppe (Frisina and Frisina, 1997). Various aspects of the wild boar have been studied, such as diet and habitat use in different ecoregions like Patagonia (Soteras *et al.*, 2017), Monte (Cuevas *et al.*, 2010, 2013a) and Espinal (Caruso *et al.*, 2018). However, studies on reproduction and behavior have not been explored.

Rodentia. Cosmopolitan species, such as the brown rat (*Rattus norvegicus*), black rat (*Rattus rattus*) and house mice (*Mus musculus*), have been the subject of different studies, particularly epidemiology (Gómez Villafañe *et al.*, 2013; Aristegui *et al.*, 2015). Muskrats (*Ondatra zibeticus*) have few studies about habitat use and ecological trends (Deferrari *et al.*, 1996, Deferrari, 2006, 2011), but there is no research about their impact or management. A substantial body of knowledge has been produced by multiple studies on the Pallas's squirrel in periurban and urban areas (Guichón *et al.*, 2015; see also Guichón *et al.*, this volume, and Gozzi *et al.*, this volume) and on the North American beaver, as an invasive ecosystem engineer in Tierra del Fuego Archipelago (Anderson *et al.*, 2009; Schiavini *et al.*, 2016).

Lagomorpha. From 1980 onwards, there has been an increase in research on the European rabbit and European hare, aiming to provide information about its, morphology, distribution, diet, diseases (*e.g.*, myxomatosis) and interspecific interaction (Galende and Raffaele, 2008, 2013; Gantchoff *et al.*, 2015; Bobadilla *et al.*, 2020), but there are no data about management for both species in Argentina. A recent publication by Bobadilla *et al.* (2022) deals with the ecology of the European rabbit in its invading front range in central Argentina.

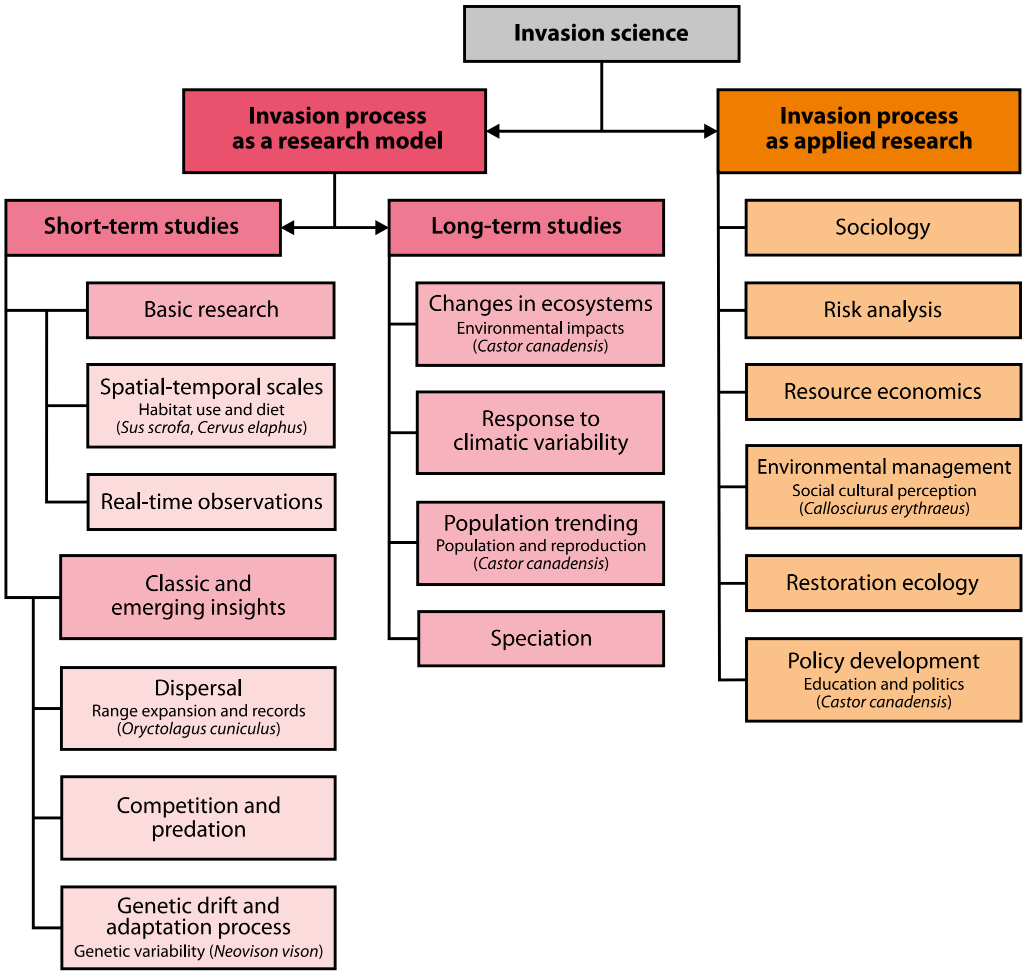

Figure 4. Invasion science research fields and examples for introduced invasive mammals in Argentina (modified from Sax, 2007).

Conclusions

Although significant advances have been made in the understanding of the phenomenon of biological invasions in South America (Jaksic and Castro, 2021, and references therein), there are still important gaps to fill (Lowry *et al.*, 2013; Ojeda, 2016). For example, more than half of the studies have been short-term and oriented to basic research on the biology and ecology of the IIMs in Argentina. Quite a few studies have quantified the ecological impacts of these species, but economic or social impacts are much less studied. However, perhaps the principal gap is in the generation of applied research and interdisciplinary studies, similar to those initial approaches that have been carried out with the North American beaver and the Pallas's squirrel (Fig. 4). At the same time, there is an overrepresentation of a few species (*e.g.*, red deer and North American beaver), while others (*e.g.*, muskrat) are almost not being studied at all. According to Pauchard *et al.* (2011), these differences in effort could be fundamentally due to contributions of the taxon or theme to general hypotheses or theories, or impacts of the taxon in conservation biology or novel taxa for the region.

IIMs provide the focus for a wide array of research dimensions, from biogeography, evolutionary biology, macroecology and community ecology, to ecosystem ecology, restoration ecology, risk analysis, and policy development, among others. A good synthesis of the diversity of research and fertile areas for future studies in the field of biological invasions is provided by Richardson (2011). There is no doubt that introduced invasive species are the research focus of a wide range of scientists and wildlife resource managers, particularly conservation biologists (Sakai *et al.*, 2001). IIMs provide the opportunity to address basic research questions in different disciplines (*e.g.*, ecology, biogeography, evolution, genetics, and conservation biology, among others) that could be used to understand the natural world in a better way. In this way, biological invasions are real-time, natural experiments, offering a scenario where processes occur faster than in most natural systems (Sakai *et al.*, 2001; Sax *et al.*, 2007). Among several examples are the unplanned experiments regarding island invaders and their ecological impacts, eco-evolutionary processes dealing with competition and character displacement, genetic change, rate of range expansion, introduction of pathogens, among others (Sax *et al.*, 2007). In this regard, the research on the North American beaver in the island of Tierra del Fuego is a good example since it represents a natural laboratory for biological and ecological studies (Fig. 4). Invasive species offer unique opportunities to study basic processes in population biology (*i.e.*, life history, demographic models, and so on), evolution (*e.g.*, rapid adaptive evolution), and ecology of interactions between invasive and native species. Some examples of these opportunities are the ecological studies on diet and habitat associations of the American mink or the invasion of new environments by the wild boar (Fig. 4).

Our main purpose in this chapter was to provide a global overview regarding the state-of-the-art in research on introduced invasive mammals in Argentina. By viewing biological invasions as a multifaceted process with major drivers and a series of sequential steps, IIMs offer an especially useful model and opportunity for a research agenda encompassing a rich diversity of topics and dimensions. Such a fundamental research program, coupled with strategic and integrated planning with governmental organisms, state agencies at several levels and different social, political and economic sectors, should provide the grounds for preventing biotic homogenization and biodiversity loss in major ecosystems of Argentina.

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2 RECONCEIVING BIOLOGICAL INVASIONS AS A SOCIO-ECOLOGICAL PHENOMENON USING THE CASE STUDY OF BEAVERS IN PATAGONIA

RECONCEPTUALIZANDO LAS INVASIONES BIOLÓGICAS COMO UN FENÓMENO SOCIO-ECOLÓGICO USANDO EL CASO DE ESTUDIO DEL CASTOR EN PATAGONIA

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Abstract. The ways we conceive biodiversity and nature determine how we investigate and manage it. In the case of introduced invasive species, they have mostly been viewed with an ecological lens, even those with clear ecological and social impacts, such as the North American beaver (*Castor canadensis*) in Tierra del Fuego. We use this case to consider how re-conceiving biological invasions as socio-ecological phenomenon, with multiple human and natural drivers and outcomes, can improve holistic and predictive capabilities of integrated research and management. Specifically, we approach the issue by evaluating how scientific paradigms in ecology have incorporated humans into ecosystems (or not), subsequently applying these perspectives to the conceptualization, study and management of *C. canadensis* in southern Patagonia. We found that most research and management efforts concerning the invasive beaver has been from a perspective that either ignores the human dimension or conceives of humans (and beavers) as agents of ecosystem disturbance. Recently, the multi-faceted roles of humans have been recognized more explicitly. However, social research has been catalyzed largely by a binational political agreement between Argentina and Chile to eradicate beavers and restore "natural" ecosystems, which still conceives of humans as separate from, or disturbers of, nature. Therefore, even though emerging perspectives of beaver research and management increasingly include a human dimension, our evaluation of this case study still finds significant limitations to fully integrated research and applications due to an unconsolidated paradigm of humans as "co-participants" in ecosystems. From this analysis, we propose three lessons that can help re-conceive biological invasions as socio-ecological phenomenon: 1) build a transdisciplinary research agenda, 2) create communities of knowledge between academics, decision-makers and other social actors and 3) teach environmental history and philosophy in the natural science curricula that produce most biological invasion researchers and managers.

Resumen. La forma en que conceptualizamos la biodiversidad y la naturaleza influye fuertemente la manera en la cual la estudiamos y manejamos. Las especies introducidas e invasoras, en este sentido, han sido analizadas principalmente desde la ecología, cuya conceptualización de la naturaleza ha excluido, en gran parte de su historia, a los seres humanos. Por esta razón, a pesar de los grandes avances en el conocimiento de las invasiones biológicas como un fenómeno ecológico, aun sabemos relativamente poco sobre los impactos y repercusiones sociales, culturales y económicas de la introducción de especies en nuevos territorios. Un caso emblemático es el castor norteamericano (*Castor canadensis*), introducido en 1946 desde Canadá al Archipiélago de Tierra del Fuego, territorio transfronterizo entre Argentina y Chile. Usamos este caso para considerar cómo la re-conceptualización de las invasiones biológicas como fenómenos socio-ecológicos podría mejorar las capacidades predictivas y de planteamiento holístico de la ciencia integrada al manejo y las políticas públicas de estas especies. Abordamos este tema, primero, a través de la evaluación de la inclusión de los seres humanos en los paradigmas científicos de la ecología.

Se encontró que los paradigmas dominantes de esta disciplina reconocen a los seres humanos en relación a la naturaleza como 1) promotores de cambio o 2) receptores de beneficios (o perjuicios). Una perspectiva emergente de los humanos es como 3) co-participantes, la cual puede ser identificada a través de la integración de perspectivas de disciplinas sociales, como la geografía humana y la etnoecología. Esta última conceptualización de la relación humano-naturaleza sería también congruente con los cambios sociales y culturales relacionados con la interculturalidad de las sociedades globalizadas y la expansión de la influencia humana sobre la biosfera en el Antropoceno. Luego, aplicamos estas tres perspectivas para analizar la forma en que los castores han sido estudiados y manejados en la Patagonia, revisando además la historia de su introducción e investigación.

Encontramos que la mayor parte de la investigación fue realizada bajo el concepto de «castores como ingenieros ecosistémicos». A partir de estas investigaciones, y en estrecha relación con la aprobación de un acuerdo binacional entre Argentina y Chile para su erradicación en 2008, se lograron importantes avances en el conocimiento ecológico del castor, pero se ignoraron, en gran parte, los aspectos sociales relacionados con su introducción y expansión hacia el continente, no confrontada por las autoridades por más de 60 años. Bajo la segunda aproximación sobre los daños o servicios del castor, agrupamos los estudios que midieron las percepciones de actores sociales específicos (p.ej. estancieros) sobre el efecto que provocan los castores en sus predios. Consideramos que la tercera perspectiva de humanos como co-participantes tiene escaso desarrollo, pero bajo esta categoría agrupamos trabajos recientes en antropología, estudios de la ciencia y la tecnología, y otras investigaciones sobre las percepciones de diversos grupos sociales sobre el castor. Además, recopilamos antecedentes que demuestran la participación de esta especie en la oferta turística y el sentido de pertenencia de los habitantes de Ushuaia en Argentina e Isla Navarino en Chile.

En base al análisis de este caso, mostramos la poca claridad que tenemos sobre la dimensión humana de las invasiones biológicas, y elaboramos tres propuestas desde las lecciones aprendidas de este ejemplo para avanzar en su reconceptualización: 1) construir una agenda de investigación transdisciplinaria, 2) crear comunidades de conocimiento con académicos, tomadores de decisiones y una variedad de actores sociales, y 3) incluir la enseñanza de la historia y la filosofía ambiental como herramienta crítica en el currículo de las ciencias naturales que formará a una nueva generación de investigadores de especies invasoras y gestores de recursos naturales capaces de generar estrategias de manejo adaptativas y socialmente vinculantes en el Antropoceno.

Introduction

References to species "invasions" are not new in the ecological scientific literature. The term is often traced to Charles Elton's (1958) seminal book, entitled *The ecology of invasions by animals and plants*, but earlier antecedents referring to the effects of species introductions were enunciated by Charles Darwin and others as early as the mid-1800s (Cadotte, 2011). However, invasion biology did not consolidate as a sub-discipline of ecology until the 1980s (Huenneke *et al.*, 1988), and its establishment coincides with broader academic efforts at that time to apply largely ecological research to identify and confront major environmental problems (see also the history of conservation biology: Meine *et al.*, 2010). In this context, the spread of introduced species around the globe came to be recognized as a major driver of global ecological change and biodiversity loss, via both species extinctions and biotic homogenization (Vitousek *et al.*, 1997; McKinney and Lockwood, 1999).

Today, invasion biology is a prominent area in ecology, and biological invasion studies account for one-quarter of all ecology publications in Latin America and the Caribbean (Pauchard *et al.*, 2011). Furthermore, articles on invasion biology have great impact, being more cited than those in other prominent areas like population biology or even climate change (Pysek *et al.*, 2006). Indeed, the study of biological invasions has become both productive and influential, with its own journals (*e.g.*, *Diversity and Distributions*, *Biological Invasions*, *NeoBiota*), textbooks (Williams, 1996), research centers and academic conferences (*e.g.*, South Africa's Centre for Excellence in Invasion Biology, the Island Invasive Conference, among others).

Notwithstanding its history of academic success and institutionalization, invasion biology has been criticized by some for being conceptually ambiguous (Woods and Moriarity, 2001; Brown and Sax, 2004), practically ineffective (Davis *et al.*, 2011), and socially or ethically controversial (*e.g.*, Mackenzie and Larson, 2010, see also review in Estévez *et al.*, 2015). These concerns, in turn, brought attention to previously unaddressed dimensions of the biological invasion phenomenon. For example, despite studies that demonstrate invasive species' negative ecological effects, ethnobotanists Pfeiffer and Voeks (2008) point out that for different social actors the cultural effects of biological invasions can indeed be negative, but also neutral or even positive. Plus, only 5–20% of all introduced species become problematic (IUCN 2017).

Yet, multiple literature reviews from regional (Patagonia: Anderson and Valenzuela, 2014), national (Chile: Quiroz *et al.*, 2006) and international scales (Latin America and the Caribbean: Pauchard *et al.*, 2011; global: Estévez *et al.*, 2015) have shown that dominant approaches to both the research and management of biological invasions are skewed towards natural science-based, descriptive quantifications of invasive species' environmental impacts. On the other hand, more mechanistic ecological work, explaining the biological invasion process and including socioeconomic and cultural aspects, has been relatively neglected (García-Díaz *et al.*, 2021). Arguably, it is precisely by labeling, highlighting and orienting our attention towards the negative aspects of the invasion phenomenon that we may be hindering our ability to holistically address the "problem" of biological invasions at the multiple scales and dimensions that it occurs (see extensive work by Larson, B. beginning in 2005 on the biological invasion metaphor).

Despite its biological bias (or perhaps due to it), invasion biology has been effective at positioning this issue as a problem for decision-makers at various political scales. Globally, for example, the discourse on biological invasions appeals to many countries' national security concerns, because the harm to local biodiversity and degradation of ecosystems by introduced invasive species represents a loss to the country's biological heritage, including water, food, and economic security (*e.g.*, Paini *et al.*, 2016). Indeed, we find the issue of biological invasions expressed in various policy-making structures at national (*e.g.*, USA's National Invasive Species Council) and regional levels (*e.g.*, European Commission Committee on Invasive Alien Species). Plus, it has been codified into international policy instruments (*e.g.*, the Convention on Biological Diversity, CBD 1992) and multilateral working groups (*e.g.*, IUCN's Invasive Species Specialist Group – ISSG, see also IUCN 2017). Indeed, the CBD's Aichi Target #9 states that by 2020 "invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment."

However, even the policy emphasis of this biological approach is focused on generic effects of invasive species (*i.e.*, to invade, to threaten) regardless of their social perceptions, local issues and feasibility and desirability of control and eradication measures. Campaigning for the eradication of agricultural pests, such as insects or weeds, is not the same as for charismatic animals (see García-Quijano *et al.*, 2011, see also Guichón *et al.*, this volume); likewise, carrying out an invasive species control program in a remote protected area is not the same as on an inhabited island or populated suburban area. Indeed, both human and biophysical geography are highly relevant to the success or failure of invasive species management, and perhaps part-and-parcel of both the problem and the solution (Estevez *et al.*, 2015). Therefore, overcoming invasion biology's inherited ecological bias is imperative not only for how we understand and study invasive species, but also how we prevent or manage them.

These global tendencies are also mirrored at the sub-regional and national levels in South America. For instance, the Argentine and Chilean governments signed a bilateral agreement to eradicate introduced North American beavers (*Castor canadensis*) to restore invaded ecosystems in southern Patagonia (Menvielle *et al.*, 2010; Malmierca *et al.*, 2011). This agreement was almost entirely informed by ecological data, science and perspectives.

The beaver was introduced to the Argentine portion of Tierra del Fuego in 1946, and for more than 50 years this biological invasion, and its noticeable effects, went mostly unchallenged. Beginning in the late 1990s, however, ecological research positioned this issue and gave rise to the current agreement, which presumes that the eradication of beavers will permit the restoration of native *Nothofagus* forests. However, little consideration was given to the multi-faceted ways that this ostensibly "biological" problem is both the cause and the outcome of interwoven human and natural processes. For example, the absence of a local hunting-trapping culture, the broader program feasibility (biological, physiological, institutional, and financial) and the ultimate desirability (social, cultural, ethical) of eradication/restoration were not considered sufficiently, even for the ostensibly long-term ecological goal of restoring "natural" ecosystems. Furthermore, beyond the authorities, diplomats, natural resource managers, biologists and conservationists involved in the bilateral process that produced the agreement, the engagement and participation of other stakeholders (*e.g.*, local communities, ranchers, tourism operators) was consigned to one clause concerning "educating the public" to encourage their support (see full text at Ministerio de Relaciones Exteriores – Chile, 2008).

The introduction of North American beavers from Canada to Tierra del Fuego constitutes a crucial historical moment in the construction of today's southern Patagonian landscape (see also Archibald *et al.*, 2020). First, as ecologists and later as socio-ecological researchers, we have worked for nearly two decades to understand the historical and present context of this biological invasion. We have discussed the issue in different venues, from local to international levels, and with different audiences, from scientific conferences to decision-making workshops and public seminars and talks. By associating our research with different audiences, we started to understand and compile historical antecedents about southern Patagonia and beaver introduction. Together, these historical processes and research findings comprise a narrative regarding beavers on both social and scientific levels. At the same time, we began to recognize the place and role different actors play in this story. In this context, as a case study, the beaver invasion also helps reveal the complex mixture of issues, beyond its mere ecological impact, that require our attention regarding the conceptual, research, societal, and practical levels of this problem. We believe that an analysis of this case may also help other scientists and practitioners broaden their understanding of biological invasions to recognize and confront them as socio-ecological phenomena. Doing so will require the engagement of other disciplinary experts and social actors, thus expanding human-nature paradigms beyond ecology.

In this chapter, we set out to elucidate how the study of this "problem" is influenced by our conceptualization of both "invasive species" and "nature" in Patagonia. To position this case study in a broader disciplinary context, we first reviewed human-nature paradigms in ecology; then, we organized the examples of beaver invasion research and management based on different ways in which humans and nature are conceived in recent scholarship, including: 1) humans as "drivers" of ecosystem change and 2) humans as "recipients" of ecosystem (dis)services. We also include a third point of view, humans as "co-participants" in socio-ecosystems (Fig. 1), as an inter- or transdisciplinary approach including perspectives traditionally found in disciplines like human geography and the humanities. We expected to find that the scientific literature and management efforts on biological invasions continue to embody the historical bias in ecology-related sciences that highlights humans' role as disturbance agents (*i.e.*, drivers), while emerging social sciences and humanities perspectives, which bring to light other aspects of human agency in nature, including the benefits we receive from it and even our co-participation with and co-production of nature (see Anderson *et al.*, 2021), would be less represented. Via the evaluation of these conceptual issues as they relate to the practice of science and management of beavers in southern Patagonia, we conclude by proposing guidance on developing a new agenda that views biological invasions as a socio-ecological phenomenon.

Paradigm	Emphasis on humans	Study unit	Research topics regarding biological invasions	Conceptual models
"Old" balance of nature paradigm	Humans omitted from ecosystems	"Natural" ecosystems	• Natural history of native ecosystems • Study and conservation of "pristine wilderness" areas	a. Humans Nature
"New" flux of nature paradigm	Humans as drivers of ecosystems	"Natural" and anthropogenic ecosystems	• Invasive species autecology • Invasive species impacts • Native ecosystem ecology • Eradication techniques • "Natural" ecosystem restoration	b. Humans → Nature
	Humans as recipients of ecosystems	"Natural" and anthropogenic ecosystems	• Ecosystem services • Ecological economics • Social perceptions • Environmental psychology	c. Humans ← Nature
	Humans as co-participants in ecosystems	Systems with "historical" and "novel" biotic, social & cultural assemblages	• Values of nature • Conservation policies • Community-based management • Decision-making • Justice & power relationships • Sense of place • Governance	d. (Humans ↔ Nature)

Figure 1. The balance of nature paradigm, which largely viewed humans as separate from nature (**a**), has been replaced by a flux of nature approach, where humans are part of ecosystems (**b-d**). However, the ways humans are conceived even as integrated parts of ecosystems can vary from humans as disturbance agents (**b**) to humans as recipients of ecosystem services (**c**) and disservices and to humans as co-participants (**d**). Such understandings of the human-nature relationship are not only conceptual or semantic, but also have practical implications for the basic study unit we address as scientists and the research topics that are considered valid.

A brief history of human-nature paradigms in ecology

Throughout its history, the scientific field of ecology has viewed humans as both a part of and separate from nature (Aggestam, 2015). While some early founders of the discipline explicitly called for the "study of man and nature (as a unit, not separately)" (Odum, 1953) and declared that "[e]cology occupies a middle ground between the physical, biological, and social sciences, and must deal with human values" (Adams, 1940), the reigning approach to ecology for most of the 20th century focused researchers' efforts on the study of self-contained, static ecosystems that were "natural" and largely excluded human influences (MacIntosh, 1985, Fig. 1a). This view of ecosystems can be termed the "balance of nature paradigm." Plant ecologist F. E. Clements (1874–1945) was influential in this early ecology paradigm via his writings on the study of vegetation succession towards climax communities. In this view, biodiversity was driven by a teleological processes (*i.e.*, nature's own apparent purpose or goal) towards maturity—or rather the final expression of how nature "should" express itself (*i.e.*, without human interference).

By the 1980s, and partially as a consequence of a new social imaginary regarding a global "environmental crisis" that arose in the 1950s and 60s in developed countries (Estenssoro Saavedra, 2007), scholars detected a paradigm shift in ecology and an increasingly explicit recognition of the role of humans in nature. After decades of ecological research under the "Clementsian" paradigm, in the 1980s and 1990s, ecosystems came to be re-conceived of as changing and inter-connected, instead of tending towards a pre-determined pathway to a final (and hypothetical) state (Pickett and Ostfeld, 1995). Humans, at different intensities and scales, undoubtedly had always been key players in many ecological processes, which vindicated ideas that were contemporary with Clements', specifically H.A. Gleason's (1926) postulates that ecosystems were heterogeneous, stochastic and dynamic. However, it was not until the last part of the 20th century that this perspective became dominant in ecological research (MacIntosh, 1985, Fig. 1b–d).

Today, rapid change and dynamism have become more profoundly characteristic in our conceptualization of the modern world through prominent concepts like the Anthropocene (Crutzen, 2002) and novel ecosystems (Hobbs *et al.*, 2006), which have been coined in the new millennium to emphasize the role of humans as the principal "driver" of ecological change, even at the planetary level (Fig. 1b). Yet, it is important to note that in this same period, the concept of ecosystem services also arose (largely in ecological economics) to link ecosystem feedback loops with human society (Norgaard, 2010). More broadly understood, though, the ecosystem services concept allows the identification of a network of benefits that nature provides to human life, both as a source of supporting natural resources and cultural meaning and social relationships (Pascual *et al.*, 2017) (*i.e.*, humans as "recipients," Fig. 1c).

Overall, understanding the history of ecological thought and of the broader social imaginaries of human-nature relationships allows us to find multiple ways of integrating humans into nature. Such an understanding provides different perspectives not only of how the world "is," but also the way we "ought" to conduct our research and management actions. For instance, scholars, with European heritage in the Americas, seeking the "balance of nature" concept, imagine ecosystems with minimal human impact, but in this process obviate millenary knowledge and interactions that many human societies have and have had with nature, including historical and large ecosystems transformations by local communities and Indigenous peoples. As a case in point, the Yucatán Peninsula's forest was only recently recognized as a "Mayan forest garden" versus a "jungle" (Ford and Nigh, 2009). On the other hand, even when we see humans as an agent mostly of change, it makes a difference if we conceive them as "disturbers" of nature or "drivers" that solely structure ecosystems. This second perspective lead Ellis and Ramankutty (2008) to reconceive biomes as "anthromes" and further to the recognition that human-created landscapes and biotic assemblages have existed in some places for thousands of years (Ellis *et al.*, 2010).

Human-nature paradigms also have influenced the application of ecological sciences on environmental management. In the applied field of conservation biology, Mace (2014) describes a time sequence from the 1960s till now that in many ways reflects the conceptualizations outlined above for the related field of ecology—passing from "nature for itself," to "nature despite people," to "nature for people," and "nature and people." Currently, conservationists are debating the multiple implications of a "nature and people" approach, including controversial proposals like "New Conservation" (Kareiva *et al.*, 2012) that seek to fully integrate Modernity's proposal of managing (even domesticating) nature and rethink the meaning of nature conservation into the future towards fostering global human welfare (Kareiva *et al.*, 2007).

Researchers from social sciences, the humanities, and interdisciplinary fields, such as human geography, environmental psychology, agroecology and ethnobiology, also have examined human-nature relationships in different cultures and epochs (Sconnes, 1999; Pretty, 2011). They too found that human societies and cultures have reciprocally shaped and been shaped by their relationship with biodiversity and ecosystems (Descola and Palsson, 1996; Ingold, 2000). Under this lens, the ideas of "nature for itself" and "nature and people" are largely cultural, and it has been empirically demonstrated, for example, by contrasting landscape preferences among people with different cultural backgrounds (Buijs *et al.*, 2009). Indeed, the idea of nature being "co-produced" (see Hinchliffe, 2007) with humans as "participants" (Fig. 1d) seems more culturally neutral and perhaps more appropriate to the current status of the planet, considering the global extent of human migration (Vertovec, 2007) and anthropogenic impact over ecosystems (Ellis and Ramankutty, 2008; Ellis *et al.*, 2010).

In synthesis, the field of invasion biology has engaged with and responded to these broader conceptual shifts (Fig. 1) and also has confronted epistemological and practical controversies regarding its future (*e.g.*, Larson, 2005; Davis *et al.*, 2011; Simberloff *et al.*, 2011). Therefore, efforts to conceptually and practically include a more socially-integrated and culturally-aware image of humans and nature are still needed. In the following sections, we seek to contribute to this academic and management debate by exploring how different human-nature paradigms relate to our current understanding of the biological invasion of North American beavers in Patagonia and what those insights can teach us for the future of addressing this issue more holistically, effectively and ethically.

Humans as "drivers" of ecological change

An invasive ecosystem engineer. Early scientific research on North American beavers in Patagonia was focused on the species' basic population ecology. For example, Lizarralde (1993) and Skewes *et al.* (2006) published seminal studies of the abundance, density and distribution of beavers in the archipelago, finding that by the late 1990s, beavers had colonized watersheds at densities on the high end of values reported in North America. Later, Anderson *et al.* (2006a) and Wallem *et al.* (2007) showed that the invasion's extent encompassed almost the entire archipelago, with the exception of the Wollaston Islands and Staten Island, and had even occupied the mainland south of Punta Arenas City, Chile by the mid-1990s. Ecologists subsequently began to characterize the beaver under the rubric of an "ecosystem engineer" for its ability to create, alter and destroy ecosystems (*sensu* Jones *et al.*, 1994). Within this body of publications, we find a large number that prioritized the quantification of ecological impacts, but to a lesser degree there are also studies on the underlying mechanisms to explain the beaver's role as an invasive ecosystem engineer in new aquatic and riparian ecosystems (Anderson *et al.*, 2009).

For instance, research shows that beavers reduce stream benthic macroinverbrate diversity by one-third, compared to un-impacted reaches. However, secondary benthic production in beaver ponds was increased by an order of magnitude (Anderson and Rosemond, 2007). Furthermore, beavers simplified pond benthic food webs in their new environment, not only lowering taxonomic diversity, but also decreasing the number of functional feeding groups (Anderson and Rosemond, 2010). At the same time, though, stream sections immediately downstream of beaver ponds displayed largely similar conditions to un-impacted sites. Based on these data, Anderson and Rosemond (2007) proposed that the mechanism by which beavers differentially affect stream biodiversity and ecosystem function in ponds is via the increase in benthic organic matter, which homogenizes substrate microhabitat for benthos, thereby reducing diversity. At the same time, beaver impacts increased benthic basal resources, thereby enhancing energy flow and the function of secondary production.

Overall, at the patch scale (*i.e.*, stream reaches, beaver ponds), beaver invasion produces the predictable effect of converting lower order streams to the conditions more representative of lentic (*e.g.*, ponds) or high order sections of the watershed. In so doing, beavers transform high latitude aquatic ecosystems (with lower rates of secondary production and decomposition) to values that are in the median of global studies. Consequently, in essence, beavers functionally converted "sub-polar" streams to "temperate" streams (Anderson and Rosemond, 2007). Additionally, considering that beaver ponds are created in a post-glacial landscape with other lentic features, such as wetlands, peat bogs and lakes, it was found that beaver ponds had a similar biotic community to other lentic habitats, but significantly higher retention of organic matter. Therefore, the effect of beavers at the landscape-scale in Tierra del Fuego did not impact benthic biodiversity, but did enhance carbon retention at the watershed scale by an average of 60%, even though the ponds themselves only constituted 10% of the stream networks total length (Anderson *et al.*, 2014).

The studies looking at beavers as a driver of ecological change have also quantified their impact to the riparian zone has the largest alteration to sub-Antarctic forests in the Holocene. In total, approximately 40% of riparian forests have been affected (Anderson *et al.*, 2009), and on the Argentine side of the archipelago this constitutes 30,000 ha that have been impacted (Henn *et al.*, 2016). Studies have also shown that beaver meadows persist as an "alternative stable state" for at least 20 years (Wallem *et al.*, 2010). In particular, the two dominant tree species (*Nothofagus pumilio* and *N. betuloides*) do not regenerate well in these new conditions. Nonetheless, *N. antarctica*, the third tree species found in the archipelago, has two adaptations that make it more resilient; it is both adapted to saturated soil conditions and also has the capacity to sprout from roots and stumps (Anderson *et al.*, 2006b).

Humans as "recipients" of ecosystems

Services and disservices from nature. In TDF, the way humans relate to nature generally and invasive species specifically is a nascent topic of scientific inquiry. Recent studies have begun to delve into how specific stakeholder groups perceive beaver as a threat or benefit, and how these views influence the support control or eradication actions. An intensive and extensive study that conducted interviews and surveys of ranchers in both the Argentine and Chilean portions of the archipelago, demonstrated that 67% supported beaver eradication (Santo *et al.*, 2015), but these same ranchers simultaneously expressed both positive and negative values regarding beavers on their land (Santo *et al.*, 2017).

One management proposal for biological invasions, which seeks to conceive humans as recipients of nature and not only drivers of change to be controlled, is known as human-centered design (Sorice and Donlan, 2015). This methodology has begun to be applied in the study of beavers in southern Patagonia and sets out to not only determine local knowledge or opinions regarding biological invasions, but also integrates stakeholder preferences for specific aspects of management programs themselves to design them in such a way as to be complementary and amenable to stakeholders' own activities. As such, this approach has the potential to attain greater social support, or "buy-in," and thereby avoid inoperable plans and social conflicts (see Estévez *et al.*, 2015; see also Scorolli, this volume). In the case of Fuegian ranchers, while 67% supported the idea of eradication, it was possible to detect specific program elements that could be modified to enhance their willingness to participate in such initiatives, including increased payments, decreased landowner involvement and increased belief in the probability of success (Santo *et al.*, 2015).

Another way to address how this biological invasion affects what humans receive from nature is to calculate their willingness-to-pay for potential management efforts. In southern Chile, researchers determined that the monetary value society is willing to contribute for the restoration of beaver-impacted forests impacted totals over seven million US dollars (Soto Simeone and Soza-Amigo, 2014). The survey respondent valuation of forests prioritized non-instrumental values, separating out into 48% inheritance value (conservation for future generations), 18% option value (conservation for the possibility to enjoy or visit them in the future), 17% existence value (conservation for the forests intrinsic worth regardless of humans) and 16% direct and indirect uses (conservation for recreation, tourism, science, etc.). Interestingly, while wealthier socio-economic groups were willing to pay more in absolute terms, the lowest strata were willing to pay a higher percentage of their total income.

Humans as "co-participants" in socio-ecological systems

Social and cultural relationships with nature. As of yet, the idea of people co-producing ecosystems with invasive species in southern Patagonia has not been fully explored or researched (but see emerging work, such as Dicenta, 2021). However, we found some insights in qualitative studies and surveys conducted in the small, isolated town of Puerto Williams (Chile, human population 2,000) on Navarino Island, and in Ushuaia (Argentina, human population 60,000) on Tierra del Fuego Island. In Puerto Williams, Berghoefer *et al.* (2008) found that the island's different social groups maintain diverse relationships with nature and consequently develop divergent valuations of invasive species. Indeed, as another study puts it, we can draw a distinction between the relationships with nature from those for whom nature is experienced by direct interaction and senses (*i.e.*, local communities) and others that see a global, endangered nature in need of conservation mediated by acquired knowledge (*i.e.*, scientists, conservationists) (Berghoefer *et al.*, 2010). In the former, invasive species, like the beaver, generate an emotional and familial response (*i.e.*, sense of place, Stedman, 2003). Some residents, therefore, have affection for the beaver, or see it as a symbol of their own identity as settlers and colonists. This "adoption" of new biota, or in other words, the mechanism of co-producing identity or place meanings with biodiversity has been documented in European settlers in Australia, adopting, for example, native species to Australia that were "new" for these European colonists (Aslin and Bennett, 2000). In this context, local relationships with an invasive species are developed through direct experience, and therefore, these people may have high awareness of their impacts, but have a divergent valuation of the species itself and its management, compared to invasion biologists and conservationists. Indeed, it is reported in southern Patagonia that some social groups demonstrate reticence to support scientifically-determined control and eradication efforts (Schuettler *et al.*, 2011; Anderson *et al.*, 2016).

In agreement with these qualitative studies on Navarino Island, quantitative surveys administered on in Tierra del Fuego National Park found that while more than 90% of visitors who were residents of Ushuaia (Argentina) know the beaver is harmful, only approximately half support the total eradication via lethal means (Anderson *et al.*, 2016). This lack of support can be partially traced to underlying ethical frameworks (*e.g.*, anthropocentric versus biocentric worldviews) held by different stakeholders regarding nature and its management (Haider and Jax, 2007). Plus, we have found that even when there is support for invasive species removal, there can often be a general rejection of lethal control options, which allows us to distinguish that there is more support for the overall goal versus the

Figure 2. The beaver is most known for the large impacts that its tree cutting and dam-building provoke to the landscape **(a)**, but at the same time the species itself is often considered charismatic and interesting by many people **(b)**. Consequently, in Tierra del Fuego, this introduced invasive species is frequently used as a "mascot" for the town of Ushuaia in tourism promotional material **(c)** and even appears incorporated into the names of some private enterprises **(d)**. (Photos: J. C. Pizarro [**a**], J. Duncnuigeen [**b**], J. J. Henn [**c**], A. E. J. Valenzuela [**d**]).

means of achieving it (Anderson *et al.*, 2016). The same study also found that only half of residents can correctly identify native species on the island, but significantly more have knowledge of the presence of specific invasive taxa, of which the beaver is the best known (Anderson *et al.*, 2016).

Beavers are also charismatic mammals with conspicuous affects to both the ecological and aesthetic landscape (Fig. 2a-b). They create an ideal narrative and novelty for animal-based tourism (Bertella, 2016), and although this aspect has not been well-studied in Patagonia, tourism operators have incorporated beavers into their offering and local narrative (Fig. 2c-d). Ushuaia, for example, is a top destination for nature-based, international tourism, and beavers have often been depicted as a city mascot, together with native species like the Magellan penguin, in tourism advertising materials and brochures. Even the name of a world-renowned ski resort on the island is *Cerro Castor* or "Beaver Mountain." In many ways, this invasive species has become part of the toponomy of Tierra del Fuego's "iconic" landscape and in some ways serves as part of its natural and social capital for tourism. Using travel blogs, tourists from North America visiting the area are confronted with the duality of the local promotion of beavers as a tourist attraction and their noticeable environmental effects they experience while hiking (*e.g.*, Henn, 2013; Russell, 2016). In this human-nature "co-production" it is also important to consider that the region's demography and economy have been dramatically changing in the last 60 years (*e.g.*, van Aert, 2013), particularly for the Argentine portion. The massive immigration to the island in the last 30 years as part of industrial promotion incentives means that for many residents the beaver and its effects are perceived as entirely normal in Tierra del Fuego.

Despite these emerging studies, we know little about the role that people take in direct actions towards invasive species. Stakeholders have been shown to have a disparity between knowledge (*i.e.*, beavers produce environmental damage) and perception (*i.e.*, beavers are part of my place), but how these people act to confront invasive species has been little considered. Willingness-to-pay, while not action *per se*, provides some indications of people's intentions towards future behavior. For example, in Chile, a government-supported beaver control program promoted significant economic incentives for the trapping of beaver, American mink (*Neogale vison*) and muskrat (*Ondatra zibethicus*), but despite these efforts, neither a fur industry nor trapping were sparked and only few self-sustaining enterprises remain today (Soto and Cabello, 2007). In contrast, between 2011–2012, a destructive wildfire impacted Torito Bay north of Ushuaia. The perceived environmental damage and danger in this case lead citizens to self-organize a social-environmental movement in defense of the native forest. This social group pressed the authorities to integrate a broader array of stakeholders into the existing native forest advisory council (Comisión Consultiva de Bosques Nativos) and implement the provincial native forestry law to improve overall management, planning and conservation (Vara and Collado, 2013). We present these two contrasting examples of social responses that were exogenous versus endogenous and ultimately having differing outcomes and sustainability. Clearly, there is not the same motivation to act on the part of the local population despite the noticeable environmental effects of invasive beavers, and as previously stated, most of these issues described in this section have not yet been empirically researched or tested.

Lessons from the invasive beaver case study

Build a transdisciplinary invasive species research agenda

Transdisciplinarity is a practice and a property that emerges when a diverse group, including social actors beyond academia, works together to analyze a complex system via the "differentiation" and "reintegration" of the system's sub-components in an iterative process (similar to interdisciplinarity, see García, 2006; but expanding beyond academia, see Star and Griesemer, 1989). In this sense, the principal lesson of the case study is the utility of a continual and iterative process of 1) understanding the study object/subject and 2) identifying and incorporating particular dimensions that have been unattended. As such, new synergies and discoveries can be found along the way that also relate to the interface of a socio-ecological phenomenon and generating mutual comprehension. If the binational agreement and its activities to confront beavers' invasion were effective bringing scientific, diplomatic and management agendas together, we propose that it would be relevant to think that repeating the same "successful" recipe of collaborative work can offer similar results in the study of other biological invasions as a social-ecological phenomenon. Specifically, mechanisms like transdisciplinary seminars and participatory workshops were useful for the modification of the agenda on beavers and similar strategies could be used elsewhere and for other problematic taxa (García-Diaz *et al.*, 2021).

We would also call attention to the emerging research topics we identified under the lens of "nature as co-production," including incorporation of introduced invasive species as social (*i.e.*, creation of research-management network), natural (nature-based tourism attraction) and cultural (place identity and belonging) capital. We show that immigration and social and demographic change can be useful factors to incorporate to the study of local cultural images of nature and invasive species (see also Dicenta, 2021). Other invasive species, such trout and salmon, could be equally interesting to explore under these perspectives. Plus, in other "southern" countries like Australia and New Zealand, we can find concrete examples of how these research topics have become increasingly important to the global literature on the socio-ecological impacts of biological invasions (see Estévez *et al.*, 2015) and informing land-use policy and decision-making (Klepeis *et al.*, 2009).

Strengthen communities of knowledge

Since the 2006 binational politico-scientific process on beaver control began, there is increasing interest in interdisciplinary, applied and social science approaches to this biological invasion. As such, a watershed moment in the way this problem was conceived, studied and confronted was the conformation of a working group that linked researchers and managers—known as "knowledge-policy communities" (*sensu* Díaz *et al.*, 2015). Now, the recent social sciences studies highlighted above demonstrate that the broadening of this set of stakeholders also diversifies the perceptions and knowledge about beavers that are involved in the process. Therefore, the integration of social science domains with ecological ones also implies the incorporation of stakeholders beyond the ecological science and natural resource management realms (Colvin *et al.*, 2016). Strengthening such communities of knowledge, then, requires attending to the question of how research should inform and encourage participative approaches in invasive species management for future actions (Star and Griesemer, 1989).

Moreover, biological invasions can be also understood even more broadly as having teleconnections and telecouplings (*sensu* Liu *et al.*, 2015), which expands the potential social actors of these knowledge communities to a global scale. For example, the case of the beaver demonstrates such long-distance socio-ecological system linkages. The introduction itself brought a species from North to South America, but currently the sharing of experiences on control has included experts from the United States, Canada and New Zealand (Malmierca *et al.*, 2011). As such, these comparative relationships provide an opportunity for research, management and conservation to be informed by other knowledge-policy communities facing similar issues or sharing the same species, but outside of academia these types of linkages between long-distance partners are less common, particularly at the local government and community levels (Ogden *et al.*, 2013).

The challenges of creating communities of knowledge exist even for simply building interdisciplinary working groups within academia and include financial, structural and implementation barriers (Anderson *et al.*, 2015). By encompassing practitioners and other local community members (*i.e.*, transdisciplinary), a new set of concerns emerge, such as power asymmetries, legitimacy and equity (Barnaud and Van Paassen, 2013). However, these issues are inherent and unavoidable if we are to transition into a paradigm of research and management as socio-ecological systems. While this represents a significant challenge for the capacity of both invasion biologists and managers, it is clear that doing so would promote not only mutual understanding, but also increase the legitimacy of information and its applicability to practical solutions.

Include environmental history and philosophy in natural science education curricula

Ecologists dominate invasion biology, given the history of this field (see above), and ecologists and natural scientists more generally have been shown to have relatively poor training in the philosophy of science (Graham and Dayton, 2002; Estévez *et al.*, 2010). To move beyond the uncritical adoption of hegemonic paradigms and principles, it is necessary to have a solid training in the humanities, particularly history and philosophy (Eigenbrode *et al.*, 2007). Doing so will give a new generation of scientists and managers involved in the study and control of biological invasions a broader understanding not only of their work, but the science-society relationship and the relationship of their discipline with other social actors. Clearly, humans do not just impact nature, nor do they simply receive benefits from it. Rather, a "humans as co-participants" perspective makes explicit that they also create multiple natures (*e.g.*, "novel ecosystems," Hobbs *et al.* 2006; "anthromes," Ellis *et al.*, 2010). However, recognizing these multi-faceted aspects of the human-nature relationship requires us to acknowledge and take responsibility for the lenses through which we view the world and our work.

Despite its inherited disciplinary biases, though, we would argue that invasion biology is well positioned to help lead other ecologists and natural scientists bridge this gap, given the applied nature of the field and the clear expression of values and priorities that invasion biologists and practitioners in Patagonia have expressed (Anderson and Valenzuela, 2014). However, there is still a need for an institutionalization of training that allows scientists and practitioners to construct their own conceptual frameworks, based on the problem, rather than an imposed and inherited disciplinary structure. Doing so also should help researchers and their students reconcile their own values and priorities, which recognize the imperative of applying their information to real world, viable solutions (Anderson and Valenzuela, 2014). Plus, taking the approach to interdisciplinarity presented by García (2006), we first must have a joint understanding of system components, which for ecologists and natural resource managers alike are traditionally "humans as drivers of change." However, by explicitly integrating a historical and philosophical perspective to this process, we are also obliged to incorporate social science understandings, such as the fact that "humans" can be differentiated into multiple social actors or stakeholders, including ranchers, scientists, local leaders and decision-makers from the local to the regional and the international levels.

Conclusions

The scientific and management attention that the beaver has received, based largely on studies that conceive of beavers as human-induced impacts to nature, make this biological invasion one of the most studied in Patagonia (Valenzuela *et al.*, 2014). The review of the research shows that both ecological and social inquiry can provide useful data and insights on the beaver's effects, the invasion processes and socio-cultural aspects regarding environmental management. At the same time, we also would like to acknowledge that the emphasis towards ecological impact studies achieved valuable outcomes, such as yielding a great deal of basic information on understudied aquatic and riparian ecosystems in southern Patagonia and permitting significant and sustained efforts to develop relationships between researchers and decision-makers, ultimately positioning this topic in the political agenda of both Argentina and Chile.

By analyzing the case of invasive beavers under the rubric of a socio-ecological phenomenon, we now find the need to explicitly recognize that a new study object or unit also requires updated conceptual models and methods (see Anderson *et al.*, 2021). In turn, this socio-ecological perspective also challenges conservation and restoration approaches that seek to maintain "natural" ecological conditions and allows scientists and practitioners instead to engage with the novel or socially-desirable conditions that recognize humans and nature together as a unit. Therefore, a greater understanding of the history and philosophy of our scientific and management paradigms should also teach us to have not only better comprehension of these disciplines' trajectories, but also greater humility of their (and our) limitations, thereby becoming better equipped to constantly search for improvements that allow us to be more effective. We should be encouraged, as well, by other successful hybrid disciplines that have played a role in helping to relate human behavior with environmental situations from other standpoints (*e.g.*, ecological economics, environmental psychology, environmental anthropology, political ecology: see Bennett *et al.*, 2016). These other fields further demonstrate that to comprehend and manage biological invasions as a socio-ecological phenomenon, natural scientists and conservation practitioners would be well-served to develop a more nuanced understanding of human values, perceptions and motivations, including acknowledging how these factors vary over time, place, and within socio-cultural contexts (Paetzold *et al.*, 2010; DeFries *et al.*, 2012).While the transformation of invasion biology into a field of inquiry and action that effectively integrates humans and nature is a major challenge, we find evidence from the case of invasive beavers, as well as in the broader academic experience, that 1) the construction of a transdisciplinary research agenda with appropriate study units and research methods, 2) the consolidation of communities of knowledge and practice, and 3) the teaching of philosophy and history to natural scientists are three concrete tasks that can help advance this proposal.

Acknowledgements

CBA recognizes the grant support of ECO-Link (GEO1262148) and PIDUNTDF A 2 /16 (*Un abordaje socio-ecológico para mejorar el entendimiento y la gestión de las invasiones biológicas en la Patagonia austral*), which provided a platform and interdisciplinary team to develop these ideas. JCP was supported by a CONICET Postdoctoral Fellowship during the preparation of the manuscript.

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3 | CHARISMA AS A KEY ATTRIBUTE FOR THE EXPANSION AND PROTECTION OF SQUIRRELS INTRODUCED TO ARGENTINA

EL CARISMA COMO ATRIBUTO CLAVE PARA LA EXPANSIÓN Y PROTECCIÓN DE LAS ARDILLAS INTRODUCIDAS EN ARGENTINA

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Abstract. The commercialization of species valued as pets or used to enrich local fauna are a constant source of introductions that may establish wild populations due to accidental escapes or deliberate releases. The most frequent pathway of squirrel introductions is the pet trade. Squirrels are successful invaders given that together with their biological attributes and tolerance to human presence, their charisma enhances their invasive potential favoring their introduction into new areas and their protection by social groups that oppose management actions. Only one squirrel species has been introduced to South America: the Asiatic Pallas's squirrel (*Callosciurus erythraeus*). This tree squirrel was introduced to Argentina in 1970, and its further expansion resulted from a combination of intentional translocations within the country and natural dispersal of individuals. The first known translocation into a new area within the country occurred two decades after the original importation of squirrels. Thirty-one translocation events, occasionally involving illegal trade, have been recorded between 1995 and 2018, giving rise to 22 invasion foci in rural and urban areas in the provinces of Buenos Aires, Córdoba, Mendoza and Santa Fe, and the city of Buenos Aires. Every year, new reports indicate the presence of *C. erythraeus* in new sites, showing that this biological invasion is an ongoing problem with a strong social component that should receive an interdisciplinary approach to also attend to public concerns. To prevent further expansion, authorities must tackle the issues of squirrel translocation and of implementing a warning-rapid response protocol in recently invaded areas. NGOs, veterinarians and pet shop owners play an important role in reinforcing responsible pet-keeping practices, including the message that wildlife species are not pets. Any management plan should be designed considering the local characteristics of the invasion process of this squirrel species, integrating the social dimension together with biological, technical, economic and political aspects.

Resumen. El comercio legal e ilegal de especies usadas como mascotas o para enriquecer la fauna de un lugar es una fuente constante de individuos que pueden iniciar poblaciones silvestres, ya sea debido a escapes accidentales o a liberaciones intencionales. La magnitud del comercio internacional

de fauna es inmensa, moviendo millones de animales vivos cada año y afectando la distribución global de especies exóticas. La vía de introducción más frecuente de ardillas exóticas es el comercio de mascotas y, en menor medida, ciudadanos particulares y zoológicos. Las ardillas suelen tener éxito como especies invasoras; el carisma de las ardillas, junto con sus atributos biológicos y sinantropía, favorecen su potencial invasor. Esto se debe a que su carisma promueve tanto su introducción en nuevas áreas como su protección por grupos sociales que se oponen a acciones de manejo.

Una sola especie de ardilla fue introducida en Sudamérica hasta el momento: la ardilla de vientre rojo (*Callosciurus erythraeus*). Se trata de una especie de origen asiático y hábitos arborícolas, que fue introducida en Argentina en 1970 por su atractivo como especie ornamental. Su continua expansión en el país se debe a la combinación de translocaciones (transporte mediado por el hombre) intencionales a nuevos sitios y a movimientos de dispersión de los individuos de corta y larga distancia. La primera translocación de ardillas dentro del país ocurrió dos décadas después de su importación. Se registraron 31 eventos de translocación entre 1995 y 2018, algunos mediante comercio ilegal, que resultaron en el establecimiento de 22 focos de invasión en áreas rurales y urbanas de las provincias de Buenos Aires, Córdoba, Mendoza y Santa Fe, y la Ciudad de Buenos Aires.

Cada año se suman reportes de presencia de *C. erythraeus* en nuevos sitios, indicando que es un problema vigente con un fuerte componente social que debería abordarse de manera interdisciplinaria teniendo en cuenta las opiniones de la comunidad, y desarrollando estrategias de comunicación honestas y que respondan a las inquietudes que surjan. La prevención de la expansión de ardillas debería enfocarse en la translocación de individuos y en coordinar respuestas rápidas cuando se detectan áreas recientemente invadidas, para lo cual es fundamental el rol de entidades de gobierno locales, provinciales y nacionales en coordinación con entidades y actores sociales vinculados a la problemática. ONGs, veterinarios y dueños de negocios de venta de mascotas juegan un papel clave en reforzar la tenencia responsable de mascotas, que incluye el mensaje de que la fauna silvestre no es mascota.

El potencial impacto sobre especies nativas alerta sobre la invasión de ardillas en áreas de alto valor de conservación. Existen algunas acciones de manejo aisladas llevadas adelante por particulares, usualmente sin autorización formal, que buscan reducir el daño que causan las ardillas mediante descortezado de árboles, consumo de frutos y roído de mangueras de riego y cables de electricidad, telefonía y televisión. Recientemente se iniciaron acciones de control en el foco de invasión de ardillas ubicado en la zona de Tupungato, Mendoza, coordinado y financiado por el gobierno provincial. Estas primeras experiencias permitirán evaluar las acciones y resultados, y trabajar de manera adaptativa para lograr un manejo exitoso. En todos los casos, los planes de manejo deberían tener en cuenta las características locales de la invasión integrando la dimensión social junto con aspectos de índole biológico, técnico, económico y político.

Invasive species and trade

Humans have transported species from one place to another since ancient times. Human-wildlife relationships have been shaped by culture, necessity, utility, beliefs, and ethical values and have been traditionally restricted to the species present in the surrounding environment. Bonds between humans and non-human species were strong enough to justify and promote the movement of animals and plants together with nomadic communities, even in long distance trips. In particular, in the period ca. 1820–1950, the development of trade and transportation infrastructure and massive European emigration facilitated the translocation and introduction of species outside their original habitats at a global scale (Hulme, 2009). This led to the establishment of wild populations of introduced species worldwide, which is an ongoing process today as more records of species introduced into novel areas are still being reported every year. In fact, in recent decades the world has entered the Era of Globalization that has led to a new phase in the magnitude and diversity of biological invasions (Meyerson and Mooney, 2007; Hulme, 2009). International trade is the most important explanatory variable to the global distribution of introduced invasive species, whereby the greater the flow of international trade, the higher the number of introduced species (Westphal *et al.*, 2008; Hulme, 2021). In this globalized era, changes in macroeconomic and geopolitical forces also change the role of different continents as donor or recipient regions for introduced species (Lenzner *et al.*, 2018).

International wildlife trade involves billions of live animals and animal products that are traded globally each year (Meyerson and Mooney, 2007; Smith *et al.*, 2009; Sinclair *et al.*, 2021). Just since 2000 in the USA, more than 1.48 billion live animals have been imported in wildlife shipments, mainly for commercial purposes (92%), such as the pet trade, and were obtained from wild populations (80%) (Smith *et al.*, 2009). Ornamental trade was responsible for all deliberate introductions in northwest Europe since 2001 (Zieritz *et al.*, 2017), while the pet trade for amphibians, reptiles and mammals has also been reported as a major invasion pathway in other regions (*e.g.*, Kopecký *et al.*, 2016; García-Díaz *et al.*, 2017; Rosa *et al.*, 2018; Carpio *et al.*, 2020). The main source of current avian invasions are pet birds that escape from cages, particularly wild-caught species (Carrete and Tella, 2008). Millions of birds are still captured annually in the wild for export to the pet markets, usually taken from developing to developed countries (Carrete and Tella, 2008). The aquarium and aquatic ornamental species industry, which has been identified as a major source of invasive species in aquatic habitats, is growing annually by 14% worldwide with more than 11 million hobbyists in the USA alone (Padilla and Willliams, 2004). The statement by Padilla and Willliams (2004) that aquatic invasive species are just a mouse click away from any home in America could be extrapolated to several other countries and species.

The legal and illegal trade of species valued as pets or to enrich local fauna are a constant source of individuals that may initiate wild populations by either accidental escapes or deliberate releases (Hulme *et al.*, 2008; Keller *et al.*, 2011; Lockwood *et al.*, 2019), as occurred with the common starling (*Sturnus vulgaris*) (Linz *et al.*, 2007) and the domestic cat (*Felis sylvestris catus*) (Duffy and Capece, 2012). Moreover, the trade of animals captured in the wild and sold in the pet market combines two sides of a threatening coin; on the one hand, it diminishes native species populations, and on the other hand, it favors exotic species introductions. Numerous species are threatened because of the high extractive pressure to sell them as pets, such as the Argentine tortoise (*Chelonoidis chilensis*) (Tortoise & Freshwater Turtle Specialist Group – IUCN, 1996) and the yellow cardinal (*Gubernatrix cristata*) (BirdLife International, 2016). The characteristics of the species traded for these purposes differ among regions and may change over time, influenced by media and fashion, and by the new species that become available in some regions, which acts as a sort of positive feedback to species introduction (Sinclair *et al.*, 2020).

Introduction of squirrels as pets or ornamental species

Species introductions are the outcome of interactions between human socio-economic pressures and the availability of species (Blackburn *et al.*, 2017). Following introduction, some species, such as several mammal and bird species associated to humans (domesticated species, pets, human commensals), have shown high invasion success independent of propagule pressure (Jeschke and Strayer, 2006). The number of species associated with humans changes over time and appears to be rising (Jeschke and Strayer, 2006), with the consequent potential increase in the probability of invasion success of new species. For squirrels, the most frequent vector of introduction is the pet trade and, to a lesser extent, private citizens and zoos (Bertolino, 2009). Squirrels have been commericalized in both legal and illegal pet markets worldwide for several decades, and numerous species have now become established in the wild, some of which are considered invasive (Palmer *et al.*, 2007; Bertolino, 2009). Eighteen introduced squirrel species have been reported in 23 countries over five continents (Bertolino, 2009; Jessen *et al.*, 2010). Squirrels are successful invaders as they combine a high reproductive potential with a high probability of establishment even from only a few founding individuals (Palmer *et al.*, 2007; Wood *et al.*, 2007; Bertolino, 2009). Several squirrel species are also able to inhabit modified and urbanized habitats (Palmer *et al.*, 2007). Moreover, their charismatic appeal is a key attribute that favors introduced squirrel invasions given that it promotes: 1) their introduction into new areas, and 2) their protection by some social groups that oppose management actions. This means that the species' charisma should also be considered, together with its biological attributes or association with humans, to analyse its invasive potential and evaluate any management action (Shackleton *et al.*, 2019; Jarić *et al.*, 2020). The well-studied case of the grey squirrel (*Sciurus carolinensis*) introduced in Europe illustrates the reason of introduction, its impact on native fauna and forest plantations, and also how social opposition prevented the development of a timely control program, thereby enhancing its invasive potential (Bertolino and Genovesi, 2003; Gurnell *et al.*, 2004; Bertolino *et al.*, 2014). The control or eradication of such appealing animals may lack public support and hence requires specific measures to gain social approval (Vane and Runhaar, 2016).

Asiatic tree squirrels of the genus *Callosciurus* have shown a particularly high likelihood of establishment from only a few released animals (Bertolino, 2009). *C. finlaysonii* has been introduced to Italy, Singapore and Japan, while *C. erythraeus* has established wild populations in Argentina, France, Hong Kong, Italy, Japan, and the Netherlands (Bertolino and Lurz, 2013; Mazzamuto *et al.*, 2016a). For a time, it was also found in Belgium, but it has been successfully eradicated (Adriaens *et al.*, 2015). In addition to the pet trade, there were intentional releases in public or private parks, or occasional escapes, which gave rise to these wild populations. In all countries where these species have been introduced, only one or two *Callosciurus* populations have established, with the exception of Argentina and Japan, where several invasion foci are known for *C. erythraeus* (Benitez *et al.*, 2013; Bertolino and Lurz, 2013; Guichón *et al.*, 2015, 2020).

Only two squirrel introductions have been reported in South America. The first case was the introduction of the Pallas's squirrel (*C. erythraeus*) in Argentina (Fig. 1) (Aprile and Chicco, 1999), and the second case was the translocation within Peru of the Guayaquil squirrel (*Sciurus stramineus*) to a site 500 km south of its original distribution (Jessen *et al.*, 2010). In Argentina, 10 squirrels were imported in 1970 and were initially kept in a large cage on a private ranch located in Luján Department, province of Buenos Aires (Aprile and Chicco, 1999). By 1973, some squirrels had escaped while others had been released, but apparently only two to five squirrels founded the first wild population of *C. erythraeus* in Argentina. After 31 years of slow spread, the invasion area in Luján occupied a region of 680 km² by 2004 (Guichón *et al.*, 2005), initiating a successful expansion process in the Pampas (Guichón and Doncaster, 2008) that yielded 1,340 km² of invaded area by 2009 (Benitez *et al.*, 2013), which is still expanding.

Figure 1. *Callosciurus erythraeus* in Luján, province of Buenos Aires, Argentina. Photo: F.A. Milesi.

C. erythraeus is a tree squirrel that inhabits tropical and subtropical evergreen and conifer forests in its native range of south-east Asia. A wide variety of arboreal habitats have proved to be suitable for this species, such as natural forests, fruit and timber plantations, and parks and gardens in rural and urbanised areas. In Argentina, *C. erythraeus* inhabits both urban and rural forested patches (Aprile and Chicco, 1999; Benitez, 2017), as was also reported in Japan (Miyamoto *et al.*, 2004). Suitable habitats include woodlands (*i.e.*, woodland patches and wooded corridors) and urbanised areas (*i.e.*, residential, suburban and urban settlements) (Guichón and Doncaster, 2008; Hertzriken, 2021). These squirrels can use highly fragmented forested patches in a matrix of non-suitable habitat (*i.e.*, open areas with no trees) (Guichón and Doncaster, 2008; Bridgman *et al.*, 2012; Benitez *et al.*, 2013).

C. erythraeus has highly arboreal habits; it nests in trees and feeds mainly on vegetable matter obtained from trees and shrubs, both in native and introduced ranges (Lurz *et al.*, 2013). In Argentina, feeding and nesting are mainly associated with introduced trees and shrub species, often used in commercial plantations, for shade, windbreaks or ornamental purposes in rural and urban areas (Benitez, 2017; Zarco *et al.*, 2018). The dependence of *C. erythraeus* on introduced trees as vital resources exemplifies how the success of one introduced species (*i.e.*, *C. erythraeus*) can be facilitated by human-modified environments and positive interactions with other introduced species (*i.e.*, exotic trees and shrubs) (Bourgeois *et al.*, 2005; Grosholz, 2005; Meyerson and Mooney, 2007; Pyšek and Richardson, 2010). Otherwise, these tree squirrels would not have successfully invaded the grasslands of the Pampas ecoregion. At the same time, squirrels could engage in mutualistic interactions that favor the regeneration of introduced trees, if viable seeds are deposited in suitable conditions far from the parental plant (Vander Wall *et al.*, 2005). The first studies on this subject suggest that *C. erythraeus* may disperse seeds of introduced vegetation through endozoochory and seed hoarding (Bobadilla *et al.*, 2016; Zarco *et al.*, 2018).

Invasion pathways

Human-mediated biological invasions often involve the movement of individuals following complex routes and multiple introduction events from different source populations (Signorile *et al.*, 2016). The range occupancy and expansion of *C. erythraeus* in Argentina can be explained by a combination of one introduction event into the country, followed by intentional translocations and releases within the country, and short and long-distance dispersal of individuals. Once the first wild population of *C. erythraeus* established in Luján Department, colonization of new areas resulted, in part, from individual dispersal into new habitat at the invasion front. Tree lines, aerial cables and roofs are regularly used by squirrels and may facilitate dispersal events among arboreal patches in fragmented landscapes. Individual dispersal plays a key role at the invasion front, determining the expansion rate and size of an established population (*i.e.*, non-human mediated dispersal, unaided spread) (Guichón *et al.*, 2020). However, the number and location of all invasion foci is determined by human-mediated introduction (*i.e.*, translocation events, aided spread) (Guichón *et al.*, 2020).

Being a charismatic species that is also easy to capture and transport, *C. erythraeus* has been intentionally carried and released into new areas within Argentina. The first invasion focus that was established in the country subsequently functioned as a source of squirrels that were translocated to other sites (Benitez *et al.*, 2013; Guichón *et al.*, 2015, 2019, 2020), as was corroborated by genetic studies (Gabrielli *et al.*, 2014). After the introduction of *C. erythraeus* in Argentina in 1970, no new squirrel releases were recorded within the country until 1995, when two translocation-release events occurred at 42 and 85 km from the original site of introduction (Guichón *et al.*, 2020). Similarly, the introduction events listed for *C. erythraeus* in Japan (Bertolino and Lurz, 2013) also indicated the occurrence of 17 new squirrel introductions or translocations after a lag period of approximately 20 years. In Argentina, this two-decade lag-phase until the onset of translocations within national boundaries was followed by a constant increase since 1995 that resulted in a total of 31 translocations, 27 of which involved released squirrels, while in the other four squirrels remained in captivity (Fig. 2) (Guichón *et al.*, 2015, 2020). Records from recent years indicate that the rate of the known translocation events has doubled in comparison to previous reports by Guichón *et al.* (2015) and now yields 1.3 translocations per year between 1995 and 2018. The number of translocation events is surely underestimated as the

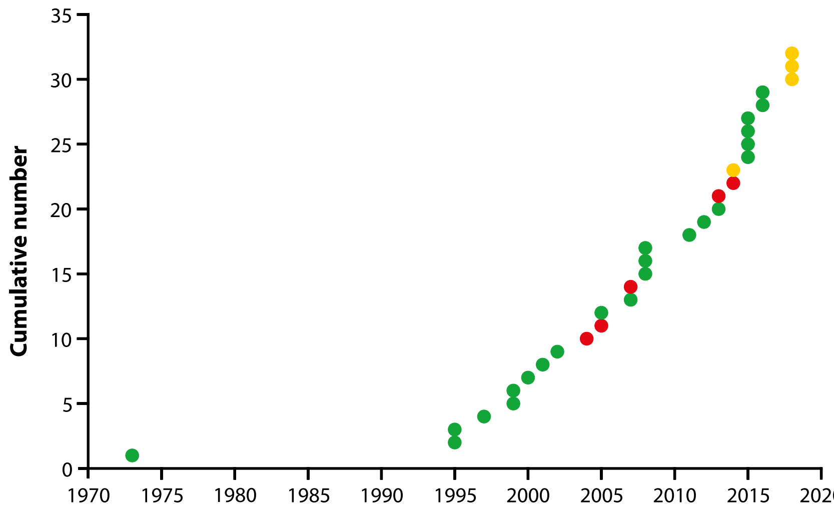

Figure 2. Cumulative number of *Callosciurus erythraeus* translocation events recorded in Argentina (data include records reported in Benitez *et al.*, 2013; Guichón *et al.*, 2015, 2020; Borgnia *et al.*, 2019). We indicate the translocations that resulted in successful (**green**) and failed (**red**) releases and those where squirrels remained in captivity (**yellow**). In those cases where the translocation date was not obtained, we indicate the year of the first reported sighting of squirrels in the wild or the year of the first interview confirming their presence or possession in captivity.

illegal transport of squirrels is difficult to document especially when individuals are released within the same invasion focus, close to their capture site, as was reported by residents (Borgnia, M., unpublished data).

The first and main invasion focus in the country (first order invasion focus centered around Luján) is still the major source of individuals (26 out of 31 translocations) (Guichón *et al.*, 2020). Five translocations recorded between 1999 and 2018 involved individuals captured in second order invasion foci, one of which originated a third order invasion focus, while after the other four translocations squirrels were kept in captivity in houses of private citizens (Fig. 2) (Guichón *et al.*, 2020). These squirrel translocations sometimes involve illegal trade, but transport of squirrels with no commercial purposes is also frequent. The introduction and subsequent translocation-release events of squirrels have usually been associated with private initiatives and/or wealthy families (Borgnia *et al.*, 2013). Squirrels are mostly released in ranches, parks, and forested and tourist areas. Five of the 27 translocation-release events failed, mostly related to individuals released in parks of the city of Buenos Aires (4 of 5). However, a high success of translocation-release events within the country (> 80%) is reflected by the 22 invasion foci that have now established in rural and urban areas from the provinces of Buenos Aires, Córdoba, Mendoza, Santa Fe and the city of Buenos Aires (Benitez *et al.*, 2013; Guichón *et al.*, 2015, 2019, 2020; Borgnia *et al.*, 2019; Coniglione and Zalba, 2019).

The translocation of squirrels into new areas is always related to their charismatic appeal as an ornamental species to "enrich wildlife" or, less frequently, to keep them as pets that usually escape or are finally released. The two-decade lag-phase in the establishment of new invasion foci indicates the occurrence of a lag in the rate of invader appearance (Crooks, 2005), which means that the onset of vector activity through translocation events took several years (Guichón *et al.*, 2015). The new phase of squirrel translocations could be related to the increase in abundance of squirrels *per se*, but also to their popularity in a region deprived of squirrels and with few diurnal wild mammals. This increase in availability and in the awareness of its presence in the region may create positive feedback in the invasion process.

Within a framework for biological invasion management (Ruiz and Carlton, 2003; Pyšek and Richardson, 2010), vector interruption consists of those actions designed to disrupt and reduce the flow of propagules to the recipient environment. In this case, disrupting translocation would not only slow down the invasion of *C. erythraeus*, but also reduce the illegal transportation of numerous species, either for economic profit or recreational or aesthetic values (McNeely, 2001; Ruiz and Carlton, 2003).

Characteristics and impacts of the invasion

The social and ecological processes involved in the successful establishment of introduced squirrel still need more studies, but at present, the propagule pressure hypothesis, which enjoys broad consensus in invasion ecology (Lockwood *et al.*, 2005; Jeschke, 2014), does not seem to play a particularly important role. Releases of 2 to 30 squirrels have initiated several *C. erythraeus* invasion foci in Argentina (Benitez *et al.*, 2013; Guichón *et al.*, 2015). On the other hand, the enemy release hypothesis (Heger and Jeschke, 2014) has found some support (Gozzi *et al.*, 2020). An advantage due to the loss of parasites and predators in the invaded community could favor squirrel survival and reproduction, resulting in high densities and further spread. Current studies on predation of *C. erythraeus* in the Pampas will provide a better understanding of the anecdotal predation events by dogs, cats or raptors recorded to date (Benitez, V., unpublished data). Parasitological studies also conducted in Argentina have shown that high density squirrel populations have low prevalence of only a few parasite species that have been acquired in the new ecosystem (Gozzi *et al.*, 2013a, 2014, 2020). No specific parasites are known to have been introduced together with the squirrels, but new interactions with local parasites are already in progress (Gozzi, 2015; Gozzi *et al.*, 2020).

It is well known, though, that the introduction of a new species may result in the introduction of novel diseases in the new environment or in a new role in the epidemiology of diseases already present in the invaded community. Zoonotic studies of *C. erythraeus* in Argentina yielded positive results for *Leptospira interrogans* in kidney samples (Gozzi *et al.*, 2013b). This is the first time that this species has been reported to be a renal carrier of *L. interrogans* and indicates that it could be involved in the epidemiology of leptospirosis (Gozzi *et al.*, 2013). Therefore, introduced populations of *C. erythraeus* could increase the prevalence of leptospirosis and the risk of contagion to humans and other wild and domestic animals, particularly taking into account that they inhabit rural and urban areas, nest close to or within houses (*e.g.*, in roofs), and are caught and handled due to their charismatic appeal.

Other concerns regarding the presence of *C. erythraeus* in rural and urban areas relate to their impact on fruit and timber production and services, due to fruit consumption, debarking, and damage to irrigation systems and cables, respectively (Guichón *et al.*, 2005; Pedreira *et al.*, 2017, 2020). As mentioned before, squirrels could favor the dispersal of viable seeds of introduced trees and shrubs, which in turn provide them food throughout the year (Bobadilla *et al.*, 2016; Zarco *et al.*, 2018). The continued spread and persistent translocations of squirrels into new areas increase the risk posed to the conservation of native biodiversity and ecosystems in Argentina, as this species will likely invade protected areas in the near future, where vulnerable species could be affected. Predation of native bird nests by *C. erythraeus* has occasionally been reported in Argentina (Pereira *et al.*, 2003; Zarco *et al.*, 2018); however, nest predation would not be the main mechanism involved in the negative effect on bird species in the Pampas (Messetta *et al.*, 2015). A trend in lower bird abundance and richness was found in sites with squirrels in comparison with non-invaded sites, and this outcome was probably related to increased competition or perceived predation risk, though results were not conclusive (Messetta *et al.*, 2015). A major concern of the potential impact of *C. erythraeus* on native species relates to its probability of establishment in the subtropical forests of Argentina, where it would enter into direct competition with native tree squirrels *Guerlinguetus brasiliensis* and *Notosciurus pucheranii* (Cassini and Guichón, 2009).

The present and potential impacts caused by *C. erythraeus* raise awareness of this problem for the people that either face damages to their production, property or services and also for those concerned with environmental problems and the ecological consequences of biological invasions in general. However, opinions and attitudes towards these squirrels range from negative (conceiving them as a harmful species that needs to be controlled) to positive (viewing them as an attractive species to be valued and protected) (Borgnia *et al.*, 2013). Personal experience with the species, its attributes, the time since its introduction in the area, and knowledge of the problems caused by this species, all affect the opinions and attitudes towards the presence of *C. erythraeus* in the Pampas (Borgnia *et al.*, 2013). Residents of Jáuregui town, where squirrels have been established for five decades, show the whole range of responses, but at present the image of this introduced squirrel is used in wall school murals, town symbols, and even illustrating the message "protect the environment" promoted by local entities (Fig. 3). Therefore, this is an example of clear cultural acclimatization, where this species has become part of the local natural heritage, and it has been added to the cultural values of local stakeholders and institutions, as a symbol of the town, shifting the cultural baseline (Pfeiffer and Voeks, 2008; Beever *et al.*, 2019). Now, this introduced squirrel could be classified as a culturally-enriching invasive species (Pfeiffer and Voeks, 2008), as has occurred with other well-known cases of introduced invasive species that are used to attract tourism and are associated with the identity of some Argentine regions (*e.g.*, salmonids, red deer *Cervus elaphus*, and sweetbriar *Rosa rubiginosa* in Patagonia) (Speziale *et al.*, 2012; Relva *et al.*, 2014).

In the last decade, the cultural impact of introduced species has become acknowledged as another consequence linked to biological invasions (see Anderson and Pizarro, this volume). Invasive species affect both biological and cultural systems, and therefore understanding these links and processes will help to better conserve our collective biological and cultural heritage (Pfeiffer and Voeks, 2008). In this context, Speziale *et al.* (2012) described

Figure 3. Iconic images of *C. erythraeus* in Jáuregui (Luján Department, province of Buenos Aires), the town where the species was introduced in 1970. The images show: **a.** sign with the legend "protect the environment;" **b-d-e.** artistic representations and murals in street walls and a bus-stop in the town; **c.** the winner entry for the town logo in a local design contest. (Photos: M. Borgnia, V. Benitez, and C. Tuis).

a shifting baseline in South America in the form of generational amnesia, which explicitly relates ecological knowledge extinction with the lack of awareness of past biological conditions by younger generations (Papworth *et al.*, 2009). Therefore, changes in the surrounding environment are not truly acknowledged and new generations get to know, interact and value the species now present in their natural and urban surroundings, ignoring the loss or replacement of species due to introductions (Speziale *et al.*, 2012; Beever *et al.*, 2019). Shifting baseline syndrome, as generational amnesia, is being considered a key issue for conservation given that it could influence participatory monitoring, local ecological knowledge and community-based conservation (Papworth *et al.*, 2009). It must, therefore, be taken into account in any communication strategy that aims for community-based monitoring and conservation actions.

Present situation

The current distribution of *C. erythraeus* in Argentina lies mostly within highly modified rural and urban areas. At present, the invasion site of highest conservation concern is the one located close to the Paraná River Delta and several protected areas, such as the Parque Nacional Ciervo de los Pantanos. This region sustains unique and biodiverse marshlands and riparian forests, composed of both temperate and subtropical flora and fauna (Malvárez *et al.*, 1999). Also, timber and fruit plantations, which could be negatively affected by debarking and fruit consumption, are important economic activities in the Lower Delta Region. Urgent actions, therefore, are needed to prevent the invasion of *C. erythraeus* into such areas of high conservation value. A collaboration strategy among local NGOs, governmental agencies, protected areas, research groups, residents, local producers and other stakeholders should work together with the goal to: 1) create an early alert network, 2) monitor squirrel spread, 3) work together in the communication of the problem to reduce translocations, and 4) facilitate rapid response actions in the invasion front near protected areas (*e.g.*, management actions in buffer zones). Such an initiative was first promoted by the Universidad Nacional de Luján and then proposed under the framework of the Global Environment Facility (GEF) project for the Argentine National Invasive Exotic Species Strategy (GEF GCP/ARG/023/GFF) that included a subproject specifically related to introduced squirrels (Guichón *et al.*, 2020). This initiative focused on the problems posed by introduced squirrels as an example of an ornamental species or a pet and it was mainly focused on communication, education and legislation. A key challenge of this project was to have a long-lasting effect, and consequently all guidelines must be incorporated into long-term ongoing projects of each institution, organisation or governmental agency, according to their own capacities and objectives.

The invasion process of *C. erythraeus* has a strong social component, and therefore, early public engagement and open, responsive communication are key aspects of any management plan that should be built using a participatory approach and taking into account the local social dimension (Crowley *et al.*, 2017a, 2017b; Novoa *et al.*, 2017; Jarić *et al.*, 2020). Traditional approaches of public education and top down, unidirectional communication can lead to destructive conflict (Crowley et al., 2017b). In turn, environmental perceptions together with emotions and past behavior can all influence community engagement in conservation initiatives (Carrus *et al.*, 2008). The new relationships between people and introduced species are major conservation challenges that need strategies accounting for participation of interdisciplinary teams and different social groups (Witmer *et al.*, 2009). Engagement in conservation activities can increase when emotional experiences are addressed (*e.g.*, joy for nature and appreciation of native fauna) and may complement messages more focused on cognitive contents (Carrus *et al.*, 2008), provided honest messages are delivered and feedback is welcomed (Crowley *et al.*, 2017b). Therefore, in the case of introduced squirrels, better communication may promote appreciation of local ecosystems and native species and illustrate the link between charismatic introduced species, such as *C. erythraeus*, and responsible pet ownership together with wildlife illegal trade. This would promote the discussion of various aspects of the *C. erythraeus* invasion, its history, impacts, risks and also its appeal as an opportunity to build from their own experience and broaden the view on the subject.

Management plans to control or eradicate introduced squirrels in European countries have been implemented for *S. carolinensis* and *Callosciurus* species (Chapuis *et al.*, 2014; Adriaens *et al.*, 2015; Bertolino *et al.*, 2016; Mazzamuto *et al.*, 2016b). Lessons learned from these management plans reinforce the importance of long-term commitment and funding, of cooperation among various institutions (governmental dependencies, conservation organizations, scientific units), stakeholders and the local community with clear roles stated from the beginning, of a clear communication strategy at a local scale, of easy access to information, and of adaptive management according to technical results and community response (Chapuis *et al.*, 2014; Adriaens *et al.*, 2015; Bertolino *et al.*, 2016; Vane and Runhaar, 2016; see also Scorolli, this volume). Successful eradication of a small *C. erythraeus* population in Belgium was achieved in 2011 (Adriaens *et al.*, 2015), while management plans were initiated in France (Chapuis *et al.*, 2014), Italy (Mazzamuto *et al.*, 2016b), Japan (Yasuda, 2015) and the Netherlands (Schockert, 2012) between 2010–2012. Until recently the only control actions conducted in Argentina were implemented by local residents, using sporadic lethal trapping or shooting in response to damage in timber and fruit plantations or property, usually with no formal authorization. In 2021, a proactive management program was initiated in the invasion focus located in Tupungato, Mendoza province, organized and funded by the provincial government in coordination with national and local authorities, and technical advice and training by researchers of the Universidad Nacional de Luján (DRNR, 2021; Benitez, V., unpublished data).

The road ahead

Once an introduced species has been established in a country, there is a high risk that it will be translocated-released to nearby regions, increasing its spread and turning control or eradication more difficult. This is particularly true for charismatic species, as shown by the repeated translocations of *C. erythraeus* in Argentina (Fig. 2) and in Japan (Miyamoto *et al.*, 2004), and also of *S. carolinensis* in Europe (Signorile *et al.*, 2016). In the context of the worldwide scenario of deliberate importation of squirrels (Bertolino, 2009), strong regulations regarding explicit prohibition of further introductions, translocations and trade of squirrels are needed. Squirrels have an innate appeal to humans and can be found in pet shops, markets and online commerce, or obtained from residents of other invaded areas. For this reason, the pet trade must be considered a high-risk pathway for new introductions, and preventive actions therefore should focus on communication and on a legal framework to regulate the import, commerce and keeping of squirrels (Bertolino *et al.*, 2013; Guichón *et al.*, 2020). In theory, intentional releases and escapes should be the most straightforward actions to monitor and regulate, but in practice there is still a need to reinforce the development of legislation and the use of information on trade and transport vectors to reduce invasions (Meyerson and Mooney, 2007; Hulme *et al.*, 2008). Moreover, the polluter-pays principle, where the agent responsible for illegal escapes/releases pays the costs of recapture, eradication and control (Hulme *et al.*, 2008), would be a desirable concept to include in the new regulations.

A comprehensive risk assessment to ban trade and keeping of *C. erythraeus* in Belgium is now available (Schockert, 2012) as a preventive measure to reduce the risk of establishment of this species (Adriaens *et al.*, 2015). Dijkstra *et al.* (2009, 2011) recommended a ban regarding this and other harmful introduced squirrels in the Netherlands, resulting in the prohibition of the commerce and keeping *C. erythraeus*, *S. carolinensis* and *S. niger* in this country since 2012 (Schockert, 2012). In the same year, the updated EU Wildlife Trade Regulation (#338/97/EC, Implementing Regulation #757/2012) suspended the introduction of live specimens of these three species in the European Union (EU), based on the threat they represent to native species and ecosystems (Adriens *et al.*, 2015). In 2013, Italy forbade selling, raising and keeping these three squirrel species (Bertolino *et al.*, 2013). Finally, *C. erythraeus* has been added to the list of introduced invasive species of EU concern (EU Regulation #1143/2014) on the basis of risk assessment and scientific evidence with the aim to address the problem of biological invasions in a comprehensive manner and to minimize effects on native biodiversity and ecosystem services, human health and economic impacts (Bertolino *et al.*, 2016). This exemplifies how national and regional regulations can complement each other to provide an adequate framework to deal with introduced invasive squirrel species.

Regulatory norms should adapt to local-regional necessities and realities because pathways can be idiosyncratic and reflect specific attributes of the species and the invaded area (Hulme *et al.*, 2008). Under the framework of the Argentine National Invasive Exotic Species Strategy, a risk assessment protocol was developed to be used before the importation of any species. This instrument was shared with national and provincial governmental agencies and made compulsory to prevent importing new invasive species. For introduced squirrels, specific legal tools regarding their import, capture, trade, keeping and release (Gozzi *et al.*, this volume) intend to slow down their spread and provide a legal framework to implement management actions. In addition, voluntary best practice codes for pet trading/keeping, also elaborated under the Argentine National Invasive Exotic Species Strategy (Zalba, S., personal communication), can facilitate the commitment of veterinarians and pet shop owners to responsible pet keeping.

Social perceptions, attitudes and actions towards charismatic introduced species play a key role in the creation of new invasion foci. Therefore, the human dimension related to introduced squirrel species must be seriously taken into account to understand the process of invasion and decide management actions (Jacobs *et al.*, 2014; Estévez *et al.*, 2015; Crowley *et al.*, 2017b). Communication linking biological invasions, illegal trade of wildlife and responsibility in the pet trade/keeping should reach a broad public and should be responsive to concerns raised by residents, although a special effort should be made to reach veterinarians and pet sellers (Episcopio-Sturgeon and Pienaar, 2020). Easy access to informed guidelines about the potential consequences and legal issues of releasing exotic species would prevent some people from buying and/or releasing these species into the wild when they cannot keep them as pets any more or with the purpose of enriching local wildlife. In this and other conflicts between socioeconomic and conservation interests, it is recommended to offer alternative solutions instead of only informing prohibitions (Carrete and Tella, 2008). The message that wildlife species are not pets could be accompanied by examples of adequate pet species and of other ways to observe, value and enjoy wildlife. A clear message of positive/negative outcomes of concrete actions should alert about the responsibility that every citizen and pet owner has on the consequences of these actions and should offer communication channels for questions and unexpected situations.

When prevention fails, the best response would be to evaluate the need and feasibility of an early warning-rapid response (Pyšek and Richardson, 2010; Simberloff, 2014). Early detection and rapid removal of introduced animals before the establishment of large populations are essential actions. A monitoring network could be built using a citizen science approach (Ricciardi *et al.*, 2017) that may be suitable for the case of introduced squirrels (Bertolino *et al.*, 2016). In fact, an early alert network to collect information from residents that observe squirrels in new sites has been promoted in Argentina by the Universidad Nacional de Luján. It was then fostered under the Argentine National Invasive Exotic Species Strategy and is currently active as a collaborative project, using the Argentine web portal of the *iNaturalist* citizen science platform (https://www.argentinat.org). However, there is still a need to build capacity to have a contingency plan to eradicate squirrels when they are still in low numbers and in relatively small areas isolated from other invaded areas. Part of the challenge resides in making the political decision to implement a management plan to tackle a problem that is not considered urgent at present and that may raise strong opposition from the community. Governmental agencies face pressing problems, have limited budgets for ongoing programs, and are sensitive to public opinion. As a result, they are reluctant to invest in these kinds of preventive actions unless a clear negative impact is foreseen (*e.g.*, squirrel damage to fruit production in a key area for regional farmers in the province of Mendoza). This is an example of spatial and temporal scale mismatch between ecological potential damage, cultural attachment to a new species and management incentive (Beever *et al.*, 2019).

In areas where *C. erythraeus* has already established large populations, managers should promote cooperation and constructive debate to develop less conflict-prone actions (Crowley *et al.*, 2017b). For invasive animals, particularly charismatic species, lack of public support derives mainly from moralistic value disagreements (Novoa *et al.*, 2017). Environmental perception, emotions and personal experiences, either positive or negative, all influence the willingness to engage in or support pro-environmental actions, such as reduction of the capture-transport of squirrels and approval of management actions (Carrus *et al.*, 2008; Borgnia *et al.*, 2013). Citizens' engagement is critical to achieve broad commitment to modify behaviors with positive/negative ecological consequences. In Luján, where introduced squirrels were first released five decades ago, a municipal regulation was sanctioned in 2011 in response to a project presented by a local school. Teachers of this school had previously participated in workshops organised by the Universidad Nacional de Luján, exposing the problem of *C. erythraeus* as a regional example of the link between biological invasions, illegal wildlife trade and pet keeping. This exemplifies how working with various stakeholders promotes citizen engagement and can have a multiplying effect. A wide spectrum of social actors, NGOs, governmental dependencies, national and regional institutions, and education institutions are needed to engage in education, communication, prevention and management, each working from their social/political role and responsibility. Specific guidelines for education in schools and broad communication in Argentina have been produced under the scope of the Argentine National Invasive Exotic Species Strategy (FAO and MAyDS, 2017; FAO and SAyDS, 2018). In each invasion focus, it is important to identify key partners that are relevant in a local-regional level, such as local NGOs or the Administración de Parques Nacionales when the invasion is close to a protected area, and local farmers associations and agricultural institutions when commercial production could be damaged.

The invasion foci of *C. erythraeus* recorded in Argentina differ in the range occupied by squirrels and their abundance, and can be placed at different stages of the invasion process (Blackburn *et al.*, 2011), which also should be taken into account to establish management priorities based on biological, economic, social and political issues (Guichón *et al.*, 2015, 2020). The social-ecological context of each region is different and so are the times elapsed since introduction and the bonds developed with the squirrels. Public awareness increases support for invasive species management (Novoa *et al.*, 2017). Residents' support and engagement could be developed in invasion foci located in rural areas, while opposition to control actions usually is stronger in tourist and urban areas (Borgnia *et al.*, 2013). As stated before, a strong limitation is the lack of political commitment to implement a management program, which results in inaction and indecision, with the exception of the recently initiated management plan in Mendoza province. Localized control actions could be taken in the short-term, following priority guidelines to select areas where urgent actions are needed and the biological, social, political and economic conditions are met. The recent management program and any new control action will not only reduce squirrel impact in priority areas, but will provide valuable insight to test methods and the commitment of all institutions, organizations and groups involved. Evaluation of these results and actions using an adaptive management framework will increase their success (Richardson *et al.*, 2020). Interdisciplinary work and community-based, pro-active environmental commitment are a promising road to tackle this complex socio-ecological conservation problem.

Acknowledgements

We thank P. Pedreira and A. Darget for her contributions, and young researchers and students that participated in several projects in the last decade. Local residents and members of governmental agencies, NGOs, protected areas and national institutions collaborated in various aspects of our studies. This project on introduced squirrels in Argentina is mainly supported by the Universidad Nacional de Luján, Argentina.

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4 | HUNTING AS A DRIVER OF MAMMAL INTRODUCTIONS

LA CAZA COMO VECTOR DE LA INTRODUCCIÓN DE MAMÍFEROS

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Abstract. Hunting is an ancestral human practice to obtain food. However, in recent times, it has become a highly lucrative economic activity and is a potential conservation tool to control populations of introduced invasive species. Ironically, though, hunting is also one of the most important drivers of mammal introductions around the world. Between the 19th and 20th centuries, at least 25 species of mammals from Europe and Asia have been introduced in game reserves in Argentina. After subsequent escapes and translocations, eight species of the introduced mammals now have wild populations outside these game reserves. Many have also become invasive, causing negative impacts to native biodiversity, economic activities and human health. These outcomes show that hunting reserves represent a source of introduced mammals, and that the lack of regulations and compliance with laws on hunting activities in the country is problematic. On the other hand, hunting on public lands, such as national parks, requires combining efforts between scientists and managers to improve legislation and management of these species in protected areas, where financial and organizational constraints may limit the scope and effectiveness of conservation actions. For example, in Argentina, two control programs provide successful experiences of carrying out inter-institutional participation between local residents, scientists and stakeholders: a short time hunting program to control red deer in Parque Nacional Lanín and a long-time hunting program to control wild boar in Parque Nacional El Palmar. Given the multi-faceted social, economic, health and ecological impacts of introduced invasive mammals, it is important to update, apply and reinforce the regulation of hunting activities, as well as consider hunting as a tool for the management of introduced invasive mammals.

Resumen. La caza es una práctica humana ancestral que se originó para buscar alimento, pero que en tiempos recientes se ha convertido en una actividad altamente lucrativa, también utilizada para

reducir o controlar poblaciones de animales plaga, e incluso con fines de conservación para proteger especies en peligro de extinción. La caza, ya sea para obtener alimento o como actividad cinegética, es uno de los motivos más importantes en todo el mundo de la introducción de mamíferos fuera de su rango nativo. Principalmente desde el inicio del siglo XV con las incursiones desde Europa para explorar y descubrir nuevas tierras, muchos animales de trabajo (p.ej. caballos) y cría (p.ej. cerdos) fueron transportados e introducidos a nuevas regiones alrededor de todo el mundo. Más recientemente, la actividad cinegética se ha convertido en uno de los vectores más importantes de la introducción de mamíferos en todos los continentes. Esto ha ocurrido en Sudamérica entre principios del siglo XIX y finales del siglo XX, y específicamente en Argentina donde al menos 25 especies de mamíferos han sido introducidas, principalmente desde Europa y Asia.

Si bien estos mamíferos fueron destinados inicialmente a condiciones confinadas en cotos de caza, campos o reservas privadas, los posteriores escapes y translocaciones de animales han provocado que actualmente Argentina cuente con ocho especies de mamíferos introducidos con interés cinegético (antílope negro: *Antilope cervicapra*, ciervo axis: *Axis axis*, búfalo de agua: *Bubalus arnee bubalis*, ciervo colorado: *Cervus elaphus*, ciervo dama: *Dama dama*, liebre europea: *Lepus europaeus*, conejo europeo: *Oryctolagus cuniculus*, y jabalí: *Sus scrofa*) con poblaciones silvestres. Muchas de estas especies son consideradas especies invasoras que provocan impactos sobre la biodiversidad nativa, las actividades productivas y la salud humana.

El elevado número de establecimientos registrados para actividades cinegéticas (>112) distribuidos en gran parte del país, presupone un potencial y latente foco de escape de mamíferos teniendo en cuenta el escaso control y falta de regulaciones en torno a esta actividad. Dichas regulaciones son muy dispares entre los gobiernos provinciales y responden en ocasiones al interés y presiones de diferentes sectores involucrados, por ejemplo, estableciendo cupos al número de animales cazados en especies de mamíferos introducidos consideradas como invasoras (*e.g.*, liebre europea). Muchas de estas especies, a partir de los primeros escapes (intencionales o accidentales) desde establecimientos cinegéticos o campos privados, se han dispersado rápidamente (*e.g.*, jabalí, conejo, liebre), invadiendo nuevos ambientes y alterando la dinámica de estos ecosistemas, afectando así las interacciones entre especies, compitiendo con especies nativas por recursos, reduciendo la cobertura y riqueza de especies vegetales, siendo vectores de enfermedades y facilitando la invasión de otras especies.

La caza deportiva es una actividad permitida en algunos sectores de áreas protegidas de Argentina como los Parques Nacionales Nahuel Huapi y Lanín, donde la caza de ciervo colorado es regulada por la Administración de Parques Nacionales (APN), emitiendo y cobrando los permisos de caza, estableciendo cupos y fechas de caza. En 1986 la APN definió políticas de manejo para que la caza deportiva se desarrolle en el contexto del manejo de poblaciones de ciervo colorado. En este sentido, el gobierno consideró que la caza deportiva puede ser una herramienta aceptable para lograr los objetivos de conservación de la biodiversidad, brindando oportunidades de caza, aplicada en el marco de un manejo y control poblacional.

El manejo poblacional a partir de la aplicación de caza deportiva y caza de control combinadas fue hasta el momento pobremente aplicada, o por cortos periodos de tiempo, principalmente en el Parque Nacional Lanín (PNL), además de en los Parques Nacionales Nahuel Huapi (PNNH), Lihué Calel, Los Alerces y Lago Puelo. Resulta indispensable que, con la vasta información generada sobre la especie y sus impactos en estos últimos años, el manejo del ciervo colorado se lleve a cabo en función de las condiciones de la población (proporción de sexos, rangos de densidad) y en relación con los objetivos de conservación de la biodiversidad amenazada por esta especie invasora, y no con el foco exclusivo en la caza de trofeos.

La caza, como se destacó anteriormente, también ha sido implementada en tiempos modernos con fines de control y conservación. En el Parque Nacional El Palmar (PNEP), el jabalí y el ciervo axis son dos mamíferos introducidos que han proliferado notablemente en el área provocando impactos negativos sobre la biodiversidad. En particular, la depredación del jabalí sobre renovales de palmera yatay *Butia yatay* (valor de conservación: emblema del área protegida) motivó la implementación de un plan de caza control para los mamíferos invasores en el parque nacional con el objetivo de reducir sus impactos y disminuir sus poblaciones. Formalmente desde 2006 a la actualidad se ha implementado este plan de control, principalmente aplicando caza desde apostaderos elevados utilizando un cebadero. Uno de los aspectos más sobresalientes del plan, además de su continuidad en el tiempo y el éxito reduciendo las poblaciones de jabalí, fue la incorporación de cazadores de las comunidades vecinas, muchos de los cuales anteriormente ingresaban al parque a cazar de manera furtiva. Estos cazadores, ahora controlados y regulados por las autoridades del PNEP, colaboran activamente con el plan de control, reforzando así las relaciones entre los sectores involucrados en el manejo de mamíferos invasores de la región.

La implementación de la caza en tierras públicas es compleja y requiere una articulación entre científicos y gestores para mejorar la legislación y la gestión relacionada con las áreas protegidas y las especies introducidas. Sumado a esto, las capacidades económicas y organizativas de las áreas protegidas muchas veces limitan el logro de un manejo integral y eficiente de los mamíferos invasores con un enfoque cooperativo para perseguir múltiples objetivos que satisfagan a los diferentes actores sociales.

La caza representa a nivel mundial una actividad altamente lucrativa, que ha funcionado como vector de la introducción de mamíferos en todo el mundo. Argentina sufre actualmente las consecuencias de este fenómeno con la invasión e impacto de especies que afectan negativamente la biodiversidad nativa, las actividades productivas y la salud humana. Es importante actualizar, reforzar y aplicar las medidas de control relacionadas con la regulación de las actividades cinegéticas en el país y, por otro lado, considerar seriamente la caza control —delineada con un estricto marco de participación interinstitucional— como una herramienta para la gestión de mamíferos introducidos.

Sport hunting in the world and Argentina: socio-economic importance

Hunting is the practice of searching or lying and waiting for animals with the intent of killing them. It has been used by humans to obtain food since prehistory. However, in Western culture, hunting can also imply a sport or recreational activity. Plus, it has been used to reduce or manage over-abundant animal populations (*i.e.*, "pests" or introduced invasive species) and their impacts (Jeschke and Strayer, 2006; Bengsen and Sparkes, 2016). Globally, hunting now represents an extremely lucrative business, but it also creates incentives for native wildlife conservation. In Africa, hunting can play an important role in the conservation of some endangered species and in the rehabilitation of wildlife areas. For example, income generated by trophy hunting has helped to recover white rhinoceros (*Ceratotherium simum*) populations in South Africa and restore its habitat in Mozambique (Lindsey *et al.*, 2007). However, hunting gets more complex when involving the introduction of species, which represents one of the greatest agents of transformation of native ecosystems (Simberloff *et al.*, 2013). For example, in North America, successful mammal introductions (and their associated ecological and economical costs) are mostly linked to the hunting industry (Pimentel *et al.*, 2005; Jeschke and Strayer, 2006).

Table 1. List of species offered for sport hunting in Argentina, indicating origin (**Af** = Africa, **As** = Asia, **E** = Europe, **N** = North America, **C** = Central America, **S** = South America) and population status at present as free-ranging populations (**FRP**) or confined populations (**CP**).

Scientific name	Common name	Origin	FRP	CP
Antilope cervicapra	blackbuck	As	×	×
Axis axis	axis deer	As	×	×
Bubalus arnee bubalis	water buffalo	As	×	×
Capra hircus	wild goat	As		×
Capra ibex	Alpine ibex	E		×
Cervus elaphus	red deer	E, As	×	×
Dama dama	fallow deer	E, As	×	×
Elaphurus davidianus	Père David's deer	As		×
Hemitragus jemlahicus	Himalayan tahr	As		×
Lepus europaeus	European hare	E	×	
Oryctolagus cuniculus	European rabbit	E	×	×
Ovis aries	Texas dall	N		×
Ovis aries	Dorset sheep	E		×
Ovis aries	Scottish blackface sheep	E		×
Ovis aries	Somali sheep	Af		×
Ovis aries orientalis	mouflon sheep	As, E		×
Ovis dalli	Dall's sheep	N		×
Ovis orientalis musimon	European mouflon	E		×
Sus scrofa	wild boar	E, As	×	×

Several reasons explain this observation of successful introductions, including the desirability of mammals as useful in food provisioning, animal husbandry, pets, animal assistance (*e.g.*, for farming), hunting, pest control, and transportation (Long, 2003; Hoddle, 2004; Forsyth *et al.*, 2013; Tedeschi *et al.*, 2021). From all fauna introduction, mammals are the group with most species' introductions at global level (Blackburn *et al.*, 2017). Historically, mammal introductions have been especially prominent in countries where native mammal fauna was non-existent or scarce (*e.g.*, oceanic islands Long, 2003); where the European colonists were unfamiliar with the endemic species to be effectively used in the agricultural or livestock systems (*e.g.*, Australia, Long, 2003, and South America, Ballari *et al.*, 2016); or where there was a perception by colonists that the faunal assemblage needed to be "improved" (Estévez *et al.*, 2015; Archibald *et al.*, 2020).

In southern South America, mammals were mainly introduced for hunting purposes (food or sport hunting) between the late 19th and early 20th centuries (Ballari *et al.*, 2016). Specifically, in Argentina, at least 25 mammal species were brought mainly from Asia and Europe (Table 1). Many of them adapted and invaded most of the country's territory (Navas, 1987; SAyDS and SAREM, 2019). Only a handful species did not prosper and were unsuccessful at invading for various reasons (*e.g.*, lack of adaptation, extreme weather, etc.) (Table 2). Most of these introduced mammals to Argentina are found within private game hunting reserves. There are at least 112 registered shooting or game reserves, most of them located in the central provinces of La Pampa, Córdoba, Neuquén, and Buenos Aires (MJyDH, 2019). These game reserves represent a latent source of potential new escapes or intentional releases that are a pool of future invasive mammals. Therefore, they are also of great importance for invasive species management and planning.

Table 2. List of mammals introduced in Argentina for sport hunting that were not successful, indicating origin (**Af** = Africa, **As** = Asia, **E** = Europe, **N** = North America, **C** = Central America, **S** = South America).

Scientific name	Common name	Origin
Ammotragus lervia	aoudad, or Barbary sheep	Af
Bison bonasus	European bison	E
Cervus elaphus canadensis	elk, or wapiti	N, As
Odocoileus virginianus	white-tailed deer	N, C, S
Rangifer tarandus	reindeer, or caribou	E
Rupicapra rupicapra	Alpine chamois	E

Many of the introduced mammals in Argentina are known to cause negative impacts on native ecosystems (Novillo and Ojeda, 2008; Sanguinetti *et al.*, 2014; Valenzuela *et al.*, 2014; Ballari *et al.*, 2016). The reported damages include changes in plant and animal communities due to overgrazing (Relva *et al.*, 2010; Barrios-García *et al.*, 2012), predation, competition (Ballari *et al.*, 2015a), and disease transmission (Flueck and Smith-Flueck, 2012). Below, we will discuss the negative impacts of invasive mammals in more detail, but importantly, the biological consequences of introduced mammals have stimulated scientists and managers to understand their biology and assess their ecological and economic impacts to manage their populations (Pyšek and Richardson, 2010, Simberloff *et al.*, 2013; Valenzuela *et al.*, 2014; Tedeschi *et al.*, 2021).

The fact that many introduced mammals represent a concomitant economic resource raises conflicts of interest where biodiversity conservation could be threatened. Indeed, introduced invasive mammals that are also game species are sometimes actually protected by laws and protected areas, such as establishing quotas and hunting periods with the aim of maintaining and improving populations (Sanguinetti *et al.*, 2014; Speziale *et al.*, 2014). In addition, game species sometimes represent a valuable socio-economic resource in rural areas (Jackson, 1988), where profit from the hunting industry (*e.g.*, hunting permits, tourist accommodation, local guides) represents an important business. These hunting businesses and their incentives can conflict with conservation goals, such as when hunters seek to improve trophies by maintaining long-term populations, rather than controlling them in the short-term (Sanguinetti *et al.*, 2014). Unfortunately, in Argentina there are many problems associated with the hunting industry, including ineffective control and enforcement of laws, and limited benefits flowing to conservation.

Hunting policy framework

An adequate legal framework is extremely important to solve environmental problems. In Argentina, there are several national-level laws that regulate the use and conservation of natural resources. However, the national constitution devolved the rights and responsibilities over natural resources to each province, where national-level policies are only valid if the provincial governments adhere to them.

The most important law related to wildlife conservation at the national level (National Law #22241) includes relevant aspects for introduced species management and control in Argentina. This law establishes the protection of wild fauna, without specific reference to their origin, taking into account individuals that live free and independent from humans, those that live in captivity or semi-captivity, and those that originally were domesticated and then became feral (Article #3). This law also regulates the importation, introduction or establishment of animals that can alter the ecological balance or affect economic activities (Article #5) and the release of captive animals without prior agreement of the corresponding authority (Article #6). These last two articles have vital importance in the species introduction processes in Argentina. Although it has not been documented conclusively, Article #6 has likely been violated on numerous occasions, contributing to the spread of introduced mammal species in much of the national territory. Specifically, regarding the impacts of introduced species, Resolution #376/97 (Ministerio de Ambiente y Desarrollo Sostenible) establishes that an environmental impact assessment is mandatory prior to the introduction of new species. The resolution even includes general guidelines for standardizing the procedure. Unfortunately, almost all game species introductions in Argentina occurred prior to this resolution in 1997.

Each year, the office that manages each province's natural resources determines the length of hunting seasons and the number of individuals that can be obtained for each authorized species (*e.g.*, Bulletin of La Pampa province and Article #16, Law #22421). In general, hunting is not allowed between June/July to March, which includes the reproductive period, without distinguishing whether species are native or introduced. In addition, the quota of hunted animals allowed varies among provinces and game reserves. On occasions, this type of regulation tends to protect and promote the development of populations (both native and introduced), and hence does not take into account the negative impacts that introduced species may have on native ecosystems. This is more relevant when hunting quotas are established for introduced species with high reproductive rates, such as the European hare (*Lepus europaeus*) or the wild boar (*Sus scrofa*). Indeed, the resolution for hunting in Argentina (National Decree #666/97), which regulates the conservation of wild fauna, establishes the classification of species into four categories of hunting, including for sport, commercial activities, control (of harmful species), and scientific, educational or cultural reasons (Article #12). Again, this resolution does not emphasize the distinction between native and introduced species, including the section "Integrated Control of Harmful Species" (Articles #19 and #20). In this case, when the regulatory frameworks from the provincial and national levels are considered together, it becomes clear that there is an incoherent philosophical and theoretical approach to native and introduced species, which complicates the definition of effective management and control strategies for introduced invasive mammals.

Lastly, the Ministerio de Ambiente y Desarrollo Sostenible de la Nación coordinated the elaboration and implementation of the project "Strengthening of Governance for the Protection of Biodiversity through the Formulation and Implementation of the National Invasive Exotic Species Strategy" (GCP/ARG/023/GFF). This project was financed by Global Environmental Facility (GEF) and assisted by the United Nation's Food and Agriculture Organization (FAO). The strategy's main objective is to reduce the impact of introduced species on biodiversity, but also proposes the improvement of socioeconomic benefits, current and future conservation and sustainable use of biological diversity (*i.e.*, natural resources and ecosystem services) (SNEEI, 2017). The initiative is based on consensus with different public and private organizations to have an efficient prevention, early warning, control and monitoring system at country level, with coordinated and planned actions, as well as consistent and effective communication to prevent further introductions and expansions.

Consequences of game introductions

Intentional releases, lack of control and poor fence structures of hunting reserves allow accidental animal escapes and subsequent establishment of feral populations. Indeed, all invasive ungulates have had escape events from the confinement from hunting ranches located in La Pampa, Entre Ríos, and Neuquén provinces (Petrides, 1975; Bonino, 1995; Novillo and Ojeda, 2008; Ballari *et al.*, 2016). The majority of invasive game species also have expanded their range from the introduction/escape locations in all directions. For example, the European hare expanded its range at a rate of 20 km/year in some areas, and now the distribution encompasses all continental Argentina (Bonino *et al.*, 2010; Monteverde *et al.*, 2019; see Valenzuela, this volume). Similarly, the wild boar is expanding its range at 3,500 ha per year in northwestern Patagonia and is now present in more than 30% of Argentina's territory (Pescador *et al.*, 2009; Ballari *et al.*, 2019).

The spread of invasive game species in Argentina causes numerous environmental consequences, which have been recorded to some extent (see Novillo and Ojeda, 2008; Ballari *et al.*, 2016). Both the European rabbit and hare are catalogued as pests in Argentina (Cuevas *et al.*, 2019; Monteverde *et al.*, 2019), and while there is little information on their ecological impacts in the country, these herbivores are suspected to have detrimental effects on vegetation, to compete for food and/or shelter with native mammals, and to disperse seeds of introduced plants (Jaksic, 1998; Bonino and Soriguer, 2009; Bobadilla *et al.*, 2020;

Bobadilla *et al.*, 2022). Indeed, Galende (2014) and Galende and Raffaele (2013) described partial diet and spatial overlap between rabbits and hares with the native rock specialist, the southern vizcacha (*Lagidium viscacia*). However, rabbits and hares also are "beneficial" to native predators by increasing the supply of prey and/or by decreasing predation pressure on native fauna (Jacksic, 1998; Novaro *et al.*, 2000). For example, up to 45% of mountain lion (*Puma concolor*) diet is comprised by European hare in Patagonia (Novaro *et al.*, 2000).

Many introduced ungulates are known to compete with native species, as they are selective browsers. Browsing usually alters plant community structure and composition by reducing regeneration, growth and survival of herb, shrub, and tree species (Côté *et al.*, 2004; Lees and Bell, 2008; Bonino *et al.*, 2010). For example, in Patagonia, red deer (*Cervus elaphus*) and fallow deer browse preferably on native plants, such as Chilean cedar (*Austrocedrus chilensis*), *Schinus patagonicus*, and maqui (*Aristotelia chilensis*), reducing plant cover and growth, while facilitating invasion of introduced trees (Veblen *et al.*, 1989; Relva and Veblen, 1998; Relva *et al.*, 2010; Barrios-García *et al.*, 2012; Relva and Sanguinetti, 2016). Moreover, diet overlap with the Patagonian huemul (*Hippocamelus bisulcus*) and Southern pudu (*Pudu puda*), which are native and threatened ungulates, has been suggested (Povilitis, 1981; Dolman and Wäber, 2008; Galende *et al.*, 2005).

Wild boar impacts native ecosystems by overturning extensive areas of vegetation to feed on roots, invertebrates and fungi (Barrios-García and Ballari, 2012). This disturbance is new to the native ecosystems of Argentina, as there are no native mammals with such foraging habits. Rooting by wild boar increases bare ground, reduces plant biomass, increase soil degradation, negatively affect perennial plant species, and facilitates further invasion by introduced plants (Barrios-García and Ballari, 2012; Barrios-García and Simberloff, 2013; Cuevas *et al.*, 2012; Nuñez *et al.*, 2013; Cuevas *et al.*, 2020; Cuevas *et al.*, 2021). Furthermore, wild boar depredates native monkey puzzle tree (*Araucaria araucana*) seeds and native rodent seed dispersers and could potentially threaten Araucaria forest regeneration and ecological processes, if boar numbers continue to increase (Sanguinetti and Kitzberger, 2010; Shepherd and Ditgen, 2012, 2013; Tella *et al.*, 2016). While the impact on animal communities (predation) in Argentina has yet to be assessed, it is known that wild boar host a number of diseases—including trichinellosis, brucellosis, and tuberculosis—that could harm both native mammals and livestock (Ruiz-Fons *et al.*, 2008; Meng *et al.*, 2009), and it could be a potential carrier of other diseases not yet registered in the country and devastating in economic aspects such as African swine fever (SENASA, 2018; see Uhart, this volume).

Some of the game species introduced in Argentina for hunting purposes were or are being controlled. Rabbits in Tierra del Fuego have been controlled by hunting, trapping, by introducing Pampa fox (*Lycalopex gymnocercus*) from mainland, and by using the myxoma virus in 1954 (Jaksic and Yañez, 1983). Nevertheless, there are still several focal areas, where populations are apparently growing (*e.g.*, the Ushuaia Peninsula and Parque Nacional Tierra del Fuego; Cuevas *et al.*, 2019; Bobadilla *et al.*, 2021). In Neuquén province, the myxoma virus is said to be used illegally since the 1980s, but rabbit populations are abundant and spreading southward (Galende, 2014). Hares, deer, and wild boar are all subject to hunting, although only during specific seasons and generally with a maximum daily limit (SAGyP, 2017). Additionally, the red deer has been successfully reduced through hunting in PNL (see Box 1, Sanguinetti *et al.*, 2014), and wild boar in PNEP (see Box 2, Ballari *et al.*, 2015a; Gürtler *et al.*, 2017). While all these efforts contribute to reducing introduced invasive species abundance and impacts, in general they are very limited in time and extent.

Sport hunting and protected areas

During much of the middle of the 20th century, the problem of introduced species as a threat to biodiversity was not included in the political agenda for protected areas, and even less for those species with value for hunting. Introduced species were mostly considered as a natural resource to be exploited for social and economic benefits (see also Guichón *et al.*, this volume). For example, wild boar, red deer and European hare, widely distributed today, have been extensively exploited in Argentina because of their attractiveness as a species of big game and/or the quality of their meat and fur (Ballari *et al.*, 2019; Monteverde *et al.*, 2019; Relva *et al.*, 2019).

In particular, although red deer and wild boar are now present in many protected areas (Ballari *et al.*, 2019; Relva *et al.*, 2019; APN – SIB, 2020), sport hunting is only permitted in some sectors within Parque Nacional Lanín (PNL) and Parque Nacional Nahuel Huapi (PNNH) (APN, 2011). Both species were introduced in Patagonia between 1917 and 1922 for hunting purposes, before national parks were created, in a historical context influenced by the recent European immigration (Daciuk, 1978; Archibald *et al.*, 2020).

By the 1950s, red deer had expanded to the southwest of Neuquén province, and the Administración de Parques Nacionales (APN) authorities already had identified it as a threat to biodiversity within Parque Nacional Lanín (PNL) (created in 1937; Dimitri, 1959). In this historical context, sport hunting was allowed in this protected area in 1955, where hunters were allowed to access over 700 km² of public land by means of a payment by auction to the highest bidder. In this way, they still were able to acquire the right of 7–8 days access to hunting areas (2,000–6,000 ha in size) to kill trophies and females if they had interest. Later, in 1987, with the increase of distribution and abundance of red deer southwards, sport hunting was allowed in over 620 km² of public land in PNNH.

Since the 1990s, with the increase of economic interest in the region and the hunting of red deer, trophy sport hunting and female elimination was allowed in private lands within the areas designated “national reserve” in both national parks (Nahuel Huapi and Lanín). These areas are equivalent to Category VI areas with the IUCN classification system (IUCN and UNEP – WCMC, 2014). This authorization aims to exert hunting pressure on wild and self-maintained red deer population on private lands, prohibiting any management that promotes the increase of their distribution and abundance. However, hunting pressure, numbers and type of animal to be felled are all defined almost exclusively by ranchers.

At the same time, during recent decades, there has been growing concern about the impact on biodiversity, based on the accumulation of local scientific evidence (Veblen *et al.*, 1989; Relva and Veblen, 1989; Veblen *et al.*, 1992; Relva *et al.*, 2009; Flueck, 2010; Relva *et al.*, 2010; Barrios-García *et al.*, 2012; Nuñez *et al.*, 2013; Relva *et al.*, 2014; Relva and

Sanguinetti, 2016). Sport hunting in protected areas is still considered a valid strategy to reduce environmental impacts against biodiversity, if it is carried out within the context of red deer population management to maintain low densities (see Box 1; Sanguinetti *et al.*, 2014).

BOX 1

Red deer sport hunting and population management needs in protected areas

In Argentina, the occurrence of red deer (Fig. 1a) within protected areas is mainly restricted to those located in northern Patagonia, due to the history of introduction and spread associated with hunting interests in the early 20th century (Merino *et al.*, 2009; Relva *et al.*, 2019). During the last 60 years, red deer management in PNL and PNNH consisted mainly in allowing sport hunters to seek trophies, and optionally females, with the idea to exert hunting pressure without investing economic resources by the government. However, the government charges hunting licenses to, at least in theory, reinvest in population management practices. In addition to this sport hunting in both national parks, in recent years some red deer control hunting projects have been developed in these and other protected areas.

The main conflict between conservation and sport hunting within protected areas lies in determining the red deer population density that is compatible with maintaining sensitive biodiversity components. To face this conflict, the APN defined in 1986 the first policy and management guidelines for red deer to put trophy hunting in the context of population management (Ramilo *et al.*, 1986). This policy defined management actions and strategies to limit new introductions and avoid the dispersion to new areas. In areas already invaded, the policy promotes control actions to maintain populations stable at low density and sex ratio close to 1:1, assuming that this demography conditions enhance the development of high-quality trophies (Mysterud *et al.*, 2001; Kruuk *et al.*, 2002; Putman, 2004). In this context, the government considered that sport hunting is an acceptable tool to achieve biodiversity conservation goals and gives hunting opportunities to different kinds of hunters (Fig. 1b), as long as it is applied within the framework of population management for the species and therefore, must be combined with complementary hunting to remove females, offspring and young individuals.

Strategies to successfully reach the overall conservation objectives (*e.g.*, avoid dispersal, limit new introductions, etc.) can be applied using different management approaches and control methods, depending on the protected area, its conservation values, and the status of the red deer invasion. Concessions and management plans with social participation for control or commercial hunting were identified as valid approaches. Aerial or ground (diurnal and nocturnal, including dogs) hunting methods were considered depending on conservation goals, biodiversity at risk and red deer invasion scenario. This approach also provides economic opportunities to settlers and residents by allowing them to participate in red deer management, while abandoning or reducing historical land degradation of livestock grazing. In synthesis, the general idea was that government mainly offered hunting possibilities and economic opportunities to local communities, with little investment in red deer population management.

After 35 years since the policy was established, it has been poorly applied regionally. Only short-period red deer population management experiences were carried out between 2008–2012 in PNL (PNL, 2012; Sanguinetti *et al.*, 2014; Fig. 1a-c), a control plan on Victoria Island (PNNH, 2020) and the Ñirihuau area within PNNH, a control plan in Parque Nacional Lihué Calel since 2013 (Pastore *et al.*, 2013), and one in Parque Nacional Los Alerces since 2019. Additionally, in Parque Nacional Lago Puelo (where the red deer does not yet have stable populations), there is an action protocol to control progress when individuals are found (Pastore *et al.*, 2017).

During the last 30 years a great deal of scientific information about red deer ecology, management and their impact in Patagonia was published (Relva and Sanguinetti, 2016). Red deer management should be carried out based on population conditions (sex ratio, density ranges) and in relation to biodiversity conservation goals threatened by this invasive species. Furthermore, the management should consider sexual and spatial segregation, as well as the influence of habitat type within environmental gradients and climate variability on population dynamic. Therefore, different population management practices should be applied, with control methods and hunting pressure against each age and sex classes, varying in space and time at public and private lands within and outside protected areas (Flueck *et al.*, 1995; Nugent *et al.*, 2011; Relva and Sanguinetti, 2016).

The debate continues about how to conserve valuable ecosystems and endangered species in the context of red deer as a threat. This debate lacks an explicit and precise conceptual and regulatory framework that links the relation between red deer densities and population structure, with the loss of native conservation targets and trophy quality. For example, although there is a solid scientific background showing that the improvement of trophy quality implies the removal of females and young individuals (Tremblay *et al.*, 2004; Milner *et al.*, 2006), local hunters do not accept this management strategy. Without a more coherent framework, no measurable conservation and management goals can be defined for an explicit agreement between stakeholder's and the government. Only with an explicit and holistic approach, will it be possible to discuss which control methods are needed to effectively reduce deer densities, while improving trophy quality.

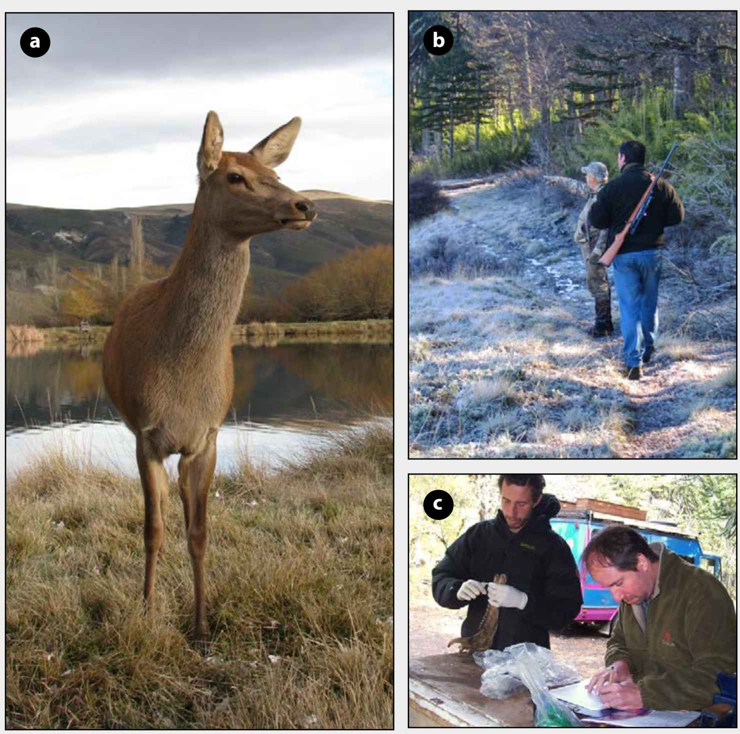

Figure 1. a. Red deer female; **b.** hunters walking through the temperate forest; **c.** technicians of Parque Nacional Lanín processing samples from deer hunting. (Photos: N. Pastore [**a**], N. Ferreira [**b-c**]).

BOX 2

Hunting control of wild boar in Parque Nacional El Palmar

Wild boar is one of the more widely distributed introduced mammals in Argentina, occurring in at least 46 protected areas (Ballari *et al.*, 2015a, Ballari *et al.*, 2019). This species causes soil disturbances, vegetation damage, diseases transmission, introduced seed dispersal, competition with native species, among other negative impacts (Barrios-García and Ballari, 2012; Cuevas *et al.*, 2012; Ballari *et al.*, 2015b). Additionally, through predation and habitat destruction, wild boar impact avian, reptile, amphibian, and small mammal populations (Ballari and Barrios-García, 2014). Lastly, wild boar affects economic human activities by damaging crops and transmitting diseases to livestock (Barrios-García and Ballari, 2012). Based on the wild boar's potential demographic growth and its wide range of negative impacts on biodiversity and ecosystem processes, there is an increasing need to design management strategies to minimize future environmental and socioeconomic impacts (Sanguinetti and Pastore, 2016).

In Argentina, the wild boar is categorized as a high priority for management by Valenzuela *et al.* (2014); however, no national initiatives are available to control their populations (Ballari *et al.*, 2016). Nevertheless, management of wild boar has been applied in some protected areas, such as the PNEP, where control efforts have been carried out for more than 10 years (Gürtler *et al.*, 2017). This protected area was created in 1965 with the aim of conserving the last remnants of yatay

Figure 2. a. Information signs to prevent tourists and visitors from entering the area where the control of introduced animals with firearms is carried out; **b.** elevated construction, called *apostadero* or deer stand, used to hunt axis deer and wild boar; **c.** park rangers, volunteers and hunters, working together to record data. (Photos: S.A. Ballari).

palm (*Butia yatay*) groves. It has an area of 8,500 ha and is located in Entre Ríos province in the Espinal ecorregion. Due to known impacts of several introduced mammals inhabiting the park (*e.g.*, wild boar on yatay palm seedlings; Pignataro, 2010), the PNEP administrators decided to carry out a control plan (Ballari *et al.*, 2015b) (Fig. 2). While introduced mammals have been sporadically hunted for control since 1983, the protected area managers began a formal and systematic Invasive Mammals Control Plan in 2006, including not only wild boar, but also axis deer and blackbuck, the latter with circumstantial presence (Gil, 2008). This program recruits local sport and subsistence hunters under a regulated framework that is controlled and directed by park rangers to contribute to the objectives of the protected area (Fig. 2a-c). In fact, this is the first management program in Argentina that allows authorized third parties to conduct controlled hunting on national park property, where there are no quotas nor trophy selection (Gürtler *et al.*, 2017).

Different hunting methods (*e.g.*, hunting with horse and dogs, hunting from a truck) have been used for wild boar with different success, but the method most used and most effective over time was hunting with firearm from a high elevated structure. These hunting fixed high points, called *apostaderos* in Spanish or deer stands in English (Fig. 2b), are located in areas with good visibility throughout the entire protected area and encompassing different habitats. Hunters use soaked corn as bait to attract the animals, which is replenished on a daily basis (Ballari *et al.*, 2015b).

The management plan in the PNEP has substantially reduced wild boar abundance during the first two years of the program, and then kept low abundances the following eight years. Furthermore, soil rooting area in the park declined (Gürtler *et al.*, 2017), and predation of yatay palm seedlings dropped to almost zero (Lunazzi, 2009; Ballari, 2014). The success of the plan may also be attributed to the joint involvement of park personnel and local recreational hunters (Fig. 2c), continued institutional support, and increased awareness of wild boar impacts, among others (Gürtler *et al.*, 2017). However, while this plan has proven to be successful for wild boar, when hunting efforts are reduced or stopped for a few months, wild boar population recovers rapidly (Ballari, S.A.; personal observation). This demonstrates that systematic control sustained over time, as well as regular monitoring, are critical for the success of the plan.

This long-term (and currently active) program is unique in Argentina because it has been effective in reducing wild boar populations, decreasing poaching, expanding the number of local stakeholders interested in the control program, and strengthening relationships between protected areas and the local communities (Gürtler *et al.*, 2017).

Changes in sport hunting within protected areas: opportunities and limitations

The sport hunting scheme implemented on public lands within protected areas needs to generate, in addition to the hunting opportunity, incentives for the people involved (*i.e.*, hunters, guides, managers, etc.). To improve trophies in the long-term it is necessary to promote the annual removal of animals of all age classes and both sexes (Flueck *et al.*, 1995). Furthermore, it is necessary to invest economic resources, improve the organizational governance capacity, and create effective educational programs for key stakeholders (Nugent *et al.*, 2011; Relva and Sanguinetti, 2016). This approach will facilitate agreements to promote management schemes and population monitoring to improve trophy quality as a product of management (Flueck *et al.*, 1995; Relva and Sanguinetti, 2016) that prioritizes native ecosystem conservation.

To implement effective management schemes inside and outside protected areas, it is essential to integrate the work between scientists and managers to achieve solid agreements to improve legislation and management related to protected areas and introduced species (Sanguinetti *et al.*, 2014). The current economic and organizational capacities in protected areas limit the achievement of a comprehensive and efficient management of introduced invasive mammals. Finally, it is also necessary to achieve a cooperative approach to pursue the multiple objectives (*e.g.*, create economic incentives, decrease animal populations) that are demanded by the different social actors (Flueck *et al.*, 1995; Nugent *et al.*, 2011; Sanguinetti, *et al.*, 2014; Relva and Sanguinetti, 2016).

Concluding remarks

Hunting represents a highly profitable activity worldwide. Indeed, hunting is the main driver of mammal introductions in Argentina, where new hunting reserves are being authorized and established every year. While most introduced mammals are confined in enclosed areas, it is well known that fences and regulations tend to be deficient and also, deliberate releases may occur. This fact raises the urgent need to improve policies and institutional frameworks related to introduced species hunting. Furthermore, it denotes that we still suffer gaps between social and ecological values, and conservation priorities and subsequent actions. This analysis reinforces the need to develop integrated research, regulations, and legislation that considers both the cultural and economic use of introduced species, as well as the ecological costs when they become invasive (Ballari *et al.*, 2016; Archibald *et al.*, 2020).

Many species introduced for hunting purposes cause direct and indirect negative impacts on native biodiversity and ecosystem processes. This issue is especially relevant when introduced species occur in protected areas. While there are successful management experiences (wild boar in PNEP, and red deer in PNL), we highlight the importance of reinforcing hunting regulations, and the development of fauna management protocols to successfully face new sources of escape, while achieving conservation objectives. Also, it is important to evaluate sport hunting management success, by monitoring population trends and environmental impacts, instead of only considering the quality and number of trophies. Lastly, management strategies, according to recent studies, need to be developed regionally with a socio-ecological vision and multi-sectorial participation of decision-makers, protected area managers and private landowners (Ballari *et al.*, 2016; Cuevas *et al.*, 2016, Sanguinetti and Pastore, 2016).

Acknowledgements

We thank the editors for inviting us to participate in this book. We also acknowledge the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), the Administración de Parques Nacionales (APN) of Argentina, and the external reviewers and editors, whose comments contributed to the improvement of the final product.

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5 | IMPACT OF INTRODUCED INVASIVE HERBIVORES IN PATAGONIAN FORESTS

IMPACTO DE LOS HERBÍVOROS INTRODUCIDOS INVASORES EN BOSQUES DE LA PATAGONIA

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Abstract. There are 13 invasive mammalian herbivore species in Argentina, which were introduced in the 15th and 19th centuries principally for livestock and hunting purposes. Currently, many of these invasive herbivores (*e.g.*, cattle, *Bos primigenius taurus*; red deer, *Cervus elaphus*; wild boar, *Sus scrofa*; European hare, *Lepus europaeus*) have greatly expanded their distributions across Argentina, causing negative impacts to native biodiversity and ecosystem processes. Selective browsing or grazing by herbivores in Patagonian forests has been shown to decrease plant growth, increase mortality, and alter flowering season, seed set, and plant tissue chemistry of many herb, shrub and tree species. At the community level, invasive herbivores often heavily browse on just a few species, favoring browse-resistant plants and thereby altering the species composition of native plant communities. Additionally, invasive herbivores can directly impact native herbivores through competition for resources and habitat modifications. Competition for food, for example, is likely to affect native herbivores like the Patagonian huemul (*Hippocamelus bisulcus*), guanaco (*Lama guanicoe*), and southern pudu (*Pudu puda*), given their diet overlap. Additionally, several studies have shown that invasive herbivores can alter entire food webs by increasing food availability for native predators or by disrupting plant-animal mutualisms that lead to trophic cascades. Lastly, invasive herbivores can also cause ecosystem level impacts by altering nutrient cycling, hydrology, and disturbance regimes. Notably, wild boar rooting and North American beaver (*Castor canadensis*) dam construction can cause long-lasting impacts to native ecosystem structure and function. While there is a relatively good understanding of introduced invasive herbivore impacts in Patagonian forests, there is still a need for more study of their impacts in other biomes and in relation to co-occurring invasive species. There is also a particular need, as with most introduced invasive species, to focus greater attention on how to manage this socio-ecological problem.

Resumen. Dentro de los mamíferos, los herbívoros son las especies que más frecuentemente se han introducido en el mundo, ya que son fuente de alimento y transporte. En Argentina, la ganadería y la caza deportiva fueron los principales motivos de introducción de herbívoros originarios de Europa y Asia. Muchos de ellos, como la vaca (*Bos primigenius taurus*), el ciervo colorado (*Cervus elaphus*), el

jabalí (*Sus scrofa*) y la liebre europea (*Lepus europaeus*) se han vuelto invasores, expandiendo ampliamente su distribución desde los sitios de introducción hasta áreas remotas y protegidas.

Numerosos estudios en la Patagonia argentina han demostrado el impacto negativo de los herbívoros invasores en las comunidades vegetales y animales nativas, así como en diversos procesos ecosistémicos. A través del ramoneo y pastoreo selectivo los herbívoros invasores disminuyen el crecimiento de las plantas y alteran la composición de las comunidades vegetales nativas. Por ejemplo, se ha reportado que la vaca disminuye el crecimiento del coihue (*Nothofagus dombeyi*) y el ciprés (*Austrocedrus chilensis*), inhibiendo la recuperación de los bosques luego de disturbios como el fuego. También se ha observado que la herbivoría afecta el éxito reproductivo de numerosas especies vegetales como el romerillo (*Baccharis obovata*), el maitencillo (*Maytenus chubutensis*), la parrilla (*Ribes magellanicum*), el maqui (*Aristotelia chilensis*) y los *Nothofagus*, reduciendo el número de flores y semillas que producen. Además, se ha reportado que la herbivoría puede alterar los rasgos foliares como el tamaño de hoja, el contenido de agua y la dureza, así como también la calidad de los tejidos vegetales. A largo plazo, la herbivoría selectiva puede también alterar la composición del sotobosque favoreciendo las especies resistentes a la herbivoría, como los *Berberis* spp., y suprimiendo a las especies palatables. Por otra parte, los herbívoros introducidos pueden afectar a las comunidades animales nativas a través de la competencia por los recursos y la modificación del hábitat. Específicamente se ha propuesto que existe competencia por alimentos entre el ganado y el huemul (*Hippocamelus bisulcus*), el ganado y el guanaco (*Lama guanicoe*), la oveja (*Ovis orientalis aries*) y el guanaco, el ciervo colorado y el pudú (*Pudu puda*) la liebre europea y la mara (*Dolichotis patagonum*), y la liebre europea y el chinchillón (*Lagidium viscacia*), debido a una superposición de ítems dietarios que estas especies utilizan. También los herbívoros introducidos pueden afectar a las comunidades animales aumentando la disponibilidad de recursos para los depredadores nativos. Por ejemplo, se ha reportado que la liebre europea y el conejo (*Oryctolagus cuniculus*) son los principales ítems dietarios del puma (*Puma concolor*), zorro gris (*Lycalopex gymnocercus*), zorro colorado (*L. culpaeus*), y aves rapaces de la Patagonia. Los impactos de los herbívoros invasores pueden también perturbar mutualismos planta-animal provocando efectos en cascadas. Específicamente, se ha reportado que el ramoneo por vaca y ciervo colorado puede reducir la abundancia de maqui (*A. chilensis*), generando efectos indirectos en la interacción monito del monte (*Dromiciops gliroides*) – quintral (*Tristerix corymbosus*) – picaflor rubí (*Sephanoides sephaniodes*). Por último, los herbívoros invasores también pueden causar impactos a nivel de ecosistema alterando el ciclo de nutrientes, la hidrología y los regímenes de disturbios. En particular, el hozado del jabalí y la construcción de represas por el castor (*Castor canadensis*) pueden causar grandes impactos en la estructura y función del ecosistema nativo. Por ejemplo, la actividad de los castores inunda grandes superficies y crea ecosistemas similares a praderas con regeneración limitada de *Nothofagus*, facilitando la invasión de plantas herbáceas introducidas. Además, la construcción de represas aumenta la concentración de nitrógeno y fósforo, y la retención de material orgánico de las cuencas hidrográficas. Estos cambios en el flujo y la calidad del agua también alteran la composición de los macroinvertebrados acuáticos y la dinámica de la red alimentaria.

Si bien tenemos una buena comprensión del impacto de los herbívoros invasores en algunos ecosistemas nativos de Argentina, aún tenemos muy poca información sobre el impacto de los herbívoros invasores en otros ecosistemas fuera de los bosques patagónicos. Además, falta información sobre el impacto de las especies invasoras cuando co-ocurren en un mismo ambiente, y finalmente acerca de cómo el manejo de estas puede revertir sus efectos.

Introduction

Herbivores are among the world's most frequently introduced mammals, as they provide a source of food, animal husbandry, and transportation (Long, 2003). In Argentina, the two main causes of mammalian herbivore introductions were livestock and hunting (Novillo and Ojeda, 2008; Merino *et al.*, 2009; Ballari *et al.*, 2016; Ballari *et al.*, this volume). In the 15th century, Spanish explorers introduced the large herbivorous livestock like cattle (*Bos primigenius taurus*), sheep (*Ovis orientalis aries*), and goats (*Capra aegagrus hircus*) (Primo, 1992; Ballari *et al.*, 2016). More recent introductions during the late 19th and 20th centuries were mostly driven by hunting practices and include the European hare (*Lepus europaeus*), red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) (Ballari *et al.*, 2016). Argentina currently hosts 23 introduced invasive mammal species, of which 56% are herbivores (Ballari *et al.*, 2016; SAyDS and SAREM, 2019; Valenzuela *et al.*, this volume) (Table 1). All of these invasive herbivores are native to Europe and Asia and have successfully established wild populations that have expanded at different rates (Novillo and Ojeda, 2008; Ballari *et al.*, 2016).

Table 1. List of introduced invasive mammalian herbivores found in Argentina's forested biomes.

Order	Scientific name	Common name
Cetartiodactyla	*Antilope cervicapra*	blackbuck, Indian antelope
	Axis axis	chital, axis deer, spotted deer
	Bos primigenius taurus	cattle
	Bubalus arnee bubalis	buffalo
	Capra aegagrus hircus	goat
	Cervus elaphus	red deer
	Dama dama	fallow deer
	Sus scrofa	wild boar, feral pig, swine
Lagomorpha	*Lepus europaeus*	European hare
	Oryctolagus cuniculus	European rabbit
Perissodactyla	*Equus africanus asinus*	donkey
	Equus ferus caballus	horse
Rodentia	*Castor canadensis*	North American beaver

Many of Argentina's introduced invasive herbivore species, including cattle, red deer, wild boar (*Sus scrofa*), and European hare, have naturally expanded their distributions from their introduction sites, thereby establishing wild populations in large areas (Novillo and Ojeda, 2008; Ballari *et al.*, 2016; Scorolli, 2018). As a consequence, the supposedly "remote" biomes of the Sub-Antarctic and Patagonian forests, which are otherwise classified as "wilderness areas" (Mittermeier *et al.*, 2003), are actually one of the most invaded ecoregions of the Southern Cone (Ballari *et al.*, 2016). Additionally, commercially valuable species have expanded throughout Argentina thanks not only to their own dispersal abilities, but also help from humans (Valenzuela *et al.*, 2014). These types of expansion have occurred by the transportation of animals for production and work, such as sheep, horses, and goats, or through escapes from game reserves or rearing facilities with poor biosecurity measures, such as the red deer. In contrast, some game species, like the fallow deer, have expanded their territory much less than others (Novillo and Ojeda, 2008; Barrios-García, this volume), while the chital (*Axis axis*) is still mostly restricted to game reserves in several provinces (Guichón *et al.*, 2016).

While among Argentina's invasive herbivore assemblage, only red deer and goats are listed among the world's 100 most harmful introduced invasive species (Lowe, 2000), many of these remaining species still are known to cause negative impacts on native biodiversity and ecosystem processes (Novillo and Ojeda, 2008; Merino *et al.*, 2009). For example, numerous authors have studied the direct and indirect impacts of invasive herbivores on plant and animal communities, as well as on ecosystem properties in Patagonian forests of Argentina, highlighting their role in altering plant species composition, decreasing forest regeneration, facilitating dispersal of introduced plants, competing with native herbivores for resources, and altering soil properties (Vázquez, 2002; Relva *et al.*, 2010; Vila and Borrelli, 2011; Barrios-García *et al.*, 2012). In the following sections of this chapter, we will discuss these impacts in more depth.

Impacts on plant communities

Selective browsing or grazing by large introduced herbivores has several direct individual-level effects by altering plant survival, growth, and fitness (Crawley, 1986; Augustine and McNaughton, 1998; Côté *et al.*, 2004; Graff *et al.*, 2007). Ultimately, these impacts can induce changes in plant traits (*e.g.*, nutritional quality and defenses) that might confer resistance or tolerance to subsequent herbivory (*e.g.*, Shimazaki and Miyashita, 2002; Rooke and Bergström, 2007; Bailey and Schweitzer, 2010), and at the same time alters plant communities by changing the richness, abundance, and composition of the native flora. Below, we will summarize the empirical data available from Argentina's Patagonian forests.

Large introduced mammalian herbivores have been reported to decrease tree seedling survival and growth, especially when natural or anthropogenic disturbances also increase the access of livestock to the forest floor. For example, following natural bamboo (*Chusquea culeou*) die-back in northern Patagonia, cattle were shown to cause more than double the seedling mortality for *Nothofagus dombeyi* and decrease seedling height more than 130% (Raffaele *et al.*, 2007). Similarly, cattle grazing in post-fire, subalpine *N. pumilio* forests decreased seedling survival ca. 30%, probably due to the combined effects of browsing and trampling and their indirect influence through the removal of potential nurse plants (Tercero-Bucardo *et al.*, 2007). In contrast, in post-fire lowland forests, seedling survival of *N. dombeyi* and *Austrocedrus chilensis* in unfenced plots tended to be higher, possibly due to lower livestock pressure and/or reduced competition from highly palatable shrub species (Tercero-Bucardo *et al.*, 2007). However, although early survival might be higher in the latter habitat, mean maximum height of all woody species and climbers, including dominant tree species, was > 70% higher in the absence of cattle than in unfenced areas (Blackhall *et al.*, 2008). For this reason, it has been proposed that large introduced herbivores often inhibit forest recovery, especially following disturbances, and favor community transitions from tall forests to shrublands dominated by resprouting woody species (Raffaele *et al.*, 2011). Similar trends had been described for the role of introduced European rabbits (*Oryctolagus cuniculus*) (Vázquez, 2002) and North American beavers (*Castor canadensis*), where direct herbivory and dam construction shift *Nothofagus* forest to grasslands (Lizarralde *et al.*, 1996).

Resilient plant species that survive and sustain viable populations might still suffer from introduced mammalian herbivory, if vigor, productivity or reproduction is impaired. Few empirical studies have explored these consequences in temperate Argentine ecosystems and have reported evidence of both the benefits and costs of browsing. For example, in *Nothofagus* forests in northwestern Patagonia, while some understory species (*e.g.*, *Baccharis obovata*, *Rosa rubiginosa* and *Maytenus chubutensis*) did not produce flowers in the presence of cattle, for others reproductive tissue output showed the opposite tendencies, depending on the shrub's palatability (de Paz and Raffaele, 2013). Specifically, whereas palatable wild currant (*Ribes magellanicum*) shrubs showed 25× fewer flowers, 10× fewer fruits, and null seed viability under livestock pressure, the less palatable box-leaved barberry (*Berberis microphylla*) increased flowers by 4×, fruits by 2×, and seed production by 9× under the same conditions (de Paz and Raffaele, 2013). Also, it is key to note that all forest strata can be susceptible to large herbivores, as ungulates have been shown to reduce 1) the number of male flowers of canopy *Nothofagus* trees in silvopastoral systems in Tierra de Fuego (Martínez Pastur *et al.*, 2008; Soler *et al.*, 2012); 2) the density of understory fruiting plants by 3× in *Nothofagus* forests in Neuquén and Río Negro (Rodríguez-Cabal *et al.*, 2013); and 3) the fitness of a common herbaceous plant, *Alstroemeria aurea*, by directly reducing its population density and thus, hindering pollen deposition on stigmas in *N. pumilio* forests in Río Negro province (Vázquez and Simberloff, 2004).

Changes in plant traits following damage by introduced herbivores have the potential to modify plant quality to subsequent herbivores (*e.g.*, Shimazaki and Miyashita, 2002; Rooke and Bergström, 2007; Bailey and Schweitzer, 2010). Such less obvious effects are particularly relevant in the case of novel plant-animal interactions. Recently, several studies in South America's temperate forests have reported changes in leaf traits, growth rate, phenology, and induced chemical defenses of remaining vegetative and reproductive tissues under introduced herbivore pressure. For example, in terms of leaf traits, two studies have shown that some browse-susceptible plant species decreased leaf size, toughness, and water content (Blackhall *et al.*, 2012), as well as leaf and shoot production (Sasal, 2009) under livestock herbivory pressure. Furthermore, phenological changes in reproductive span were reported for several understory species, with some palatable species shortening their blooming periods (*e.g.*, *R. magellanicum*, *Schinus patagonicus*), while browse-resistant species have shown to lengthen their flowering periods (*e.g.*, *B. microphylla*), favoring reproductive success (de Paz and Raffaele, 2013). Induced chemical defenses post-browsing, which aim at reducing subsequent herbivore damage (Karban and Baldwin, 1997), have not been assessed for temperate forest species, but indirect evidence suggests changes in secondary chemistry due to livestock grazing. Studies of tissue flammability in *N. antartica* shrublands described patterns of decreased tissue ignitability at the community level (Blackhall *et al.*, 2017) and species-specific changes in foliar flammability (Blackhall *et al.*, 2012) due to cattle browsing, suggesting changes in plant allelochemical content as some secondary metabolites, such as terpenes, often correlate with tissue flammability (*e.g.*, Owens *et al.*, 1998; Ormeño *et al.*, 2009; Page *et al.*, 2012; Pausas *et al.*, 2016). Moreover, in the neighboring Patagonian steppe, Cavagnaro *et al.* (2003) showed that *Senecio filaginoides*, the least preferred shrub species grazed by sheep, employs both high concentrations of constitutive allelochemicals and induced resistance following damage, especially by increasing oil and hydrocarbon fractions.

Alternatively, browsed plants could compensate the removed tissue by enhancing growth and photosynthetic rates, activation of dormant meristems, changing biomass allocation, or increasing nutrient uptake. All of these responses increase tolerance capabilities by minimizing the negative effects of damage on plant fitness (Tiffin, 2000; Fornoni, 2011), but evidence of these strategies in native species in the face of biological invasions by herbivores in Argentina's temperate forests is still scarce. Increased growth rates following cattle browsing have been reported for *N. antarctica* in northwestern Chubut, with such a response being stronger in larger rather than smaller saplings (Echevarría *et al.*, 2014). In addition, tolerance might depend on browsing pressure, with *N. antarctica* saplings being able to rise compensatory regrowth only under low stocking rates, while heavy browsing pressure suppressed tree regeneration and led to shrubby architecture and lower growth rates (Echevarría *et al.*, 2014). Lastly, only one study to date has measured resource allocation post-damage by introduced ungulates. Six years after cattle exclusion in a post-fire subalpine *N. pumilio* forest, the browse-resistant shrub *B. microphylla* showed similar vegetative, reproductive and root biomass as browsed plants and even increased in size, suggesting compensatory growth. In contrast, the more palatable *R. magellanicum* was unable to compensate, showing decreased overall size and biomass of all vegetative and reproductive tissues, and low shoot : root ratios compared to undamaged individuals in the exclosures (de Paz and Raffaele, 2015).

Through differences in seedling establishment and survival, plus selective browsing of understory species, introduced herbivore mammals also substantially modified vegetation cover and species composition of native plant communities. For instance, in northwestern Patagonia, long-term livestock presence reduces plant species richness and cover of subcanopy trees, shrubs and bamboo up to 80%, while simultaneously increasing the relative cover of ground-layer herbs (Veblen *et al.*, 1989; Raffaele and Veblen, 2001; Raffaele *et al.*, 2007; Blackhall *et al.*, 2015; Piazza *et al.*, 2016; but see Blackhall *et al.*, 2008). Besides cattle, browsing by introduced deer species, such as red and fallow deer, also strongly inhibit growth of native tree saplings, decrease cover of native understory plants, and change understory species composition (Relva *et al.*, 2010; Barrios-García *et al.*, 2012; Rodríguez-Cabal *et al.*, 2013). Given their generalist diet, these large ungulates can exert damage on ca. 30 woody species and several forbs and grasses (Vila and Borelli, 2011; Barrios-García *et al.*, 2012; Soler *et al.*, 2012), but often heavily browse on just a few selected species (Relva *et al.*, 2010; Vila and Borelli, 2011; Barrios-García *et al.*, 2012), favoring browse-resistant over browse-sensitive species (Relva *et al.*, 2010; Blackhall *et al.*, 2015), and decreasing plant evenness and species turnover along environmental gradients (Piazza *et al.*, 2016). For example, it has been reported that *Berberis* spp. increases its abundance in heavily browsed sites (Relva and Veblen, 1998). Moreover, although introduced herbivores could aid to control introduced plant species (*e.g.*, Zamora Nasca *et al.*, 2018), preferences towards more palatable native species often actually favor the invasion of introduced tree species, such as pines (Nuñez *et al.*, 2008; Relva *et al.*, 2010), as has been seen in other ecosystems worldwide (Oduor *et al.*, 2010). Such preferences are likely driven by the tissue quality of native plants (*e.g.*, Forsyth *et al.*, 2002), but such assessments are still missing for Argentine ecosystems. Furthermore, not only large but also medium-sized introduced herbivores like the European hare have been shown to reduce woody native plant cover, while increasing the area occupied by introduced forbs (Raffaele *et al.*, 2011).

Besides cattle and deer, Barrios-García and Simberloff (2013) reported that wild boar rooting increases by as much as 2× the establishment and biomass of non-native seedlings, compared to unimpacted sites. Additionally, the same authors showed that soil disturbance by wild boar, rather than endozoochorous dispersal, facilitates plant invasions. Another well-known biological invasion by an introduced herbivore is the huge impact on native plant communities attributed to beavers. In the 1940s, 20 beavers were introduced to the Argentine portion of Tierra del Fuego in an attempt to help start a fur industry. Beavers have colonized nearly all streams in the Fuegian Archipelago and are found in many watersheds on the mainland south of Puerto Natales, Chile, reaching as many as 100,000 individuals (Anderson *et al.*, 2009). Introduced beavers can devastate *Nothofagus* forests by cutting and killing the dominant tree species (*N. pumilio*, *N. betuloides*), but can actually favor regeneration of *N. antarctica* and ultimately create resilient grasslands dominated by introduced herbaceous species (Martínez Pastur *et al.*, 2006; Wallem *et al.*, 2010; Henn *et al.*, 2014). However, the greatest impact on riparian communities comes from the flooding associated with dam construction (Lizarralde, 1993). Beaver dams can reach up to 100 meters in length and cause floods, which has serious impacts on the native vegetation. This introduced herbivore is also an invasive ecosystem engineer and has directly modified around 30,000 ha on the Argentine side of Tierra del Fuego's main island (Isla Grande), constituting the largest ecosystem alteration in this biome in the Holocene (Henn *et al.*, 2016; see Anderson and Roulier, this volume).

Impacts on animal communities

Besides their effects on plants, introduced herbivores can also directly impact native herbivores through competition for resources and habitat modifications (Vázquez, 2002; Valenzuela *et al.*, 2014). Large native mammalian herbivores in the Andean Patagonia region include the guanaco (*Lama guanicoe*) and two species of endangered deer: the Patagonian huemul (*Hippocamelus bisulcus*) and the southern pudu (*Pudu puda*) (Vázquez, 2002). Competition for food has been presumed to occur between cattle and huemul (Vila *et al.*, 2009; Briceño *et al.*; 2013, Díaz *et al.*, 2013), cattle and guanaco (Fernández Pepi *et al.*, 2015), sheep and guanaco (Soler *et al.*, 2012), as well as between red deer and pudu (Silva-Rodríguez *et al.*, 2016). However, the suggestion that introduced herbivores likely affect native herbivores through exploitation competition stemmed from studies that described patterns of resource use and partitioning among sympatric species; establishing the potential for competition, but rarely demonstrating its action or effect (Dolman and Wäber, 2008). Similarly, Bonino *et al.* (1997) found a 50% trophic overlap between the native mara (*Dolichotis patagonum*) and the introduced European hare; and Galende *et al.* (1998) and Galende and Raffaele (2013) showed diet and spatial overlap between the native southern mountain viscacha (*Lagidium viscacia*) and the introduced European hare.

Introduced mammalian herbivores may also affect animal communities by increasing food availability for predators. This process is known as "apparent competition" (Holt, 1977), and occurs when prey species, in this case introduced herbivores, elevates predator abundance above levels that would have been maintained by native prey, which then increases predation pressure on native prey assemblages. In the temperate forests of Patagonia, puma (*Puma concolor*) and foxes (*Lycalopex gymnocercus* and *L. culpaeus*) prey upon introduced herbivores, and sometimes these non-native species contribute most of their diets (Novaro *et al.*, 2000). Similarly, avian predators consume introduced herbivores. A study by Barbar *et al.* (2016) found that the composition of the Patagonian raptor community is altered as a consequence of the introduction of European hare and rabbit. These authors found that the relative abundances of large and medium-sized raptor species have increased, probably because these introduced lagomorphs represent a new food resource, thereby providing higher biomass than native prey species and favoring large and medium-sized raptors compared to other smaller species of the same trophic level.

In addition to the impacts on vertebrates, introduced mammalian herbivores affect native invertebrates in several ways, directly by trampling on its nests, or indirectly through their effects on the quantity and quality of food sources, or by changing the habitat. For example, cattle browsing in post-fire *Nothofagus* forests increased beetle richness 18% by altering environmental heterogeneity, but reduced pollinator visits by increasing flower production through a "resource dilution effect" (Sasal *et al.*, 2015, 2017). In contrast, browsing on *Aristotelia chilensis*, one of the most common understory plants in Patagonian temperate forests, by cattle and red deer reduced foliar arthropod species and individuals compared to un-browsed plants in un-invaded sites (Rodríguez-Cabal *et al.*, 2019).

Cascading impacts—disruption of plant-animal mutualisms

Mutualisms are essential interactions not only for the persistence of these beneficial relationships' partners, but also for the maintenance of biodiversity and the integrity of ecosystems (Janzen, 1980; Feinsinger, 1987; Bond, 1994; Levey and Benkman, 1999; Traveset, 1999; Herrera, 2002). Patagonian temperate forests present a high degree of endemism (Heywood and Watson, 1995), and a large portion of its flora depends on mutualistic partners (Aizen and Ezcurra, 1998). Introduced mammalian herbivores may indirectly impact native plant communities by disrupting such plant-animal mutualisms (Mack and

D'Antonio, 1998; Rodríguez-Cabal *et al.*, 2013), ultimately leading to consequences at multiple levels via trophic cascades.

In the northern portion of this temperate forest, we find a unique interaction, including the world's southern-most hummingbird (*Sephanoides sephaniodes*), a mistletoe (*Tristerix corymbosus*), the most common host of mistletoe and dominant understory shrub (*A. chilensis*), three seed dispersers—a marsupial (known as monito del monte, *Dromiciops gliroides*) and two birds (the white-crested elaenia, *Elaenia albiceps*, and the austral thrush, *Turdus falcklandii*). The nectar produced by the mistletoe is the primary food resource for the hummingbird during the winter (Aizen, 2003). During the austral spring, the hummingbird pollinates nearly 20% of the endemic woody genera in Patagonian forests (Aizen and Ezcurra, 1998). The marsupial disperses seeds of at least 25 fleshy-fruited species and is the only known disperser of the mistletoe, allowing its seed to establish by fecal deposition on *A. chilensis* branches (Amico and Aizen, 2000). The elaenia and the thrush are generalist seed dispersers and carry the seeds of more than 80 plant species in these forests (Amico and Aizen, 2005). When *A. chilensis*, which is preferred forage for cattle, red and fallow deer (Veblen *et al.*, 1992; Jaksic *et al.*, 2002), is browsed, the close interaction network between these native species can be disrupted. Indeed, Rodríguez-Cabal *et al.* (2013) demonstrated

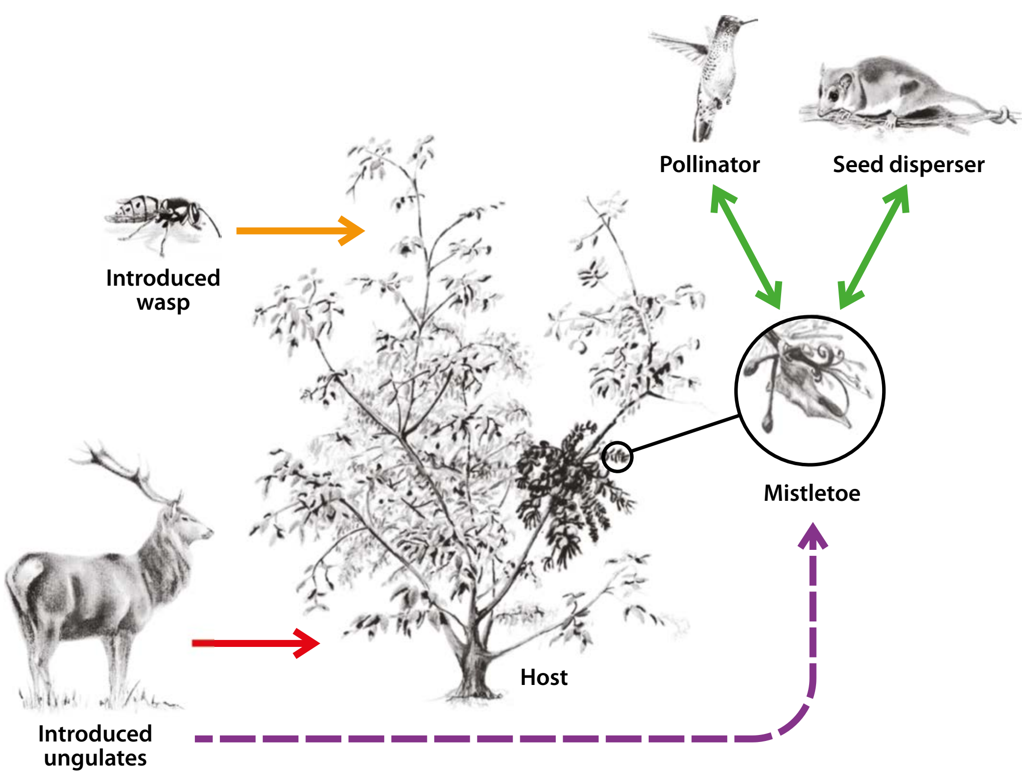

Figure 1. A keystone plant-animal mutualism in the northern portion of Patagonia's temperate forest biome. The red arrow indicates the direct negative effect of introduced ungulates on the most common host of the mistletoe, and the purple arrow indicates the indirect effect. The green arrows indicate native mutualistic interactions. Figure modified from Fig. 1 in Rodriguez-Cabal *et al.* (2013). (Drawings: Ezequiel Rodriguez-Cabal).

how the reduction of *A. chilensis* abundance by introduced ungulates caused indirect effects that lead to the disassembly of the entire web (Fig. 1). These authors showed a 16× reduction in the abundance of *A. chilensis* in sites invaded by introduced ungulates, compared to uninvaded sites (*i.e.*, intact sites). In turn, invasive herbivore browsing on *A. chilensis* indirectly reduced the abundance of the species in the keystone mutualistic interaction. Specifically, the abundance of mistletoe was 83× greater in intact compared to invaded sites, triggering the disassembly of this key mutualistic web. Another example of the negative effects of introduced ungulates on mutualisms comes from the study of Vázquez and Simberloff (2004), who showed that invasive ungulates indirectly alter the pollination and reproduction success of the herb *A. aurea* by decreasing population density via trampling. Also, pollination quantity (number of conspecific pollen grains) and quality (as determined by contamination with heterospecific pollen grains) were found to dramatically decrease at invaded sites, which in turn decreases reproductive performance of *A. aurea* at these invaded sites.

Another interesting effect of non-native herbivores was reported by Nuñez *et al.* (2013), who described facilitation among introduced species (pines, an ectomycorrhiza, and mammals) in northern Patagonian forests. Members of the family Pinaceae require an obligatory mutualism, an introduced ectomycorrhizal fungi, to thrive; however, both of them may disperse independently using different vectors. These authors found that introduced mammals, such as red and fallow deer and wild boar, disperse spores of ectomycorrhizal fungi in their feces via fungi consumption. Thus, introduced mammals may indirectly facilitate pine invasions via fungi dispersal in sites where they co-occur.

Ecosystem level impacts

While most studies of introduced species focus on the impact on native population and community properties, comparatively less is known about the role of biological invasions by mammalian herbivores on ecosystem-level properties. We know that invasive herbivores can change ecosystem structure and processes, such as productivity, nutrient cycling, hydrology, and disturbance regimes, thus altering fundamental rules of existence of all species living in the ecosystem (Vitousek, 1990; Ehrenfeld, 2010). In Argentina, very few studies have determined the consequences of invasive herbivores on native ecosystems and have mainly focused on the impacts of the beaver as an invasive ecosystem engineer. However, some effects by other introduced herbivores have been reported.

As described above, selective browsing by introduced herbivores can alter plant community composition and litter quality; these changes may, in turn, alter the rates of organic matter decomposition and/or nutrient cycles. For example, cattle grazing in grasslands in the wet Pampas biome (Buenos Aires province) reduces standing biomass by 65% relative to an exclosure, and total above-ground nutrient stocks decreased by half or less, compared to those in the ungrazed exclosure (Chaneton *et al.*, 1996). The same study showed that grazing increases N and P concentrations, and nutrient uptake by roots, enhancing mineralization rates. Similarly, rooting by introduced wild boar in the Monte desert biome (Mendoza province) results in decreased soil bulk density and soil respiration rates, but higher C:N (Cuevas *et al.*, 2012). In forested ecosystems, only two studies have looked at the impact of introduced deer and wild boar on soil properties after 6–7 years of exclusion and found mostly non-significant effects on soil N and C stocks and cycling, suggesting that forested ecosystems are either more resilient to disturbance or that longer-term studies are needed (Relva *et al.*, 2014; Barrios-García *et al.*, 2014).

The beaver again provides the most striking example of how an introduced species can alter ecosystems (Lizarralde *et al.*, 1996; Anderson *et al.*, 2009). As stated above, in the 1940s, 20 beavers were introduced in Tierra del Fuego, and since then the population has spread throughout the archipelago and onto the mainland (Valenzuela *et al.*, 2014). Beavers are semi-aquatic rodents that build dams with logs and branches to create a refuge from predators and a "garden" in the forest with patches containing more palatable forage. This activity modifies both riparian and stream ecosystems, creating meadow-like ecosystems with limited *Nothofagus* trees regeneration and facilitating the invasion of introduced herbaceous plants (Anderson *et al.*, 2006; Martínez Pastur *et al.*, 2006; Wallem *et al.*, 2010). Furthermore, dam construction increases the flow of terrestrial organic matter subsidies to in-stream systems (Anderson *et al.*, 2009). Specifically, dams increase nitrogen and phosphorus concentration (Lizarralde *et al.*, 1996), and enhance the retention of organic material and thereby carbon-standing stock by approximately 72% in watersheds (Anderson *et al.*, 2014). These changes in water flow and quality also alter the structure and function of the aquatic macroinvertebrate assemblage and food web dynamics (Anderson and Rosemond, 2007, 2010).

Conclusion

In this chapter, we have synthesized how invasive mammalian herbivores directly and indirectly alter biodiversity from the individual level to the ecosystem scale in the temperate forests of Argentine Patagonia. Furthermore, we have shown that invasive herbivores in Patagonian forests can have cascading effects on different trophic levels. While we now have some understanding of the distribution of introduced herbivores in Argentina and their consequences on some native species and ecosystems, there is still much to be studied. Particularly, we have very little information on ecosystem-level impacts in biomes outside of Patagonian forests. There is also a relative dearth of information on how invasive herbivores interact with other co-occurring invasive species or drivers of global change. Finally, as noted by Anderson and Valenzuela (2014), there is still a tremendous need to concentrate on applied research concerning how management can address or reverse these effects.

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6 | MANAGEMENT OF FERAL HORSES AS INVASIVE MAMMALS: BIODIVERSITY CONSERVATION VERSUS CULTURE?

MANEJO DE CABALLOS CIMARRONES COMO MAMÍFEROS INVASORES: ¿CONSERVACIÓN DE BIODIVERSIDAD VERSUS CULTURA?

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Abstract. Feral horses (*Equus ferus caballus*) are large, herbivorous mammals considered invasive in many countries. Their populations are managed to reduce impacts on biodiversity, and conflicts often arise between government agencies and horse defenders. In Argentina, feral horse management has been inconsistent. In Parque Provincial Ernesto Tornquist (PPET), a grassland ecosystem reserve in the Pampas region, the feral horse population was reduced by 50% in 2006–2007. The management goal was to eradicate the species. In 2011, a conflict arose between the park's authorities, university researchers and a group of horse protectionists. This chapter describes the process surrounding this conflict, analyzes the arguments of the opposing sides, and compares the experience with invasive species conflicts in other countries. A *Facebook* group, which later transformed into a non-governmental organization with the goal of protecting the feral horses of PPET, attacked researchers and government authorities studying and managing this invasive population. The conflict persisted for two years and caused management efforts to be suspended. Researchers provided evidence of the feral horse's Eurasian origin, taxonomic status, and demographic rates that would lead to rapid recovery after control efforts ended. Impact on biodiversity was quantitatively studied and significant changes were reported. Argentine legislation clearly states that invasive mammals should be managed. Horse protectionists invoked the following aspects justifying their opposition: the horse's cultural and historical role in Argentina, aesthetic value, genetic uniqueness, and the horse as a reintroduced "native" species (based on paleo-records). There are important differences with the management of feral horses in other countries. Argentine governmental agencies were passive and did not have a management plan or any court-based legal process. Important challenges that were identified include: having an official science-based management plan, providing more substantiated evidence, attaining active government participation, and including human dimensions of this biological invasion from a socio-ecological perspective.

Resumen. El caballo (*Equus ferus caballus*) es un mamífero herbívoro de gran tamaño miembro de la familia Equidae y del orden Perissodactyla, originario de Eurasia, fue domesticado aproximadamente hace 5.000 años. Cuando los caballos domésticos escapan del control del ser humano o son liberados se denominan cimarrones. Fueron introducidos en Argentina en el siglo XVI por los colonizadores españoles. Rápidamente se volvieron cimarrones y se dispersaron ampliamente en varias regiones del

país, como la Pampa, Noreste y Patagonia. En el siglo XIX prácticamente se extinguieron en estado silvestre por la aparición de las estancias y el uso del alambrado para dividir la tierra. Actualmente existen varias poblaciones de caballos cimarrones en áreas poco pobladas de las regiones de Cuyo y Patagonia. También habitan en áreas protegidas como los Parques Nacionales Los Glaciares y Bosques Petrificados de Jaramillo en la provincia de Santa Cruz. La mayor población conocida, y la más estudiada, se encuentra en el Parque Provincial Ernesto Tornquist (PPET) en el sudoeste de la provincia de Buenos Aires.

El caballo cimarrón es considerado una especie introducida invasora en varios países. Dado su potencial impacto sobre la biodiversidad a altas densidades poblacionales son considerados un serio problema de conservación y su manejo resulta una prioridad. Usualmente, el manejo implica la reducción del tamaño de las poblaciones para minimizar el impacto causado. Es frecuente el uso de métodos letales y de captura viva con posterior adopción de los animales. En varios países, como EE.UU., Australia y Nueva Zelanda, el manejo de caballos cimarrones ha sido muy conflictivo y controversial. En la Argentina, el manejo ha sido esporádico y no organizado. Solo se ha manejado la población de caballos del PPET. Esta área es considerada de gran valor para la biodiversidad por conservar una muestra del ecosistema de pastizal serrano y numerosas especies endémicas. Este capítulo describe el conflicto que generó dicho manejo y analiza los argumentos propuestos por los grupos involucrados. Además, compara el conflicto con situaciones similares ocurridas en otros países y propone algunos desafíos pendientes para el futuro manejo de los caballos cimarrones en Argentina.

Los caballos fueron introducidos en el PPET en 1942. El grupo original era de raza Criolla Argentina, derivada de caballos andaluces-bereberes. Estos caballos rápidamente se asilvestraron, ocupando una amplia zona de la reserva. Su población creció paulatinamente hasta aproximarse a la capacidad de carga del ecosistema, alcanzando una densidad muy alta (35 caballos/km^2 en 2002). En ese período, los caballos cimarrones estuvieron limitados por alimento. La mortandad por inanición fue alta y el impacto sobre la biodiversidad significativo. Durante 2006 y 2007, las autoridades del área protegida manejaron la población de caballos cimarrones reduciendo un 50% su tamaño. Se capturaron mediante corrales 220 animales, la mayoría fueron relocalizados y 80 fueron eliminados por decisión del cuerpo de Veterinarios Equinos del Ejército. Este manejo fue implementado sin asesoramiento técnico y sin conocimiento del público. En 2011, un grupo de defensores de los caballos inició una serie de protestas contra las autoridades a cargo del PPET y los científicos que estudiaron a los caballos y asesoraron al gobierno. El conflicto, de tono muy agresivo, duró dos años. El escenario principal fueron las redes sociales, pero también tuvo lugar en los medios locales y regionales. Se formó un grupo de *Facebook* con más de 5.000 miembros, que luego fundó una organización no gubernamental, la Asociación Civil Cimarrón Equino (ACCE). Su misión es proteger a todas las poblaciones de caballos y burros cimarrones del país. Los investigadores de la Universidad Nacional del Sur (UNS), institución local, participaron del conflicto brindando evidencia de los siguientes argumentos: los caballos cimarrones son una especie introducida invasora, causan impacto sobre la biodiversidad, su demografía sugiere que crecen rápidamente y se recuperan fácilmente del control poblacional. Los defensores de los caballos cimarrones se opusieron al manejo. Presentaron argumentos asignando a los caballos cimarrones los siguientes valores: importancia cultural e histórica, estética, composición genética única, estatus de especie «nativa» reintroducida (en términos paleohistóricos), y parte del ecosistema. Las autoridades del PPET decidieron suspender el manejo en 2012, finalizando así el conflicto, pero no resolviendo el problema socio-ambiental de fondo.

Existen interesantes paralelismos entre el conflicto en Argentina y los ocurridos en otros países. Los actores involucrados son similares y los argumentos se repiten. Algunos rasgos particulares de este conflicto son: ausencia de un plan de manejo basado en evidencia científica, escasa participación del gobierno en las discusiones e inexistencia de procesos legales. En el año 2013 los investigadores de la UNS presentaron oficialmente una propuesta de Estrategia de Manejo de los caballos cimarrones en el PPET. Si bien aún no ha sido implementada, recientes conversaciones con las presentes autoridades y también con el Presidente de ACCE auguran un futuro promisorio. La dimensión humana del conflicto es un aspecto crucial a tener en cuenta para arribar a una posible solución en el manejo de caballos cimarrones. Algunos autores han propuesto recientemente que los problemas de conservación, incluyendo el manejo de especies invasoras, sean abordados desde una perspectiva socio-ecológica. Esto implica el estudio de los valores y las actitudes de los distintos actores de la sociedad en pos de soluciones más efectivas y éticas. Existen importantes desafíos a futuro para un mejor manejo de las poblaciones de caballos cimarrones en la Argentina: difundir ampliamente las evidencias científicas, lograr una participación activa y transparente de las autoridades, contar con planes de manejo de caballos cimarrones basados en ciencia y con amplia participación del público, y con inclusión de profesionales de las ciencias sociales. Además, se debería integrar esta especie en la Estrategia Nacional de Especies Exóticas Invasoras (Ministerio de Ambiente y Desarrollo Sostenible).

El manejo de caballos cimarrones como mamífero invasor en la Argentina es complejo y con múltiples aspectos. Para hallar una solución en el futuro, este problema debe ser tratado de manera estratégica y colaborativa. Si bien hay importantes desafíos por delante, existen evidencias y antecedentes de la voluntad de llegar a un manejo participativo y basado en ciencia está disponible.

Introduction

Horses (*Equus ferus caballus*) are large, herbivorous mammals and members of the family Equidae in the order Perissodactyla (Bennet and Hoffman, 1999). Horses originated in North America four million years ago and migrated through the Bering Isthmus to Eurasia and through the Panama Isthmus to South America during the Great American Biotic Interchange (GABI); later, they dispersed widely (Mc Fadden, 2005). By the end of the Pleistocene, all horses in America had become extinct (Alberdi and Prado, 2004; Mc Fadden, 2005). When domestic horses escape from human control or are liberated in natural areas, they can revert to a form of life similar to that of wild equids and are termed “feral” (Berger, 1986; Douglas and Leslie, 1996).

During European colonization of the Americas, horses were re-introduced to the continent. In Argentina, the first horses were brought by Spaniard colonizer Pedro de Mendoza, when he founded Buenos Aires in 1536. The first settlement was destroyed by indigenous inhabitants of the area, and when Pedro de Garay founded a new settlement in the same place, he discovered there were already thousands of feral horses descended from the original introduction (Cabrera, 1945). During the 16th century, many other horses entered Argentina from Chile and Peru, accompanying the colonists that established the first Euro-colonial cities. These horses, and many others that escaped, founded the first feral horse populations, which expanded rapidly to inhabit the Pampean region, northeast and central Argentina and the Andes mountains region (Cabrera, 1945). These early introductions were of horses of Andalusian-Barb ancestry, and they later became the Argentine Criollo horse breed.

Horses as introduced invasive species

Introduced invasive species are defined as those species that are transported outside of their native range, establish populations and cause environmental damage (CBD, 2017). Introduced invasive mammals are present worldwide and are deemed by some sectors of society to be a serious biodiversity conservation problem (Lever, 1994; Long, 2003; White *et al.*, 2008). In particular, feral ungulates are a highly successful group of invasive species, and their management has motivated considerable effort and investment in many countries, including Australia (Bradshaw *et al.*, 2007), New Zealand (Parkes and Murphy 2003), and the United States of America (USA) (Douglas and Leslie 1996; Witmer *et al.*, 2007).

Horses were introduced by humans outside their native range in many countries on every continent except Antarctica (Lever, 1994; Long, 2003). Feral horses are considered invasive in many of these countries (Lever, 1994; Long, 2003), including Argentina (Novillo and Ojeda, 2008; InBiAr, 2017). They are especially abundant in Australia and the western USA, and at high population densities, they have large impacts on the environment through overgrazing and trampling (Dobbie *et al.*, 1993; Beever and Brussard 2000a; Dawson et al., 2006).

Feral horse populations in Argentina are mainly distributed in the Andean zone of the Cuyo and Patagonia regions, but their geographic location, size and origins remain understudied (Scorolli, 2016). Some populations occur in natural protected areas, like Parque Nacional Bosque Petrificado de Jaramillo and Parque Nacional Los Glaciares, both of which are in Santa Cruz province, and the largest and most-studied population is found in Parque Provincial Ernesto Tornquist (PPET), located in the Pampas region of southwestern Buenos Aires province (Merino *et al.*, 2009; Scorolli, 2016).

Feral horse management is often very conflictive and controversial (Dobbie *et al.*, 1993; Symanski, 1996; Beever and Brusard, 2000b; Dawson *et al.*, 2006; NRC, 2013). Where the species is considered invasive, management is usually aimed at reducing the population size or density to minimize damage (Nuñez *et al.*, 2016). These goals are achieved in different ways, including lethal methods or live capture and subsequent adoption by the public. Conflicts usually arise between governmental agencies or authorities and non-governmental organizations (NGOs) or horse protection groups, as has occurred in the USA, New Zealand, Canada and Australia.

In Argentina, feral horse management has been inconsistent and relatively unorganized. Formal efforts have only been initiated in one natural protected area: PPET (Scorolli, 2016). The conflict that arose between a group of horse defenders and government authorities when management of PPET's feral horses was attempted has been briefly described elsewhere (Scorolli, 2016, 2018). The aim of this chapter is to elaborate on these previous descriptions to analyze the values involved and arguments offered by the opposing groups and add a comparison with conflicts that have arisen in other countries. These findings provide insights to potential solutions and highlight gaps and challenges for future feral horse management in Argentina.

The conflict over management

The management and conflict of horses in a protected area

PPET is a natural provincial protected area, consisting of 6,770 ha located in the Ventana Hills of the Pampas region in southwestern Buenos Aires province (38°00 S and 38°10' S; 61°45' W and 62°8' W). Its main goal is to preserve the biodiversity of the hill-grassland ecosystem (Fiori *et al.*, 1997). The area has a rich plant community with more than 600 species (Long and Grassini, 1997), and the presence of endemic plant and animal species brings special value to this reserve (Kristensen and Frangi, 1995).

Domestic Argentine Criollo horses were introduced to the area in 1942, but soon became feral and increased their population without management. They were studied for the first time in 1995 (Scorolli, 1999). In 2002, their density was extremely high, at 35 horse/km², and the population was approaching carrying capacity (Scorolli and Lopez Cazorla, 2010). Researchers studied their demography and population dynamics (Scorolli and Lopez Cazorla, 2010), as well as their impacts on vegetation (Loydi and Distel, 2010), the bird community (Zalba and Cozzani, 2004) and interactions with introduced invasive plants (de Villalobos *et al.*, 2011). In 2006, government authorities in charge of the protected area, based on an assessment from previous years made by university researchers, decided to initiate management efforts for this feral horse population (Scorolli, 2016, 2018). The goal, defined by a provincial government decree (PEPB, 2006), was to eradicate the population. The Universidad Nacional del Sur (UNS) was not involved nor consulted, and the plan proceeded without public knowledge (Scorolli, 2016, 2018). Feral horses were trapped with mobile-corrals, and in two years of management, 220 horses were captured. Most of them were relocated, and 80 were euthanized by the Army Equine Veterinary Division (Scorolli, 2016, 2018). At this time, during a political speech made by the former provincial governor in a meeting of the local ranchers' society (Asociación Rural), some public protests and verbal attacks were made on the authorities. In 2011, a group of horse defenders initiated a series of protests in the local and regional media against the described management actions. They attacked the authorities and also the researchers who had provided the evidence that promoted control (Scorolli, 2016, 2018). The horse defenders opposed this goal, denying the impacts on biodiversity and opposing the labeling of horses as an introduced invasive species. When biologists responded to these criticisms with scientific evidence, the conflict escalated. A *Facebook* group was created that in only a few months reached 5,000 members. Members posted messages and gave radio interviews, uploaded videos and wrote notes in online newspapers (Scorolli, 2016, 2018). The group consolidated and later founded an NGO called Asociación Civil Cimarrón Equino (ACCE – the Wild Horse Civil Association) with the explicit goal of conserving all feral equine populations, including horses and donkeys (*Equus africanus asinus*), in Argentina (ACCE, 2011).

The controversy persisted for two years and also involved conservation NGOs and PPET park rangers. Government agencies remained almost silent during this time, perhaps because they were finishing their mandate period (Scorolli, 2018). After the election, the new responsible authorities, who were staff from a newly created environmental agency called the Organismo Provincial para el Desarrollo Sostenible (OPDS – the Provincial Agency for

Sustainable Development), contacted the ACCE group. They promised them a participatory meeting and even agreed to give them control of the feral horses, but this never happened. Finally, managers made the decision to stop feral horse management and the conflict ended. However, the socio-ecological problem of feral horses as a biological invasion continues today (Scorolli, 2018).

The arguments of researchers

Feral horses as invasive species. Domestic horses originated in Eurasia approximately 5,000–6,000 BP (Pennisi, 2001; Olsen, 2016) and are considered an introduced species in Argentina (Novillo and Ojeda, 2008; InBiAR, 2017). In PPET, they were established in the 1940s, and the population expanded to occupy all available areas in the reserve. They are the dominant large herbivore, and in 2001–2002 were found to have reached very high densities and cause significant environmental impacts (Scorolli and Lopez Cazorla, 2010).

There is some uncertainty about the current taxonomic status of feral horses (Groves, 2002). The modern horse species was first described by Linnaeus from a domestic specimen type (Bennett and Hoffman, 1999). The taxonomy and phylogeny of the *Equus* genus is complex and still not fully understood (Groves, 2002). It is not completely clear who was the domestic horse's ancestor (Kefena *et al.*, 2010). The Eurasian tarpan (*E. ferus ferus*) is one candidate, but insufficient evidence supports this claim. The Mongolian wild horse or takhi (*E. ferus przewalskii*) is the only true wild horse at present. However, recent research strongly suggests that it is not the domestic horse's ancestor, but rather these are two separate lineages (Orlando *et al.*, 2013). Some authors consider that the scientific nomenclature *E. caballus* should be retained for both the domestic form and feral populations of horses (Gentry *et al.*, 2004).

Demography and population dynamics. Feral horses in many countries have few if any predators. They show moderate fecundity, very high survival rates, and their average annual population growth rate worldwide is 18% (Ransom *et al.*, 2016). These life history characteristics allowed feral horses to recover rapidly, even after population size reductions, and clearly limits the efficacy of inconsistent control methods (NRC, 2013). There is evidence that the PPET population shows density-dependence and has been food-limited, with annual mortality as high as more than 80 horses, dying mostly from starvation (Scorolli and Lopez Cazorla, 2010). After two important population reductions, one of 30% caused by mass-mortality in 2002 and another of 50% by management in 2006–2007, the population recovered its initial size in just four to five years (Scorolli, 2016, 2018).

Impact on biodiversity. Feral horses are considered to be a problem species by environmental scientists and managers in many countries, and their environmental impacts were studied in the USA (Beever and Brussard, 2000a, 2004; Beever and Herrick, 2006), New Zealand (Rogers, 1991) and Australia (Dawson *et al.*, 2006; Cherubin *et al.*, 2019; Robertson *et al.*, 2019). In PPET, important evidence was obtained from 2000 onwards about the impacts on the grassland bird community (Zalba and Cozzani, 2004), vegetation composition and structure (Loydi and Distel, 2010; de Villalobos and Zalba, 2010; Loydi *et al.*, 2010; Loydi *et al.*, 2012; de Villalobos, 2016), impact of dung-piles as dispersers of introduced invasive plants (Loydi and Zalba, 2009), and facilitation of introduced invasive trees like pines (*Pinus halepensis*) (de Villalobos *et al.*, 2011). Habitat modification would also be expected to affect the population of endemic animals, such as rodents and lizards, but this has not been studied.

Legal framework. Argentina has ratified the Convention on Biological Diversity (CBD, 2017), and as part of this multi-lateral treaty has obligations concerning biodiversity conservation and invasive species management. Also, the Administración de Parques Nacionales (APN – National Parks Administration) published a report that presents its official position about the need to prevent and control invasive species in national parks (APN, 2007). The Argentine National Fauna Conservation Law (#22,421) and Resolution #376/97 from the Secretaría Nacional de Ambiente y Desarrollo Sostenible (SAyDS – National Secretary of Environment and Sustainable Development) similarly made pronouncements against invasive species in any area of national biodiversity value, particularly protected areas. Plus, a provincial law in Buenos Aires province about Natural Protected Areas (#10,907) clearly states that introduced species should be managed.

Even when some "post-modern" critics suggest that expert opinion, including that of scientists, is almost without any value to society (Symanski, 1994, 1996), the legal normative framework represents the legitimized norms, standards or compromises that guide the actions of a nation's policies and inhabitants. To institutionalize further its position with regards to introduced and invasive species, Argentina is also developing and implementing a National Invasive Exotic Species Strategy with the financial support of the Global Environment Facility (GEF), administered through the Food and Agriculture Organization (FAO) and broad participation of government and academic institutions (FAO, 2016).

Arguments from horse protectionists

Cultural and historical value. The members of ACCE claim, as one of the main arguments against management, that feral horses are a very important part of Argentine rural culture and history. Popular culture is defined as a group of practices and manifestations that express the way of life in a place or country (RAE, 2017). It is true that Argentine Criollo horses have played a vital role in the rural way-of-life throughout history since European colonization (Brailovsky and Foguelman, 1991; Taboada, 1999; Dowdall, 2003). Historically, Argentina and the Pampas have been famous around the world for their livestock, and still today Argentina is often considered a "horse nation," where livestock breeding is a traditional and economically important activity.

Many travelers and historical chroniclers, such as Faulkner, Paucke, Dobritzhoffer, Azara, D'Orbigny, and Darwin, referred in their works that in the rural landscape of the past, feral horses were incredibly abundant and mostly used as a source of tamed animals for work and as a renewable resource that produced meat and fat for consumption and leather for export (Taboada, 1999). Later, when the era of ranches consolidated, feral horses were viewed by ranchers as a problem or a pest, because the big herds often destroyed fences, infrastructure, and even "stole" domestic horses, causing considerable damage to commercial ranching activities (Brailovsky and Foguelman, 1991; Taboada, 1999).

Indigenous peoples also have intensely used feral horses since the 18th century; they ate their meat, used their fat, and traded live animals and hides (Alioto, 2011; Pedrotta, 2016). During the 18th and 19th centuries, hundreds of thousands of Argentine Criollo horses were used in the independence war against Spain, as well as in wars against neighboring countries and in Argentina's own fierce civil war (Cabrera, 1945; Taboada, 1999). Many domestic horses died in the battles during this period. The ACCE proposes that feral horses must be honored as war heroes or "patriots."

The domestic Argentine Criollo horse was, and still is, highly valued by rural people, but that is not the case of feral horses. However, this distinction between domestic and feral is apparently poorly understood in many social contexts. At present, only 10% of the Argentine human population lives in rural areas (INDEC, 2010). Therefore, most of the public's experience with feral horses is indirect. Only in PPET is it possible for tourists to have some

Figure 1. Herd of feral horses in Parque Provincial Ernesto Tornquist, Argentina.

contact with feral horses, but this possibility is reduced by the deteriorated conditions of the inner roads that cross the area.

Aesthetic value. The value assigned to a species due to its beauty or symbolism is frequently a reason for its protection and conservation (Pearson, 2016). Feral horses are viewed as beautiful animals by most people (Fig. 1), and aesthetic value is one of the reasons for their protection in many countries (Dawson *et al.*, 2006; NZ DOC, 2012; NRC, 2013; ITRG, 2016).

Genetic uniqueness. The ACCE also proposes to value PPET's feral horses based on a supposed unique genetic composition. The breed that was the reported source of this population is Argentine Criollo, from the famous horse breeder Emilio Solanet in Ayacucho. This is the most common breed in rural Argentina. However, there has yet to be any genetic study of the PPET feral horses that could help to clarify this purported value.

Reintroduction of a "native" species. Some researchers in the USA and Europe have proposed "rewilding" as a conservation restoration tool to reintroduce large mammals that went extinct during the Pleistocene by bringing back the same or ecologically similar species to their former habitat (Donlan *et al.*, 2006; Donlan, 2007). This proposal has been highly criticized (Rubenstein *et al.*, 2006; Rubenstein and Rubenstein, 2016), but in a recent work by Naundrup and Svenning (2015), the potential area suitable for reintroduction of horses was analyzed for Argentina and a large part of South America.

During the Pleistocene in Argentina, there were horses of the genera *Equus* and *Hippidion* (Alberdi and Prado, 2004). The *Equus* species found in Argentina included *E. neogeus*, perhaps somewhat similar to the *E. caballus* of the Pleistocene (Prado and Alberdi, 1994), but different from the domestic breeds that were artificially selected by humans for millennia. The factors that caused the Pleistocene extinction of horses in the Americas are still not entirely known and have been the subject of great debate among paleontologists (Alberdi and Prado, 2004; Prado and Alberdi, 2017). Recently, some evidence suggested vegetation change was one of most probable causes (Sánchez *et al.*, 2006; Prado and Alberdi, 2017). If the vegetation change since the Pleistocene has been as significant as many ecologists believe (Beever and Brussard, 2000b; TWS, 2011), and present plant communities evolved without horses, then the reintroduction as part of a "rewilded" landscape restoration strategy would need to be carefully analyzed.

"Wild" species that "belong" to the ecosystem. Many horse defenders consider feral horses to be an integral part of the ecosystems where they now have populations (NRC, 2013; ITRG, 2016) and even playing crucial functions that benefit the habitat and other species (Kirkpatrick and Fazio, 2010; Downer, 2014). In Argentina, ACCE indistinctly uses the terms "wild" and "feral" for naming these horses. The word *cimarrón* (the most used synonym of feral in Spanish) indicates an animal that has escaped from domestication, but the term is sometimes used to mean wild or untamed. In Argentina, *cimarrón* has been used for centuries to name escaped horses or cattle (Taboada, 1999) and is widely known and unambiguously used by the rural people. Most horse protectionist groups prefer the term "wild" for feral horses and invoke their rights as a wild "native" species that is part of the ecosystem. They even propose to treat them as threatened fauna, not controlling the population nor allowing their culling, but instead caring for their welfare and even giving them veterinary care or supplementary food if needed (HSU, 2010; ACCE, 2011; ITRG, 2016).

Comparison between conflicts in different countries

There are many differences and variations between the conflicts that have occurred around the topic of feral horse management in Argentina and other countries. Some interesting parallels and common arguments exist (Table 1). The conflict in PPET had some particular features that could be mentioned, including that no legal court processes have yet occurred, and that the OPDS (Currently Environment Ministry of Buenos Aires province) has not written a formal management plan, despite the UNS having been proactive in conducting research that has provided sufficient results to elaborate one.

Table 1. Comparison of feral horse management conflicts in different countries.

Feature of conflict	Countries				
	Argentina	Australia	USA	New Zealand	References
Long-term duration (decades)		×	×		1, 2
Short-term duration (some years)	×			×	3, 4
Government, scientists and horse defenders involved	×	×	×		1, 2, 3
Gave rise to legal processes			×		2
Science-based management plan		×	×	×	6, 7, 8, 9
Participatory planning		×	×		5, 6, 8
Protests against goals, lethal methods and scientific evidence	×	×	×	×	3, 10, 11

References: 1. Dawson *et al.*, 2006; **2.** National Research Council, 2013; **3.** Scorolli, 2016; **4.** New Zealand Department of Conservation, 2012; **5.** Independent Technical Reference Group, 2016; **6.** Parks Victoria, 2021; **7.** Office of Environment and Heritage, 2017; **8.** United States Bureau of Land Management, 2011; **9.** United States Bureau of Land Management, 2015; **10.** Asociación Civil Cimarrón Equino, 2011; **11.** Humane Society of United States, 2010.

Challenges for the future

A crucial aspect of feral horse management success is addressing the problem's human dimensions (Dawson *et al.*, 2006; Nimmo and Miller, 2007; NRC, 2013). Recent reviews have highlighted the surprising paucity of studies that quantify this issue (Nimmo and Miller, 2007; Linnell *et al.*, 2016). Only some such research exist, including Bhattacharyya *et al.* (2011) in Canada, Chapple (2005) in Australia, and Rikoon (2006) in the

USA. Recently, in the Argentine portion of Tierra del Fuego, the perceptions about threats to nature were studied, including free-roaming horses (Mrotek *et al.*, 2019). It would be very important to evaluate in other regions of Argentina how different social actors perceive this type of conflict and the underlying issues (see Anderson and Pizarro, this volume; Car *et al.*, this volume; Guichón *et al.*, this volume).

The polarized situation of ecologists *vs.* horse defenders is perhaps not an accurate reflection of reality, and it could be more productive to look for solutions that incorporate multiple perspectives (Estévez *et al.*, 2015). In this context, some authors have remarked on the importance of managing the environment, and in particular biological invasions, from a socio-ecological perspective (Knight, 2019; see also Anderson and Pizarro, this volume). This framework applied to addressing the feral horse conflict provides an interesting venue and a potentially positive direction for the near future. A correct diagnose of values and risk perception of the different stakeholders involved in the conflict, as proposed by Estévez *et al.* (2015), could be an important first step in the right direction.

Recently, the university researchers involved in the conflict have officially presented OPDS authorities with a draft management proposal for feral horses in PPET (Scorolli, 2016, 2018). The document focuses on technical aspects with the main goal being to reduce the feral horse population size through corral live trapping and relocation or adoption of the captured horses. The proposal considers adaptive management to be a key issue, with careful monitoring of both ecosystem and social responses. A public debate of the management strategy, including participation of diverse stakeholders, has not yet happened, but clearly is needed and expected. At present, this proposal has not been implemented, but recent conversations with authorities, and also with the President of ACCE, are promising. Some challenging tasks, however, are urgently needed to improve feral horse management, including:

- Better communication of scientific evidence to the general public.
- More effective participation and transparency by governmental agencies and authorities.
- Further debate with and participation of different citizen social groups in the planning process and communication strategy.
- Greater engagement of the public regarding biodiversity's multiple values.
- Enhanced integration of knowledge (*e.g.*, values, opinions, perspectives) gained from other stakeholders to improve feral horse management plans.
- Inclusion of feral horse management plans in the current National Invasive Exotic Species Strategy (ENEEI).

Conclusions

Managing feral horses as an introduced invasive mammal in Argentina is a complex and multi-faceted task. If we are to arrive at a solution in the future, this issue should be treated in a more strategic and collaborative context that recognizes and incorporates its human dimensions, beyond merely expecting society to accept ecologists' statement of scientific values. Clearly, many challenges remain, but the basis for a sound, participative, knowledge-based management plan is already available. There is a clear path forward regarding the expansion of this issue to understand it as a social-ecological system (see also Anderson and Pizarro, this volume).

Acknowledgements

Thanks to the Secretaría de Ciencia y Tecnología of Universidad Nacional del Sur (UNS) and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) for the financial support to the projects PGI 24/B213 and PIP 112 201201 00413 CO. Special thanks as well to Dr. Jason I. Ransom for critically reading the manuscript and providing valuable suggestions.

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7 | PROGRESS OF BIOLOGICAL INVASION GENETICS AND THE MANAGEMENT OF INVASIVE MAMMALS IN ARGENTINA

AVANCES SOBRE GENÉTICA DE LAS INVASIONES BIOLÓGICAS Y EL MANEJO DE MAMÍFEROS INVASORES EN ARGENTINA

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Abstract. Introduced invasive species generally have a wide geographic distribution, characteristic life cycles and great ability to adapt, establish and spread in a new environment. Invasion genetics is a relatively new discipline that investigates the genetic variation patterns of introduced invasive species and their ecological and evolutionary consequences. A pioneer in this discipline was Charles Elton, who published *The ecology of invasions by plants and animals* in 1958, although later *The genetics of colonizing species* was considered the founding document for invasion genetics in 1965. Gradually, the advances in emerging molecular technologies, use of higher resolution genetic markers, and research development on genetic variation of invasive species consolidated the importance of genetic aspects in the invasion process. Undoubtedly, the growing concern for the disturbances generated by invasive species on biodiversity and ecosystem functions was also determinant for the inclusion of invasion biology within the broad field of conservation biology. Recently, several scientific journals have expanded their editorial scope, including conservation-relevant articles that address the genetic aspects of biological invasions. In Argentina, it is striking that genetics is not being used frequently for species that have become invasive, even when they are causing countless impacts and disturbances in various ecosystems. Although the number of introduced invasive mammals in Argentina exceeds 20, only five of them have been assessed genetically. Presuming that invasion genetics is better incorporated into the agenda of invasion biology research and application, it would allow integrating ecological, genetic, and evolutionary aspects for more effective management, control or eradication of invasive species widely distributed in Argentina.

Resumen. La genética de la invasión investiga los patrones de variación genética de las especies exóticas invasoras y sus consecuencias ecológicas y evolutivas. Un precursor del tema fue Charles Elton (1958) por *The ecology of invasions by plants and animals*, aunque esta monografía, que reúne varios casos de estudio, no tuvo un impacto significativo quizás por su temprana aparición. El interés por

este tema surgió como consecuencia de la publicación del volumen *The genetics of colonizing species*, editado por Baker and Stebbins (1965), considerado una destacada síntesis sobre la genética y evolución de especies colonizadoras y el documento fundacional de la «genética de la invasión». Sin embargo, el verdadero ímpetu por su estudio surgió a fines de la década de 1980, con la publicación sobre problemas ambientales del SCOPE (Scientific Committee on Problems of the Enviroment), que daba cuenta de esta problemática. Consecuentemente, la biología de la invasión experimentó un crecimiento exponencial para fines de la década de 1990, puesto en evidencia con la aparición de la revista *Biological Invasions*, dedicada a publicaciones específicas sobre introducciones e invasiones de especies. Más tarde, el incremento del uso de marcadores genéticos en el desarrollo de la biología de la invasión y el lanzamiento de la revista *Molecular Ecology*, que concentró gran cantidad de artículos sobre variación genética en invasoras, culminaron por consolidar la importancia del estudio de los aspectos genéticos en el proceso de las invasiones. Recientemente, varias publicaciones científicas han ampliado sus objetivos editoriales incluyendo artículos relevantes a la conservación que tratan aspectos genéticos de las invasiones biológicas.

En líneas generales, las especies introducidas invasoras siempre han despertado interés, no solo por sus características distintivas de amplia distribución y ciclos de vida, sino también por la aptitud que evidencian para la adaptación, establecimiento y expansión en un nuevo ambiente, que les permite transformarse en invasoras exitosas. Sin duda, la temprana disociación que existió entre los estudios sobre ecología de las invasiones y aquellos relacionados a su genética y evolución, lentamente está siendo superada gracias al desarrollo de investigaciones que integran ambos enfoques en el estudio de las especies exóticas. En particular, durante las últimas décadas, se incrementó el desarrollo de nuevas metodologías moleculares basadas en el ADN, que permitieron la detección, identificación y monitoreo de diversas especies invasoras de forma certera. De igual forma, también el análisis de la variabilidad y estructura genética poblacional, incluso su aplicación en el manejo, control y/o erradicación de las especies invasoras, fueron los avances más contundentes que durante las últimas décadas llevaron al nacimiento de la «genética de la invasión». Paulatinamente, y en particular durante los últimos años, los estudios sobre genética de la invasión se incrementaron con el objetivo de identificar los determinantes de la invasividad y los rasgos que caracterizan a las especies introducidas invasoras usando análisis filogenéticos, filogeográficos y otros enfoques experimentales que incluyen factores históricos, biogeográficos y ecosistémicos.

Sin duda, la genética de la invasión es una herramienta de estudio para reconstruir la historia biogeográfica y evolutiva de las invasiones, evaluando entre otras cosas la magnitud que tuvieron los cuellos de botella genéticos y eventos fundadores. Ambos procesos evolutivos pueden reducir drásticamente la variabilidad genética (deriva génica), con lo cual se espera que las especies introducidas presenten un potencial limitado para adaptarse a nuevos ambientes.

En Argentina, a pesar de la cantidad de especies introducidas que se han convertido en invasoras, pocos estudios integran un enfoque genético. Es así que, de las especies de mamíferos invasoras registradas en nuestro país, solo cinco de ellas incluyen datos sobre su estructura y variabilidad genética.

Introduction

Invasion genetics investigates the patterns of genetic variation of introduced invasive species. A pioneer in this discipline was Charles Elton with *The ecology of invasions by* *plants and animals* (Elton, 1958). Although his monograph collects several study cases, it did not have a significant impact on research and policy at the time, most likely due to its early emergence in the consolidation of ecology as a field. Most interest in this subject arose later, starting with the publication of *The genetic of colonizing species* (1965), edited by H.G. Baker and G.L. Stebbins, which is considered a remarkable synthesis on the genetics and evolution of colonizing species and the founding document for invasion genetics, even before there was a field of "invasion biology." However, the real momentum for its study emerged in the late 1980s (Simberloff *et al.*, 2013) with the identification of biological invasions in the context of the priority environmental research issues included in a report by the Scientific Committee on Problems of the Environment – SCOPE (Mooney and Drake, 1986). Consequently, invasion biology experienced exponential growth by the end of the 1990s, evidenced by the emergence of the journal *Biological Invasions*, dedicated to specific publications on species introductions and invasions. Later, the increased use of genetic markers in the development of the invasive biology and the launch of the journal *Molecular Ecology*, which concentrated a large number of articles on genetic variation of invasive species and consolidated the importance of the study of genetic aspects in invasive processes. More recently, several scientific publications have expanded the editorial scope of this sub-discipline, including conservation-relevant articles that addressed genetic aspects of biological invasions. Undoubtedly, the early dissociation that existed between the studies on the ecology of biological invasions and those related to their genetics and evolution is slowly being overcome due to the development of research that integrates both approaches in the study of introduced invasive species. During the last decades, the development of new DNA-based methodologies allowed the detection, identification and monitoring of several invasive species accurately. In addition, the analysis of the variability and genetic structure of the populations, including its application in the management, control and/or eradication of invasive species, were the most significant advances that led to the origin of invasion genetics.

Biology of invasions

Introduced invasive species have raised interest among biologists, not only because of their distinctive characteristics of wide distribution and life cycles, but also because of their ability for adaptation, establishment and expansion in a new environment, which allows them to become successful invaders. Invasion biology is the scientific sub-discipline of ecology that studies the worldwide introduction and dispersal of introduced invasive species. One of the characteristics of these species is that they are easily adaptable to new habitats, thus allowing them to rapidly increase their population size and geographic distribution. Environmental damage and disturbances caused by biological invasions represent significant economic costs for various activities, also involving health risk situations (Mack *et al.*, 2000). Certainly, they are one of the main causes of species extinctions, range retractions and restructuring of biological populations (Williamson, 1996; Cox, 2004; Sax *et al.*, 2005). Growing concerns about the disturbances caused by invasive species on biodiversity and ecosystem functioning were determinant for definitively including invasion biology within the broader field of conservation biology.

Colonization of a new area by an introduced species involves a process that begins with the translocation of propagules from the source population to new areas and continues through the establishment and population growth in the colonized area or region. Invasion occurs when this population expands to such a point as to cause some kind of negative impact, as defined by people (including ecological damages, but also social, economic and cultural effects). The obstacles at each stage of the process will determine that only a limited number of species will be established as successful colonizers in the new region (Lee, 2002; Gilchrist and Lee, 2007). As a result, the magnitude of the invasion has important genetic consequences that are transferred from one place to another, which could influence the probability of establishment, the future distribution, and the adaptability of the invasive species.

A relevant stage of the process is the expansion phase, since the colonizing species is exposed to new selective forces arising from the biotic and abiotic conditions prevailing in the new environment where dispersion is occurring. Although most introductions fail at this stage, species that successfully adapt to the new environment may become highly invasive, achieving a rapid expansion. If the adaptive response occurs in the short-term, these cases become true natural experiments, which are very useful for the study of ecological and evolutionary responses.

The early dissociation between studies on the ecology of invasions and studies related to genetics and evolution of introduced species is slowly being overcome due to the development of research that integrates both approaches. In the last few years, DNA-based methods were developed for the detection, identification and monitoring of invasive species (Darling and Blum, 2007) and for the analysis of the variability and genetic structure of populations (*e.g.*, Tsutsui *et al.*, 2000; Abdelkrim *et al.*, 2005; Zhan *et al.*, 2012; Chau *et al.*, 2015) to apply these results to the management, control and/or eradication of introduced invasive species. All these advances led to the origin of invasion genetics.

Invasion genetics: how can invasive populations overcome founder effects?

Invasion genetics is a relatively new discipline that investigates patterns of genetic variation in invasive species populations and their ecological and evolutionary consequences (Barret, 2015). During the last decades, the use of genetic markers at the experimental level has been diversified to include Random Amplification of Polymorphic DNA (RAPDs), isoenzymes, Amplified Fragment Length Polymorphism (AFLPs), chloroplast DNA (cpDNA), microsatellites, DNA sequences and Single Nucleotide Polymorphism (SNPs), which together gave rise to molecular ecology as a new sub-discipline. This area of study answers many questions relevant to both ecology and evolution by applying molecular genetic techniques and including research on biological invasions. Studies on invasion genetics have increased gradually, with the aim of identifying the determinants of invasiveness and the traits that characterize introduced invasive species, using phylogenetic and phylogeographic analyses, and other experimental approaches, which include historical, biogeographical, and ecosystem factors. Certainly, invasion genetics is a tool for reconstructing the biogeographic and evolutionary history of invasions, evaluating among other things, the magnitude of genetic bottlenecks and founding events. Both evolutionary processes can drastically reduce genetic variability (gene drift), and consequently it is expected that introduced species might have limited potential to adapt to new environments.

The genetic approach provides a way to solve the genetic paradox of biological invasion (*i.e.*, "how introduced populations, whose genetic variation has been depressed by a genetic bottleneck or founding effect, persist and adapt to new conditions") (Sakai *et al.*, 2001). This is a paradox because somehow, it rejects concepts of conservation genetics that indicate that reduced genetic variation due to founding effects and genetic drift restricts the ability of a population to adapt, increasing the risk of extinction of small populations (*e.g.*, those resulting after a bottleneck). Despite this, the adaptive potential of some invasive species might be significant.

Although both phenotypic plasticity and epigenetic variation have been proposed as compensatory for this lack of genetic variation (Liebl *et al.*, 2015), many invasive species may have benefited from repeated introductions, increasing propagule pressure and genetic variation into the new range or habitat. For example, one factor that contributes to the adaptive potential of introduced species and that could contribute to invasion success is the intraspecific hybridization (admixture) produced by multiple introductions from different native populations into one area (Sakai *et al.*, 2001; Keller and Taylor, 2010; Verhoeven *et al.*, 2011). Unlike many threatened species, introduced species can counteract bottleneck or founder effects, producing adaptations that allow them to thrive in new environments, which is a genetic paradox (Frankham, 2005; Dlugosch and Parker, 2008; Estoup *et al.*, 2016). In addition, some invasive populations showed greater genetic diversity, when compared to native populations (Kolbe *et al.*, 2004; Lavergne and Molofsky, 2007).

To adapt to new environments, species will either have to tailor their phenotype by epigenetic changes (*i.e.*, methylations that induce changes in gene expression) or by phenotypic plasticity in response to environmental variables, which enables individuals to adapt rapidly to environmental changes (Liebl *et al.*, 2015). It is important to note that there are increasingly more studies reporting evolutionary changes in invasive populations at ecological time scales, such as the case of copepods adapted to different salinities (Lee and Petersen, 2002). Likewise, there are several other studies reporting adaptations in response to climate change within a few decades for *Drosophila* flies (Huey *et al.*, 2000), *Oryctolagus* rabbits (Williams and Moore, 1989) and *Solidago* plants, also known as goldenrods (Weber and Schmid, 1998).

One of the key factors in invasion genetics is that if we want to study adaptation of introduced species to new environments, we have to stop using neutral markers and begin determining how particular gene variation influences the introduction and successful expansion of species. Recent advances in molecular tools (*i.e.*, Next Generation Sequencing) will undoubtedly provide great contributions to genetic studies. At present, the most commonly used markers for studying individual adaptations to environmental changes are the SNPs, which are variations in the DNA sequence that affect one or a few nucleotides of a genomic sequence.

Molecular technology and studies on invasion genetics

There are several new technologies for the analysis of genetic variability in invasive species that use a variety of molecular markers, whether they are nuclear, mitochondrial or chloroplastic and some of which were mentioned above as examples. In 2003, Paul Herbert proposed DNA barcoding as a new way to identify species (Hebert *et al.*, 2003a; 2003b). Barcoding uses a very short genetic sequence from a standard part of the genome for species identification. The main roles of the International Barcode of Life (iBOL) are to extend the geographic and taxonomic coverage of the DNA barcode reference library, store the resulting barcode records, provide community access to the knowledge they represent, and create new devices that ensure global access to this information. For example, DNA barcoding will enable rapid identification of invasive species, allowing quarantine and eradication efforts to begin far earlier, with significant reductions in costs and increased chances of success.

Another technique known as metabarcoding is a rapid method for biodiversity assessment (Taberlet *et al.*, 2012). Environmental DNA (eDNA) is a surveillance tool used to monitor for the genetic presence of a species in a variety of environmental samples. For example, in samples that have many potentially invasive species, the presence of the targeted invasive species can be confirmed through the direct detection of its DNA. Compared to traditional methods of surveying for species, the increased sensitivity of this technique could be a valuable tool not only for invasive species, but also for threatened and endangered ones, as well. Furthermore, early detection by metabarcoding can significantly reduce the costs of managing invasive species. There is considerable interest in the use of eDNA barcoding for ballast water monitoring in ships, which is an important source of aquatic invasions, as well as for the study on the functioning of microbial invasions.

Over the past decade, genetics gave way to genomics, which sequences the entire genome rather than single genes. The study of the genome brings much more comprehensive insights into the DNA and allows the analysis of the variability between invasive populations in greater detail and sensitivity. Genomics is an extremely powerful tool for reconstructing the evolutionary history of invasive species (Luikart *et al.*, 2003) and enables scientists to differentiate between neutral (*i.e.*, those changes in which natural selection does not affect their spread in a species) and positive DNA changes (*i.e.*, those that improve chances of survival and reproduction of an organism and thus spread through a population). This positively selected evolution drives the fast adaptation of invasive species. Consequently, by understanding the effects of positive evolution we can predict how species could be able to adapt in the future.

Invasion genetics is gradually proceeding to invasion genomics. Both disciplines provide a cost-effective solution to the monitoring and management of invasive species (see eDNA above). Therefore, studies using these new technologies will be key for analyzing the functional role of candidate loci and will represent a step forward for invasion genetics.

Despite the remarkable increase in research on biological invasions in Latin America in the last decades (*e.g.*, see Pauchard *et al.*, 2011), some gaps in information still exist. A major challenge is to integrate invasive genetics with other approaches, such as demographic and ecological studies. Although there are numerous research programs on population genetics and higher resolution molecular markers, there are very few studies in Argentina that integrate the genetic and ecological data of invasive species, which therefore represents a new field to explore. It should be noted that so far in Argentina, no management or eradication plans have employed eDNA or genetic/genomic information.

Advances in genetic research of introduced invasive mammals in Argentina

The problem arising from the introduction of organisms requires integrating multiple approaches to end or at least control their impact. It is not just about investigating the ecology of species in both their places of origin and in their introduced distributions, but also about the development of working methods and multisector collaborations, which enable control and management actions. In this sense, the current linkage between science and management and between provincial and national jurisdictions is insufficient (Lizarralde, 2016; Ojeda, 2016).

In this context, there is surprisingly little research on the genetic aspects of introduced mammals in Argentina and even less research regarding those that become invasive and cause a countless number of damages and disturbances in diverse ecosystems (Lizarralde *et al.*, 2016; 2018). It is necessary to consider that the study of the genetic variability and population structure is the key to develop control and management plans for introduced invasive species. At present, the use of this information is essential for various management agencies worldwide. Depending on the source of information and criteria one considers, there are 21 (Ballari *et al.*, 2016; SAyDS and SAREM, 2019; Valenzuela *et al.*, this volume) or 27 (Lizarralde, 2016) introduced invasive mammal species in Argentina, without considering those that are native to the mainland, but were introduced onto islands, such as the Pampa fox (*Lycalopex gymnocercus*) and the large hairy armadillo (*Chaetophractus villosus*), which were introduced onto Tierra del Fuego's main island (Isla Grande).

Only five of these introduced invasive mammals have had studies about either i) a molecular genetic approach analyzing their population genetic structure and variability, or ii) some preliminary data that requires further research. These invasive species are: 1) the North American beaver, *Castor canadensis* (Lizarralde *et al.*, 2004, 2008; Fasanella *et al.*, 2010; Fasanella and Lizarralde, 2012); 2) the Asian squirrels, *Callosciurus* spp. (Gabrielli *et al.*, 2014); 3) the European rabbit, *Oryctolagus cuniculus* (Bonino and Soriger 2008); 4) the wild boar, *Sus scrofa* (Gabrielli *et al.*, 2008a, 2008b; Sagua *et al.*, 2014, 2018); and 5) the large hairy armadillo (Poljak *et al.*, 2010).

Beavers had a striking population expansion shortly after introduction to Tierra del Fuego, making them responsible for the most drastic landscape alteration since the last glaciation, affecting not only the hydrology and composition of the southern beech forest, but also allowing other introduced species to invade the ecosystem. From 20 individuals intentionally released in 1946 (Pietrek and Fasola, 2014), beavers have increased their numbers to a current population size of approximately 100,000 or more individuals (Lizarralde *et al.*, 2004). Genetic studies analyzing the variability and population structure of mitochondrial DNA of this species in the Tierra del Fuego Archipelago showed the presence of seven linages; three of them proved to be the most abundant and distributed throughout the archipelago (Lizarralde *et al.*, 2008; Fasanella *et al.*, 2010). According to this information, the authors concluded that the main island should be considered a single management unit (MU) and the archipelago's small islands each as a separate MU. They also proposed long-term control and management measures, considering that it was not possible to clearly identify eradication units (EU) on the main island, given that the Strait of Magellan is the only geographic barrier that would prevent gene flow in the population. This scenario makes it difficult to decide whether eradicating, controlling or even tolerating the species is the most effective and efficient strategy. Beaver invasion is certainly one of the most complex topics regarding introduced invasive mammals in Argentina, and a molecular biology approach would allow integrating different strategies to ensure a more successful management program of this invasive mammal.

Gabrielli *et al.* (2014) also conducted a genetic characterization of two *Callosciurus* squirrel species originally from Asia (*C. finlaysonii* and *C. erythraeus*) that have been introduced into Argentina. These authors compared them with native and introduced Asian populations. They also analyzed the genetic variation in mitochondrial and nuclear DNA markers between the four Argentine invasion foci to corroborate if the invasion pathway has been a single event, as believed. Unexpectedly, sequences from Asian squirrels introduced into Argentina were more related to *Callosciurus finlaysonii* than to *C. erythraeus*, according to D-loop and Cytochrome b mitochondrial markers. In addition, introduced squirrels from the different invasion foci formed a monophyletic group that, together with one haplotype for the D-loop and Cytochrome c oxidase subunit I (COI) markers supported the hypothesis of one single introduction event into Argentina, followed by subsequent translocations. The phylogeny of *C. erythraeus* and *C. finlaysonii* and their different subspecies is not yet resolved, since intraspecific variation among sequences of *Callosciurus* belonging to different subspecies or collected from different regions is large and comparable with the distance to the sequences from Argentina. Gabrielli *et al.* (2014) finally concluded that the genetic and intraspecific variations between *Callosciurus* species require further research to obtain a more comprehensive phylogeny. This demonstrates the need for applying genetic studies to get a clear understanding of the parental origin of introduced populations and an updated review of their phylogenies. Thus, by comparing with parental populations in their native environments, we can generate basic information for the development of adequate preventive management strategies.

The European rabbit is another species that invaded Argentina and is present throughout mainland Patagonia and parts of the Tierra del Fuego Archipelago. A genetic study of Patagonian populations (Bonino and Soriger, 2008) determined the main existing lineages and the genealogical relationship between rabbit populations introduced in Argentina and their original distributions. This study was the first, and so far the only one for this introduced invasive species. Undoubtedly, there is still much to investigate in relation to intra and inter-population genetic variability of this species and its implication in the identification of MUs and implementation of control actions.

A similar situation arises from studies on the genetic structure of *S. scrofa*. Gabrielli *et al.* (2008a, 2008b) analyzed the population of this species from Parque Nacional El Palmar (Entre Ríos province) and identified new mitochondrial haplotypes of great homology with reference haplotypes of pig breeds native to Asia. The low genetic variability detected in this study suggests that there was a unique introduction source for populations from Parque Nacional El Palmar and at least so far, it was not the result of hybridization with other variants. Analyzing another mitochondrial marker, Sagua *et al.* (2014; 2018) reaffirmed what was preliminarily observed by Gabrielli *et al.* (2008b) and proposed that the origin of the remaining wild boars from central and southern Argentina is not only related to European populations, but also shows variability with respect to these populations. Consequently, this suggests the existence of multiple wild boar introductions in Argentina. Nevertheless, it is still necessary to unravel the complex genetic structure in the original populations. This structure, common everywhere the boar is introduced, is marked by domestication events in Asia and Europe, large numbers of breeds, ingression of Asian genome into the breeds and the interbreeding of domesticated swine and wild boars (Wu *et al.*, 2007; Scandura *et al.*, 2008). The characteristics of an expanding invasive species are combined with the decrease in populations of pure specimens by hunting pressure and reduction of habitats.

Finally, the large hairy armadillo is a particular case, because it is native to Argentina, except on the main island of the Tierra del Fuego Archipelago, where it was introduced by humans around 1982 (Poljak *et al.*, 2007). All armadillos from Patagonia and Tierra del Fuego belong to the same mitochondrial linage. Recent monitoring of this species' population on Tierra del Fuego shows that their distribution has increased since its introduction (see Poljak *et al.*, 2020).

Despite the considerable number of species introduced in Argentina (Novillo and Ojeda, 2008; Ballari *et al.*, 2016; Lizarralde, 2016), no genetic studies have been carried out for almost any of these species, not even descriptive studies suggesting the need to relate ecological aspects and population genetics. Although the magnitude that the translocation and introduction of species can cause seems to be understood, it is necessary to further progress toward greater awareness at the global level. In Argentina, there is still much to be known about the adaptations of introduced species in the new environments they inhabit and about the potential of many other species that are not yet invasive. In any case, the genetics of both potentially and already invasive species should be studied in depth to establish adequate control measures and prevent major problems.

Implications for the management and genetic control of invasive species

Preventing introduction of invasive species is the most effective management approach (Hulme *et al.*, 2008). Early detection of invasive species soon after their introduction, when populations are still limited to a small area and are at a low density, maximizes the probability of effective management (Simberloff, 2001). Comparing genetic variation within and between populations enables biologists to understand how invading species spread, are intermingled, and compete with native species. This has given researchers a better understanding of the routes that invasive animals, such as sea squirts (*Microcosmus squamiger*, Rius *et al.*, 2012), ladybird beetles (*Harmonia axyridis*, Lombaert *et al.*, 2010) and many invertebrate pests (Kirk *et al.*, 2013), have used when they colonized new areas. Elucidation of introduction is essential for effective management of invasive species and for sustainable policy decisions. In addition, markers like microsatellites and mitochondrial

DNA have been widely used to understand population dynamics of different pests and disease vectors, helping control programs to limit their impact, as in the case of some mammal species (Hebert *et al.*, 2003a; Abdelkrim *et al.*, 2005; Lizarralde *et al.*, 2008; Berry *et al.*, 2012; Fasanella *et al.*, 2010; Bebber *et al.*, 2013; Adams *et al.*, 2014; Gabrielli *et al.*, 2014).

Molecular techniques enhance management of invasive species because they are faster, more specific and have greater standardization than surveillance programs based on morphological identification (Pochon *et al.*, 2013). Biologists use molecular techniques to catch invasions earlier by detecting animals' DNA in the environment (eDNA) from skin, urine, feces, air, sediment, soil or water samples. Environmental DNA surveillance for a species' presence is an indirect genetic method to detect rare and cryptic species (Mahon *et al.*, 2014). There are two kinds of eDNA monitoring: 1) Targeted surveillance, which screens for and targets DNA of a particular species in the sample (*e.g.*, Ficetola *et al.*, 2008; Wilcox *et al.*, 2013); and 2) Metagenomics, which sequences all DNA from a sample and then uses established databases to recognize the genetic identity of the species (*e.g.*, Thomsen *et al.*, 2012; Pochon *et al.*, 2013; Kelly *et al.*, 2014; Mahon *et al.*, 2014). For example, Ficetola *et al.* (2008) detected the DNA of the invasive bullfrog (*Lithobates catesbeianus*) in French ponds, even before the invasion had been noticed by visual, audio or other observations.

Genetic control strategies, which involve genetic engineering, are area-wide and species-specific methods. This species-specific aspect is very attractive from an environmental perspective, as it targets only the species of interest (Alphey *et al.*, 2013). Most genetic strategies that take benefit of the mate-seeking behavior of the modified species provide a control agent that self-disperses and actively seeks the invasive population. Although scientists have recognized the potential for applying genetic technologies to the control of invasive species for several years, the application has been primarily restricted to insects.

The most common genetic-based strategy for population suppression that uses classical genetics for biological insect control is the Sterile Insect Technique (SIT) (Klassen and Curtis, 2005). This technique has been used successfully for more than 50 years against several major agricultural pests, using radiation-sterilized insects. In Argentina, this technique has been employed mainly in agricultural regions, where insects cause large losses in fruit and vegetable production.

Clustered regularly interspaced short palindromic repeats (CRISPR)-Cas9 is a recently developed technology that has great potential for controlling invasive species and has resumed discussions on the use of gene drive for invasive species control (Esvelt *et al.*, 2014). Once transgenic organisms, bearing the gene drive, are constructed in the laboratory, they must be released into the wild to mate with wild-type individuals to begin the process of spreading the drive to wild populations. The total time required for spreading to all members depends on the number of transgenic organisms released, the generation time of the invasive species, the impact of the drive on individual fitness, and the dynamics of mating and gene flow in the population. In general, it is expected that spreading out the drive throughout the population will take many generations (Esvelt *et al.*, 2014). Given the potential of gene drives to alter entire wild populations and consequently ecosystems, the development of this technology must include robust safeguards and control methods (Esvelt *et al.*, 2014; Oye *et al.*, 2014). This technology can be applied for controlling or even eradicating invasive species from islands or even possibly from entire continents, but this can also have risks related to undesired spread. First, rare mating events may allow the drive to affect closely related species, and second, this could spread from the invasive population back into the native habitat. Because this technology involves transgenic organisms, experiments are not completely without risk (Esvelt *et al.*, 2014). Therefore, researchers, policymakers, and resource managers must carefully evaluate implementation risks of these technologies that could threaten rather than assist a given ecosystem (Webber *et al.*, 2015).

Much remains to be done in terms of genetic control using modified organisms, so we believe that making a consultative and regulated risk-cost-benefit analysis in a biosecurity context might be a careful step forward before the use of gene drive technologies in invasive species populations. In this sense, we consider that for the time being, in Argentina it would be more useful to use genetic information to detect invasive species in time (eDNA) and to study their genetic structure, so that they can be quickly combated with traditional eradication and control measures. It is also extremely important to inform and educate researchers, policymakers, resource managers and the general public to avoid new species introductions (see Campos *et al.*, this volume; Car *et al.*, this volume).

We are already well equipped to use molecular data to understand invasive species dispersal and adaptation, and this knowledge has valuable applications at a time when these are urgently required. We believe that the extensive experience of regulatory successes and failures in the context of classical biological control offers an existing framework to provide meaningful guidance for assessing risks and benefits for applications related to invasive species control within this emerging field. The time to develop this regulatory framework is today.

Final considerations

New genomic tools provide an unprecedented view of past and present population processes. In addition, genetic tools add much more than simply improving the detection and understanding of the expansion. High-density markers are used to detect changes in different parts of the genome, processes of hybridization and introgression and adaptation to the climate change. Since climate change and other anthropogenic effects at smaller geographic scales increase disturbed habitats, a higher rate of changes in biological communities is expected, particularly those caused by introduced species (Chown *et al.*, 2015).

Invasion biology has recognized that the direction of research is clearly changing (Simberloff *et al.*, 2013). Although most studies hitherto were purely ecological (at the level of organisms, species, populations, or ecosystems), we need to recognize the usefulness and increasing growth of genetic studies and the significance of evolutionary processes in invasive species for generating management actions and controlling the impact of biological invasions. As shown above, there has been a resurgence of interest in this subject. Indeed, the significance of the genetic approach and of the evolutionary perspective is now globally recognized as important, not only for understanding the species' ability to move forward through different stages of the invasion, but also for improving management interventions that could reduce rates and impacts of invasions.

In other words, genomic tools are very useful for the management and control of invasive species. Although they might be considered as overly expensive for the resources allocated to management, several studies have shown that they are actually far more effective than traditional monitoring tools (see above). Technology is advancing so rapidly that users do not need to be familiar with its complexities, and in this sense, different technology assistance programs exist in several international agencies. As a result, countless genomic tools can be used for enabling the society to reduce the economic cost of biological invasions. To mitigate these costs, a better understanding of the causes, consequences and progression of the invasion is necessary. Consequently, genetic information will serve to identify and predict the risk of source populations and address the problem when potential invasions are detected. Finally, molecular approaches should not be considered as a magical solution to invasive species control. On the contrary, they should be considered as a new tool that, together with current control methods, could provide better results.

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8 | DISEASE RISKS FROM INTRODUCED MAMMALS

RIESGOS DE ENFERMEDAD POR MAMÍFEROS INTRODUCIDOS

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Abstract. Many pathogens brought with introduced species have caused extinctions and dramatic ecosystem changes worldwide. Global literature illustrates how pathogens can facilitate biological invasions by "spilling over" into vulnerable, non-immune native hosts, or by "spillback," whereby introduced species become hosts for native pathogens that then affect local species. Introduced pathogens may even persist where the exotic host species fails. Moreover, if these pathogens establish disease cycles between domestic and wild species, they become virtually impossible to eliminate. Interventions to halt disease in wildlife populations are complex, expensive, controversial and often ineffective. Thus, strong biosecurity and prevention practices are needed to avoid pathogen introduction in the first place. Dealing with this threat requires interdisciplinary expertise and inter-agency coordination. In Argentina, introduced animal diseases are listed as one of the main conservation threats for nearly every threatened native mammal. Yet, current knowledge on whether or how invasive species' pathogens impact and alter ecosystems in the country is scarce. In recent years, disease surveillance in native and introduced wildlife has increased in Argentina. Several targeted and opportunistic investigations are being conducted via an *ad hoc* network reporting to the national veterinary service, thus providing reasonable species and geographic coverage. As more research enables a diagnosis of the present situation and assessment of future risks, systematic monitoring (*e.g.*, via sentinel or easily accessible species) is recommended for early warning and rapid response. Meanwhile, best practices, such as avoiding contact between introduced (wild and/or domestic) and native species, enhanced surveillance, and strict biosecurity, particularly in wildlife strongholds, can buffer against accidental pathogen invasions. With increased connectivity and globalization, introduced pathogens are becoming more prevalent and widespread worldwide. Like all countries, Argentina must strive for healthy wildlife and functional ecosystems, free of introduced invasive species and pathogens. Therefore, readiness for early detection and response must be of the highest priority.

Resumen. Las especies introducidas, y los patógenos asociados a esas especies, son reconocidos factores de pérdida de biodiversidad y cambios ecosistémicos. A nivel mundial, muchos patógenos invasores han causado epidemias severas y extinciones de especies. Según la literatura global, las enfermedades no son solo una consecuencia de las invasiones biológicas. Los patógenos pueden también ser actores clave para que la especie invasora se establezca exitosamente. Hay dos mecanismos comunes de facilitación de la invasión. Uno es el *spillover*, en que la especie invasora trae consigo patógenos nóveles para los cuales las especies locales no tienen inmunidad. El otro es el *spillback*, en que las especies invasoras se convierten en hospederos de patógenos nativos, y así impactan sobre

especies de la fauna local. Incluso, si un patógeno invasor encuentra hospederos locales adecuados, puede establecerse y persistir en el nuevo ambiente, aun cuando su hospedero invasor original no lo logre. Numerosos patógenos de mamíferos introducidos han causado graves trastornos ecosistémicos, modificando la ecología de enfermedades existentes o removiendo especies clave de cadenas tróficas y hábitats sensibles. Es más, muchos han causado importantes pérdidas de servicios ecosistémicos que se traducen en graves pérdidas económicas y de otros beneficios sociales. Cuando los patógenos introducidos logran establecerse en ciclos que incluyen especies domésticas y silvestres, son casi imposibles de eliminar. Peor aún, estos ciclos suelen incluir componentes ambientales que sostienen e incrementan las reinfecciones, limitando todavía más las opciones de control o erradicación. Esto es grave porque las intervenciones en poblaciones silvestres son de por sí complejas, costosas, controversiales y a menudo ineficaces. La clave se centra entonces en la prevención. Y esta depende, en gran medida, de una sólida bioseguridad y una adecuada capacidad de detectar tempranamente las invasiones. Lidiar con esta amenaza requiere colaboración interdisciplinaria y coordinación entre instituciones gubernamentales y de la sociedad civil.

Aunque la Argentina sostiene un número preocupante de especies introducidas invasoras, que se expanden por casi toda su geografía, casi no existen estudios sobre el rol de los mamíferos introducidos como reservorios de patógenos. Es más, considerando que las enfermedades introducidas se señalan como una de las principales amenazas para prácticamente todos los mamíferos amenazados del país, es preocupante este enorme vacío de información. Los estudios existentes muestran que en áreas de solapamiento entre especies introducidas y nativas los problemas de salud pueden ser significativos, principalmente cuando se asocian a cambios ambientales bruscos (antrópicos o naturales) que generan fuerte estrés sobre las poblaciones silvestres. Afortunadamente, en los últimos años se han ido incrementando las investigaciones en salud de fauna silvestre (nativa e introducida) en el país. Además, y siguiendo modelos de otros países, numerosos investigadores contribuyen a la vigilancia de enfermedades por medio de una red de apoyo al servicio oficial de sanidad animal (SENASA). Muchos de estos estudios se basan en muestras colectadas a partir de especies cosechadas para consumo (p.ej. ciervo colorado, *Cervus elaphus*), o programas de control de especies introducidas y cacería deportiva (p.ej. jabalí, *Sus scrofa*), lo cual permite una mayor cobertura de especies y áreas, con costos menores.

Las especies invasoras pueden cambiar la dinámica de las enfermedades en los ecosistemas que colonizan de diversas maneras. Estos cambios pueden tener efectos profundos y altamente costosos para la fauna nativa, pero también para la producción animal (y la seguridad alimentaria) y la salud de las personas. Hasta donde se sabe, la Argentina se encuentra aún mayormente libre de las principales enfermedades problemáticas en especies no domésticas. Por ello, urge generar más conocimiento que permita un mejor diagnóstico de la situación actual y una evaluación informada de futuros riesgos. Se requiere, además, y tal como ocurre para las especies productivas, poner en práctica un monitoreo sistemático (p.ej. usando especies indicadoras o centinela) para la detección y respuesta temprana a posibles invasiones. Al mismo tiempo, es recomendable la implementación de buenas prácticas básicas, como evitar el contacto entre especies exóticas (silvestres y/o domésticas) y especies nativas, particularmente en áreas protegidas (p.ej. restringiendo o eliminando la presencia de ganado y mascotas). También se sugiere mejorar la capacidad para la vigilancia de enfermedades en especies nativas y la aplicación de medidas básicas de bioseguridad, como por ejemplo el uso de «lava pies» en el ingreso de senderos turísticos, para evitar la introducción accidental de patógenos exóticos.

Con la creciente conectividad y globalización, la contaminación por patógenos se está haciendo más prevalente, dispersa y común a nivel mundial. Al igual que otros países, la Argentina debe aspirar a que su fauna esté saludable y sus ecosistemas funcionales, libres de especies y patógenos invasores. Las lecciones aprendidas de otras regiones demuestran que estar adecuadamente preparados y alertas tiene un incalculable valor para proteger a nuestras especies y paisajes nativos, debiendo ser, por ello, de nuestra más alta prioridad.

Introduced pathogen-species association

Biological invasions are well-recognized drivers of biodiversity loss and ecosystem change (CBD, 2007). Similarly impactful, yet notably less acknowledged, are the pathogens often brought with introduced species (Daszak *et al.*, 2000). In this chapter, relevant aspects of the introduced pathogen-species association are described, and global literature is used to exemplify known impacts of introduced pathogens on native species and to summarize information on potentially harmful pathogens linked to introduced mammals in Argentina. Finally, this evidence is used to identify opportunities to enhance local conservation efforts by reducing risk and improving disease management practices.

Pathogens are an intrinsic part of biological diversity and ecological complexity in natural, healthy ecosystems. Furthermore, they are critical natural selection factors by which only the fittest individuals survive (Altizer *et al.*, 2003; Vander Wal *et al.*; 2014). In natural systems, complex host-pathogen co-evolution processes allow for a delicate balance, which keeps infections from necessarily leading to disease. However, when novel agents are introduced, disease-defense mechanisms may be quickly overcome (Roelke-Parker *et al.*, 1996; Hochachka and Dhondt, 2000; Altizer *et al.*, 2003). Introduced pathogens are more likely to produce severe wildlife epidemics than pathogens that locally evolved with their host (Dobson and Foufopoulos, 2001). Yellow fever, introduced to the Americas in association with the commercial practice of trading enslaved Africans, illustrates this fact. Lack of evolution-acquired immunity in New World primates (particularly in the genus *Alouatta*) leads to recurrent and devastating mortalities that have placed some species on the verge of extinction (Holzmann *et al.*, 2010; Moreno *et al.*, 2015; Kowalewski and Oklander, 2017). At the same time, even at sub-lethal levels, diseases can influence reproduction, survival, fitness, and abundance of wildlife populations, and pose a particularly significant risk for threatened and endangered species (Smith *et al.*, 2009; Pedersen *et al.*, 2017).

The close link between introduced invasive species and pathogens is revealed in the IUCN's list of the world's 100 worst introduced invasive species (Lowe *et al.*, 2000). Several of the fourteen mammal species on that list are notable for their roles in transmission of infectious diseases to native wildlife, livestock, or humans (*e.g.*, wild boar, *Sus scrofa*; red deer, *Cervus elaphus*; red squirrel, *Sciurus vulgaris*; brushtail possum, *Trichosurus vulpecula*; black rat, *Rattus rattus*; Lowe *et al.*, 2000; Dunn and Hatcher, 2015). Moreover, some have been responsible for species extinctions and dramatic ecosystem changes. Several examples worth highlighting include the extinction of the endemic Christmas Island rat (*Rattus macleari*) at the turn of the 20th century, due to the introduction of black rats hosting a pathogenic trypanosome carried by their fleas (Wyatt *et al.*, 2008). Also noteworthy is the morbillivirus, which caused rinderpest and was introduced to Africa from India with cattle (*Bos primigenius taurus*) to feed invading Italian troops in 1887. Rapidly spilling over to wild ungulates, in two years it exterminated 95% of buffalo (*Syncerus caffer*) and wildebeest (*Connochaetes* spp.), in addition to causing incalculable loss of farmed cattle and famine in humans, as it spread across the entire continent (Mack, 1970). The effects of rinderpest were so severe that it modified the distribution of several native ruminants and shattered human pastoral civilizations (Mariner *et al.*, 2012).

Disease is not only a consequence of biological invasion; pathogens can be key players in the success of the invasion itself. That is, introduced invasive species' pathogen loads are part of the mechanisms that enable their successful establishment in a new area (Vilcinskas, 2015). A common mechanism described in the ecology of biological invasions is that of the "novel weapon," also termed "spillover" of a co-invasive pathogen or pathogen pollution (Daszak *et al.*, 2000; Morand *et al.*, 2015; Vilcinskas, 2015). That is, the invasive species benefits from carrying pathogens that are harmless to the invasive host, but lethal to native species. For example, in the United Kingdom (UK), native red squirrels (*Sciurus vulgaris*) are being rapidly replaced by the invasive North American gray squirrel (*S. carolinensis*) because the latter carries a poxvirus which causes fatal disease only in the native species (Tompkins *et al.*, 2003). Red squirrel declines and replacement are up to 25 times higher in areas where squirrel poxvirus is present in gray squirrel populations (Rushton *et al.*, 2006). Similarly, introduced species can also "spillback" pathogens when they become part of an existing local pathogen cycle, amplifying its impact on the native host (Kelly *et al.*, 2009; Dunn *et al.*, 2012). While several examples of this mechanism exist for invasive plants, fish and marine invertebrates, there appears to be limited evidence for mammals (Kelly *et al.*, 2009).

Upon introduction, such pathogens rely on many host-dependent parameters, including rates of encounter, transmission, co-infection, mortality, and recovery, for their establishment and spread (Telfer and Brown, 2012). Worryingly, however, if native species prove to be competent hosts, some pathogens may persist even where the introduced host species fails. Such is the case of West Nile virus (WNV), which arrived in the United States of America (USA) in 1999 with an unknown carrier. Regardless of its original host, the virus quickly became established in local passerine birds and mosquitoes and within four years had reached nearly every corner of the USA and southern Canada (Sejvar, 2003). Despite the dominant role that avian species play in WNV transmission (McLean *et al.*, 2001), dozens of mammal species have since been exposed to the virus in North America (Root, 2013). Yet only a few, such as the fox squirrel (*Sciurus niger*), become viremic enough to be competent hosts (Root, 2013). Also, wild boar have been proposed as sentinels for WNV, since they are commonly exposed, are regularly available for sampling from control operations, and are widespread, particularly in rural areas where practicality of surveillance via report of dead birds is limited (Gibbs *et al.*, 2006).

An invasive species may also act as a facilitator for the subsequent invasion of an introduced pathogen. In Svalbard, Norway, the establishment of the tapeworm (*Echinococcus multilocularis*), which causes a rare, but potentially lethal human disease, known as alveolar echinococcosis, was enabled by the preceding introduction of the sibling vole (*Microtus* *levis*) (Henttonen *et al.*, 2001). This small mammal filled the previously inexistent role of intermediate host in the parasite cycle, which has the Arctic fox (*Vulpes lagopus*) or domestic dog (*Canis lupus familiaris*) as definitive hosts (Fuglei *et al.*, 2008).

Impacts of introduced pathogens on native species

Many introduced mammal pathogens have led to major ecosystem disruptions, modifying the ecology of an existing disease, or removing key species from food chains and habitats. For example, it is thought that the profound ecological and social changes following rinderpest's devastating path led to a massive epidemic that caused over 250,000 human deaths from African sleeping sickness in Uganda alone (Fèvre *et al.*, 2004). When tsetse flies (*Glossina* spp.), which are vectors of the deadly trypanosome parasite that causes sleeping sickness, were left without their primary food source (*i.e.*, cattle and wild ruminants), they turned to humans (Mariner *et al.*, 2012). This was facilitated by the colonization of tsetse flies as depopulated pasturelands reverted to shrubs and by large-scale restocking with trypanosome-infected livestock from remote locations (Fèvre *et al.*, 2004). Also of note, the arrival of *Rattus* spp., one of the most widespread introduced mammals, to the USA onboard ships in the late 1890s drove significant and lasting changes to prairie ecosystems. With the rats came fleas infected with the bubonic plague bacterium (*Yersinia pestis*) (Kugeler *et al.*, 2015). Plague, possibly the deadliest disease of all times, is considered to have shaped modern civilization through three massive pandemics (*i.e.*, Europe lost 60% of its population in the 14th century), according to the Center for Disease Control and Prevention from USA. Fortunately, plague's human death toll in the USA was halted by the timely discovery that it was treatable with antibiotics in the 1920s (Kugeler *et al.*, 2015). By then, however, plague had already reached the prairie dog (*Cynomis* spp.), its most emblematic native mammal victim. Completely vulnerable to plague, prairie dogs suffered about 98% reductions in population size and range during the 20th century, worsened by persecution as agriculture pests. Then, in a typical negative cascading effect, black-footed ferrets (*Mustela nigripes*) became the next casualty, both directly from plague infection and indirectly through mortality of prairie dogs, which is their main prey-base. The effect was devastating, and black-footed ferrets were declared extinct in the wild in 1987. They are currently listed as endangered and are supported by massive reintroduction efforts from captive populations (IUCN, 2012). The plague-prairie dog-ferret example illustrates the cascading, ecosystem-level impacts of an introduced pathogen removing a keystone species (*i.e.*, those with a much larger role in the structure and function of the ecosystem than would be expected from their abundance) (Walsh *et al.*, 2016). Moreover, loss of many grassland-dependent ecosystem services has recently been linked to prairie dog absence (Martínez-Estévez *et al.*, 2013). Invasive species can also directly disrupt ecosystem services linked to health, such as disease regulation. Wild boar in Hawaii are known to create breeding habitat for introduced mosquitoes by hollowing out ferns they feed upon, thus favoring vector-borne diseases, such as avian malaria and dengue fever that impact both wildlife and humans (Pejchar and Mooney, 2009). Likewise, the death of over seven million bats in the USA since 2006, due to the introduced fungal disease white-nose syndrome (WNS) (presumably introduced by scientists studying caves), entails massive losses in pest control services. It is estimated that one million little brown bats (*Myotis lucifugus*), the species most affected by WNS, can consume up to 1,320 metric tons of insects a night (when multiplied by seven the result is stunning). In financial terms, the value of this bat-dependent pest suppression plus concomitant reduction in pesticide use has been estimated to reach $53 billion US dollars per year (Boyles *et al.*, 2011; Kunz *et al.*, 2011).

Diseases associated with livestock are worth highlighting for two interrelated reasons. First, food animals are both vectors and victims of introduced pathogens, many of which are shared with native and introduced wildlife (*e.g.*, brucellosis, tuberculosis, influenza; Miller *et al.*, 2013). Second, in productive systems, perceived or actually failing yields from disease often lead to heightened conflict at the wildlife-livestock-human interface. Retaliatory killing of wild animals and, in the best-case scenario, controlled culling operations, are often the unfortunate result of disease-mediated livestock wildlife interactions (Miller *et al.*, 2013; Gortázar *et al.*, 2015). Moreover, once bidirectional transmission of pathogens between domestic and wild species is established, they become almost impossible to eliminate. Even well-designed or well-intended disease management efforts have suffered from the inherent complications of such shared cycles, particularly since interventions in wildlife populations are complex, expensive, controversial, and often ineffective (Gortázar *et al.*, 2015; Woodroffe *et al.*, 2016). Furthermore, these wildlife-livestock cycles often include a persistent environmental component by which re-infection continuously occurs. The badger (*Meles meles*)-cattle-tuberculosis (TB) triangle in the UK is a contemporary example of such a situation. Recent studies suggest that infectivity of pastures is so high and prolonged, that even with reciprocal cattle-to-cattle transmission control, badger culls to reduce wildlife-to-cattle transmission repeatedly fail to lessen disease burdens (Woodroffe *et al.*, 2016). Furthermore, localized reactive badger culling triggers both badger movement and changes in TB infection prevalence, increasing risk of new infections in cattle farms by 27% within a 1 to 5 km radius (Bielby *et al.*, 2016). Thus, contrary to expectations, these unfruitful attempts nurture generalized dissatisfaction, leading to intensified frustration in the farming sector and reactive distrust and antagonism in the observing public (*The Guardian*, 2016). A somewhat less contentious scenario exists in New Zealand, where TB is sustained by a suite of hosts, yet uniquely centered on an introduced marsupial, the brushtail possum (*Trichosurus vulpecula*) (Warburton and Livingstone, 2015). Since the 1950s, before possums were acknowledged as a wildlife vector of TB, they had already been recognized as a significant conservation pest and were under targeted control (Warburton and Livingstone, 2015). Despite its aggressive culling approach and the many impacted wildlife species (target and non-target casualties), the "TB-free New Zealand" campaign has been highly effective, is socially accepted, and shows promise for eradication of the disease in the next few decades (Warburton and Livingstone, 2015). Notwithstanding this success, control of livestock-threatening diseases can be even more challenging if the introduced pathogen accompanies a widespread, well-established, and culturally-valued invasive species, such as the wild boar (Keuling *et al.*, 2016; Ballari *et al.*, this volume). A current open-ended example is the ongoing and seemingly unstoppable expansion of African swine fever (ASF) across Europe and Asia (Gaudreault *et al.*, 2020). ASF is highly contagious and causes death from hemorrhagic disease in domestic and feral pigs, with mortality rates up to 100% (Gavier-Widén *et al.*, 2015). Originating from a food-borne geographic jump (food scraps from a ship from southern Africa were fed to pigs in the country of Georgia) in early 2007, pig-boar contact kick-started the ongoing epidemic (Sánchez-Vizcaino *et al.*, 2013). ASF quickly spread to neighboring countries, reached the European Union (EU) in 2104 and had affected at least eight EU countries by 2018 (Chenais *et al.*, 2018). In August 2018, the virus was also found in China and within the next year and a half had spread to 11 additional countries in Asia (Mighell and Ward, 2021). By 2021, the Asian outbreak had resulted in the death or culling of more than five million pigs (over 10 percent of the total pig population in China, Mongolia and Vietnam) and huge economic and food security consequences (Gaudreault *et al.*, 2020; You *et al.*, 2021). Of relevance for this chapter are the different pathways by which the disease is expanding. While in Asia it is mostly linked to pig farms and products (the latter oftentimes illegally transported by humans), in Europe the epidemic spread is closely linked to wild boar (Bosch *et al.*, 2017; Chenais *et al.*, 2018). Recent risk analyses for Europe suggest that wild boar habitat (contaminated by infected carcasses) and wild boar presence are the most important factors enabling the geographic spread of the disease. Concurrently, contact between wild boar and domestic pigs allows for repeated introductions of the virus (Bosch *et al.*, 2017; Chenais *et al.*, 2018). Under very different conditions, it took over 30 years to eradicate ASF from a previous introduction to Europe in the 1960s (Bosch *et al.*, 2017). In the current scenario, it is unlikely that such a success will occur anytime soon. The only effective containment and eradication of ASF thus far was achieved by the Czech Republic through a combination of quick reaction to the initial (small) outbreak, intensive surveillance and proper disposal of dead wild boar, and strict biosecurity to avoid transmission to domestic pig (State Veterinary Administration, Czech Republic, 2019). In the absence of a vaccine, early detection of infected wild boar remains the most relevant measure to stop ASF spread, in addition to quick removal of carcasses and strict control of pig and by product (including feed) movement (Guinat *et al.*, 2017; Cwynar *et al.*, 2019). In July 2021, ASF was detected in the Americas, specifically in Haiti and Dominican Republic, raising alarms for the region and activating a strong response to control the spread of the disease (World Organization for Animal Health, 2021). As will be discussed later in this chapter, expertise and multi-sectorial collaborations for surveillance are essential for timely detection and prevention of diseases that affect both wild and domestic animals.

Diseases of free-roaming pets or their feral counterparts, namely cats (*Felis sylvestris catus*) and dogs (*Canis lupus familiaris*), may reach native wild populations by mechanisms as straightforward as incursions of unvaccinated animals into wildlife heavens, or by intricate ecosystem changes, facilitating high environmental pathogen loads and consequent wildlife exposure. Canine distemper virus (CDV) has caused massive die-offs in endangered African wild dogs (*Lycaon pictus*) and no-longer-abundant African lions (*Panthera leo*) in the Serengeti ecosystem in Tanzania (Roelke-Parker *et al.*, 1996; Goller *et al.*, 2010). The Ethiopian wolf (*Canis simensis*), the rarest canid species in the world and the most threatened carnivore in Africa, is almost extinct due to the combined effects of rabies and CDV infections (Gordon *et al.*, 2015). In all the above cases, viral strains were backtracked to dog populations and were associated with poor healthcare and lack of vaccination. Irresponsible pet ownership is an all-too-common condition in human dwellings adjoining wildlife reserves (often intensified by poverty), which not only implies health risks, but also leads to wildlife losses from predation. Locally in Argentina, Ferreyra *et al.* (2009) found CDV—which was 97% identical to non-vaccine dog viral strains—killing crab-eating foxes (*Cerdocyon thous*) in the Parque Nacional El Palmar. The exact origin of the fox-killer virus remains unconfirmed, but at the time of the outbreak hunters with dogs had been allowed into the park as part of an introduced invasive species control program for wild boar and axis deer (*Axis axis*). Incursions of stray dogs from neighboring towns into the park might have been an alternative or additional entry options for the disease. In any case, while control of dog movements is known to be nearly impossible in vast areas with permeable boundaries, red flags should be raised whenever domestic species are purposely introduced to or placed in close proximity with wildlife in protected areas of any kind.

A contrasting, convoluted introduced-to-native wildlife pathogen pathway is exemplified by the feline protozoan *Toxoplasma gondii* infections in endangered southern sea otters (*Enhydra lutris nereis*) in California, USA. In a complex setting of intertwined land-use changes, this terrestrial cat-originated parasite ended up in a main sea otter food item (marine turban snails, *Tegula* spp.), exposing the highly specialized and voracious otters to life-threatening *T. gondii* loads (Conrad *et al.*, 2005; Mazzillo *et al.*, 2013). Investigations by several authors revealed a situation in which human population growth and urban development of coastal areas lead to unfiltered runoff and sewage heavily contaminated with *T. gondii* ending up in the sea. VanWormer *et al.* (2016) estimated a 44% increase in oocyst (the infective form of the parasite) delivery from land to sea between 1990 and 2010. The loss of estuarine wetlands is thought to have further contributed to the problem by eliminating natural filtering mechanisms. Shapiro *et al.* (2010) projected that erosion of 36% of vegetated coastal wetlands may increase the flux of oocysts by more than two orders of magnitude and that total loss of wetlands would result in a number three times higher. Sadly, a similar scenario seems to be unfolding in Hawaii, where at least 13 endangered Hawaiian monk seals (*Neomonachus schauinslandi*) have died from toxoplasmosis since 2001 (National Oceanic and Atmospheric Administration, 2022). *T. gondii* is only shed by felids. Thus, infection reduction can only be achieved by controlling feline sources of the parasite. A decade-old estimate reports a daunting 60 to 100 million feral cats in the USA (Loyd and DeVore, 2010).

From food reserves for shipwrecked sailors to sprouting businesses based on fur-bearing or agriculture animals, over the course of history humans have managed to re-arrange the natural distribution of animal species on every corner of the planet (McNeely, 2001). Recognizing the previously inadvertent impacts from such actions, current trade restrictions and biosecurity protocols are modern tools used by governments to prevent new invasions. International bodies, such as the World Organization for Animal Health (WOAH), set standards for the health of traded agriculture animals to which most countries adhere (WOAH, 2022). Yet no method has succeeded in yielding zero risk (Early *et al.*, 2016), and food mammals can still become invasive. For example, in Brazil the water buffalo (*Bubalus bubalis*) is thriving in feral populations and may be involved in the transmission of zoonotic and livestock-relevant pathogens (Barbosa da Silva *et al.*, 2014; Minharro *et al.*, 2016). Of additional concern is the shift in the drivers for non-agriculture animal movement worldwide. Today, demand for vertebrate wildlife species in the pet trade is exponentially increasing as more countries achieve higher wealth and living standards (Ding *et al.*, 2008). The current scale of the legal and illegal global wildlife trade is in the billions of animals and tens of billions of US dollars annually (Smith *et al.*, 2009; Rosen and Smith, 2010; Scheffers *et al.*, 2019). Beyond its impact on species extinctions and abundance, there is an underlying, but poorly recognized, risk of the pet trade becoming a source of introduced invasive species and diseases (Rosen and Smith, 2010; García-Diaz *et al.*, 2016; Lockwood *et al.*, 2019). Lockwood *et al.* (2019) provide several examples of pet trade-originated invasive reptiles, amphibians, birds and fish in North America and the EU. Moreover, Hulme *et al.* (2008) determined that pet escapes were the source of establishment for several introduced taxa in the EU, including mammals. Likewise, Ikeda *et al.* (2004) blame irresponsible ownership and release of pet raccoons (*Procyon lotor*) for their naturalization in Japan. The recent finding of raccoon roundworm (*Baylisascaris procyonis*), which causes serious disease in humans with a >40% case fatality rate (Sapp *et al.*, 2018), adds to the danger of this popular pet. The gravity of wildlife trade lies in the inadequacy of current regulations to detect the diversity of wildlife imported and assess the risk they pose as potential invasive species or hosts of harmful pathogens. In an analysis of the USA imports from 2000–2006, the majority of shipment records did not contain the appropriate level of taxonomic information, nor did they undergo mandatory testing for pathogens before or after shipment (Smith *et al.*, 2009).

A recent study showed that most countries have limited capacity to predict, detect, and act against invasions (Early *et al.*, 2016). This is particularly worrying in the context of increased trade and commerce, since successful prevention (via rapid eradication) hugely depends on early detection as well as rapid response to newly discovered invasions (Early *et al.*, 2016). It is also worth highlighting that once established, eradication of pathogens is just as complex, or likely much more, than that of any other introduced invasive species. Proof of this fact is that despite huge expense, technological progress, high social relevance, and concerted effort, only two diseases have been eradicated worldwide since the advent of modern medicine, namely smallpox in humans (in 1979; World Health Organization) and rinderpest in animals (in 2011; WOAH).

As shown in the global literature, the pervasive impacts of invasive pathogens (alone or in association with their introduced host) span the full spectrum from native to domestic species, natural to agriculture ecosystems, food security to human health and wellbeing. Importantly also, introduced pathogens place a substantial financial burden on the global economy, costing many hundreds of billions of US dollars each year (Pimentel *et al.*, 2001).

Links between potentially harmful pathogens and introduced mammals in Argentina

Despite bewildering numbers, broad geographic presence, and recognition of their likely impact on native wildlife health, very few studies have assessed the role of introduced mammals as disease hosts in Argentina. This is particularly notable for non-reportable diseases (*i.e.*, those not listed by the WOAH as mandatory due to their lower significance for international trade). The main exception is regular testing for a few pathogens of public health concern in species consumed by humans (*e.g.*, trichinellosis in wild boar, brucellosis in European hare, *Lepus europaeus*).

A non-comprehensive list of potential health hazards posed by introduced mammals and feral/free-roaming pets and livestock in Argentina is presented in Table 1. A focus was placed on pathogens linked to species previously identified as probable health risks (see Valenzuela *et al.*, 2014; Ballari *et al.*, 2016), as well as those known or suspected to be of concern for conservation, agriculture, or public health in other parts of the world. While not exhaustive, this table allows for a quick glimpse of latent risks based on reports from other countries or regions and locally, when available. It also permits a visualization of existing knowledge gaps and data restrictions, which abound. Diseases of non-feral livestock and domestic animals transmissible to wild mammals were purposely not included, as they are too vast to discuss in this chapter and can be found in specialized literature.

It is worth mentioning that livestock diseases are broadly believed to have had a significant role in the decline of several native ungulates. Such is the case for the Pampas deer (*Ozotoceros bezoarticus*) and the Patagonian huemul (*Hippocamelus bisulcus*), presumably affected by foot-and-mouth disease (FMD) and other cattle and sheep illnesses (summarized in Pastore and Vila, 2001; Uhart *et al.*, 2003; Uhart and Chang Reissig, 2006). While many historical reports were based on empirical observation, and diagnoses were not always confirmed, nowadays some of these risks are likely mitigated given active national plans for control of reportable diseases, such as FMD, brucellosis and tuberculosis in livestock (SENASA, 2017). Notwithstanding, forced sympatry with livestock in most areas where these endangered cervids remain is a matter of concern and should be proactively addressed to avoid pathogen spillover. Regardless of scale, livestock rearing and/or grazing concessions have been repeatedly acknowledged as a problem requiring immediate attention in national parks in Argentina (Martinez, 2008; Chang Reissig *et al.*, 2010). An urgent and timely call to action stems from several viral, bacterial, and parasitic livestock-origin diseases currently affecting the huemul in Chile. Vila *et al.* (2019) reported on severely incapacitating foot lesions caused by a parapoxvirus closely related to bovine papular stomatitis virus (BPSV) and pseudocowpoxvirus (PCPV) in Parque Nacional Bernardo O'Higgins. Likewise, huemul affected by ovine caseous lymphadenopathy (LAC – *Corynebacterium pseudotuberculosis*) require frequent medical interventions and suffer occasional mortality at Reserva Nacional Cerro Castillo (Morales *et al.*, 2017). Recently, a huemul killed by LAC in this protected area was found with lung cysts from a livestock strain of *Echinococcus granulosus*, a parasite spread by carnivores and responsible for hydatid disease in humans (Hernández *et al.*, 2019). But not only cervids are affected by livestock diseases. Between 2014 and 2019, sympatric populations of vicuña (*Vicugna vicugna*) and guanaco (*Lama guanicoe*) from Parque Nacional San Guillermo in Argentina were decimated by an epidemic of sarcoptic mange (Ferreyra *et al.*, 2022). It is hypothesized that this debilitating skin disease was introduced to the area by infected llamas (*Lama glama*) given to farmers near the national park in the context of a governmental livestock incentive program. Mange nearly extirpated the native camelids from the protected area, which had profound cascading ecological impacts,

Table 1. **(A)** Mammal species introduced to Argentina (* refers to species native to the mainland that have been introduced to Tierra del Fuego); **(B)** Pathogen transmission to environment and/or native species; **(C)** Impact area: relevant for wildlife (conservation concern); relevant for agriculture; relevant for public health. Impacts are either potential, known, unknown, or considered not relevant; **(D)** Reports of pathogen in alien species host in America and/or Argentina; **(E)** Reports of pathogen in native species in Argentina (disease, infection or exposure). Pathogens are either reported (reference) or not reported.

Introduced species (A)	Associated pathogen	Relevance (B)	Impact area (C)			Reports of the pathogen/s (D)		
			Conservation	Agriculture	Public health	Americas	Argentina	Native species (E)
American mink (*Neogale vison*)	*Leptospira* spp.	Potential source of waterborne pathogens	Unknown	Known	Known	Reported Chile[1]	Reported serology[2]	Not reported
	Canine distemper virus	Potential source for native mustelids and carnivores	Known	Not relevant	Not relevant	Reported Chile[3]	Not reported	Not reported
	Aleutian disease virus	Potential source for native mustelids and carnivores	Potential	Not relevant	Potential	Reported Canada[4]	Reported serology[2]	Not reported
	Toxoplasma gondii	May infect multiple hosts	Known	Known	Known	Reported Chile[5,6]	Reported serology[2]	Not reported
	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Potential	Known	Known	Not reported	Reported serology[2]	Not reported
	Brucella abortus	May infect multiple hosts; potential transmission to predators or native herbivores	Known	Known	Known	Not reported	Reported serology[2]	Not reported
	Neospora caninum	Potential source for native carnivores	Known	Known	Not relevant	Reported USA[7]	Reported[2]	Not reported
	SARS-CoV-2	May infect multiple hosts; transmission to and from humans	Potential	Known	Known	Reported USA[8]	Not reported	Not reported
North American beaver (*Castor canadensis*)	*Giardia* spp., *Cryptosporidium* spp.	Potential source of waterborne pathogens	Unknown	Known[77]	Known	Reported USA[9,10]	Not reported	Not reported
Chital (*Axis axis*)	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Potential	Known	Known	Reported USA[11,12]	Reported[13]	Not reported
	Leptospira spp.	Potential source of waterborne pathogens	Unknown	Known	Known	Reported USA serology[14]	Reported serology[15,16]	Reported serology pampas deer[17], marsh deer[18,19]

Table 1. (Continued).

Introduced species (A)	Associated pathogen	Relevance (B)	Impact area (C)			Reports of the pathogen/s (D)		
			Conservation	**Agriculture**	**Public health**	**Americas**	**Argentina**	**Native species (E)**
Fallow deer (*Dama dama*)	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Potential	Known	Known	Reported USA[11,12]	Not reported	Not reported
Red deer (*Cervus elaphus*)	Paratuberculosis (*Mycobacterium avium* ssp. *paratuberculosis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Known	Known	Potential	Reported USA[20,21]	Reported[22]	Not reported
	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Potential[23]	Known	Known	Reported USA & Canada[12]	Not reported	Not reported
	Leptospira spp.	Potential source of waterborne pathogens	Known	Known	Known	Reported USA serology[78]	Reported serology[24]	Not reported
Wild boar (*Sus scrofa*)	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Known[23]	Known	Known	Not reported	Reported[25]	Not reported
	Herpesvirus (Pesudorabies or Aujezky)	Potential source for wild carnivores	Known[23]	Known	Not relevant	Reported USA[26,27]	Reported serology[28,29,30]	Not reported
	Leptospira borgpetersenii	Potential source of waterborne pathogens	Unknown	Known	Known	Reported Brazil[31]	Reported[32]	Reported white-eared opossum[31]
	Leptospira spp.	Potential source of waterborne pathogens	Unknown	Known	Known	Reported Brazil[33]	Reported serology[29,34]	Not reported
	Trichinella spiralis	Potential source for carnivores and rodents	Unknown	Known	Known	Reported Chile[35,36]	Reported[37,38]	Reported puma, South American sea lion, opossum, armadillo[39,40,38,41]
	Toxoplasma gondii	May infect multiple hosts	Known	Known	Known	Reported USA[42]; reported Brazil[43]	Reported serology[44]	Not reported
	Brucella spp.	May infect multiple hosts	Known	Known	Known	Reported USA[45,46]	Not reported	Not reported
	Brucella suis	May infect multiple hosts	Known	Known	Known	Reported USA[47]	Not reported	Not reported

Table 1. (Continued).

Introduced species (A)	Associated pathogen	Relevance (B)	Impact area (C)			Reports of the pathogen/s (D)		
			Conservation	Agriculture	Public health	Americas	Argentina	Native species (E)
European hare (*Lepus europaeus*)	*Brucella* spp.	Potential source for other species	Unknown	Known	Known	Not reported	Reported[48,49]	Not reported
	Paratuberculosis (*Mycobacterium avium* ssp. *paratuberculosis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Known	Known	Potential	Reported Chile[50]	Reported serology[48]	Reported serology mara[48]
	Neospora caninum	Potential source for native carnivores	Known	Known	Not relevant	Not reported	Reported serology[51]	Not reported
Mice and rats (*Mus* spp.; *Rattus* spp.)	*Yersinia pestis*	Source for wildlife; wild felids and other carnivores are highly susceptible	Known	Known camel, llama, goat, sheep[52]	Known	Reported USA[52]	Not reported	Not reported
	Trichinella spiralis	Potential source for carnivores and rodents	Unknown	Known	Known	Reported[53]	Reported rat[39]	Reported puma, South American sea lion, opossum, armadillo[39,40,38,41]
Muskrat (*Ondatra zibethicus*)	*Giardia* spp. *Cryptosporidium* spp.	Potential source of waterborne pathogens	Unknown	Known	Known	Reported USA[54,55]	Not reported	Not reported
	Toxoplasma gondii	May infect multiple hosts	Known	Known	Known	Reported USA[42]	Not reported	Not reported
	Alveolar echinococcosis (*Echinoccocus multilocularis*)	Potential source for humans and wildlife	Unknown	Not relevant	Known Europe[56]	Not reported	Not reported	Not reported
Feral cattle (*Bos primigenius taurus*)	Bovine tuberculosis (*Mycobacterium bovis*)	May infect multiple hosts; potential transmission to predators or native herbivores	Known	Known	Known	Reported USA[57]	Not reported	Not reported
	Brucella abortus	May infect multiple hosts; potential transmission to predators or native herbivores	Known	Known	Known	Not reported	Not reported	Not reported

Table 1. (Continued).

Introduced species (A)	Associated pathogen	Relevance (B)	Impact area (C)			Reports of the pathogen/s (D)		
			Conservation	**Agriculture**	**Public health**	**Americas**	**Argentina**	**Native species (E)**
Feral cat (*Felis sylvestris catus*)	Feline leukemia virus	Potential source for native carnivores	Known Florida panther (*Puma concolor coryi*)[58]	Known	Not relevant	Reported USA and Canada[58,59]	Reported serology[60]	Not reported
	Toxoplasma gondii	May infect multiple hosts	Known	Known	Known	Reported USA[61]; reported serology Brazil[62]	Reported serology[60]	Reported Geoffroy's cat[60], armadillo[63]
Feral dog (*Canis lupus familiaris*)	Canine distemper virus	Potential source for native carnivores and mustelids	Known	Not relevant	Not relevant	Reported Chile free-roaming and rural dogs[64,65]	Not reported	Reported mortality crab-eating fox[66,67]
	Rabies	Potential source for humans, domestic dogs and wildlife	Potential	Not relevant	Known	Reported USA[68,69] and Brazil[70]	Not reported	Reported bats[71,72], red fox[73]
Pampa fox* (*Lycalopex gymnocercus*)	Hydatid disease (*Echinococcus granulosus*)	Potential source for humans and wildlife	Unknown	Known	Known	Reported Chile[74]	Reported[75]	Not reported
Large hairy armadillo* (*Chaetophractus villosus*)	Brucellosis (*Brucella suis*)	Potential source for other species	Unknown	Known	Known	Not reported	Not reported	Reported[76]

References: [1]Barros *et al.*, 2014; [2]Martino *et al.*, 2017; [3]Sepúlveda *et al.*, 2014; [4]Nituch *et al.*, 2012; [5]Sepúlveda *et al.*, 2011; [6]Barros *et al.*, 2018; [7]Almería 2013; [8]Shriner *et al.*, 2021; [9]Dunlap and Thies, 2002; [10]Fayer *et al.*, 2006; [11]Waters *et al.*, 2011; [12]Griffin and Mackintosh, 2000; [13]Mc Cormick *et al.*, 2018; [14]Pedersen *et al.*, 2018; [15]Petrakovsky *et al.*, 2015; [16]Tammone *et al.*, 2018; [17]Uhart *et al.*, 2003; [18]Brihuega *et al.*, 2008; [19]Orozco *et al.*, 2020; [20]Jessup and Williams, 1999; [21]Williams, 2001; [22]Paolicchi *et al.*, 2001; [23]Gortázar *et al.*, 2007; [24]Brihuega *et al.*, 2003; [25]Winter *et al.*, 2016; [26]Pedersen *et al.*, 2013; [27]Witmer *et al.*, 2003; [28]Serena *et al.*, 2015; [29]Abate *et al.*, 2015; [30]Carpinetti *et al.*, 2017; [31]Jorge *et al.*, 2012; [32]Brihuega *et al.*, 2017; [33]Vieira *et al.*, 2016; [34]Abate *et al.*, 2021; [35]Landaeta-Aqueveque *et al.*, 2015; [36]Hidalgo *et al.*, 2019; [37]Cohen *et al.*, 2010; [38]Lauge *et al.*, 2015; [39]Ribicich *et al.*, 2010; [40]Castaño Zubieta *et al.*, 2014; [41]Pasqualetti *et al.*, 2018; [42]Ahlers *et al.*, 2015; [43]Santos Brandão *et al.*, 2019; [44]Winter *et al.*, 2019; [45]Leiser *et al.*, 2013; [46]Pedersen *et al.*, 2017; [47]Pedersen *et al.*, 2014; [48]Marull *et al.*, 2004; [49]Fort *et al.*, 2012; [50]Salgado *et al.*, 2011; [51]Baldone *et al.*, 2009; [52]Abbott and Rocke, 2012; [53]Ortega-Pierres *et al.*, 2000; [54]Kirkpatrick and Benson, 1987; [55]Bitto and Aldras, 2009; [56]Umhang *et al.*, 2013; [57]Miller and Sweeney, 2013; [58]Cunningham *et al.*, 2008; [59]Gibson *et al.*, 2002; [60]Uhart *et al.*, 2012; [61]Conrad *et al.*, 2005; [62]Costa da Silva *et al.*, 2014; [63]Kin *et al.*, 2015; [64]Garde *et al.*, 2013; [65]Acosta-Jamett *et al.*, 2015; [66]Megid *et al.*, 2009; [67]Ferreyra *et al.*, 2009; [68]Bergman *et al.*, 2009; [69]Velasco-Villa *et al.*, 2018; [70]Carnieli *et al.*, 2013; [71]Piñero *et al.*, 2012; [72]Torres *et al.*, 2014; [73]Ibañez Molina and Chang Reissig, 2019; [74]Aguilera, 2001; [75]Zanini *et al.*, 2006; [76]Kin *et al.*, 2014; [77]Gow and Waldner, 2006; [78]Bender and Briggs Hall, 1996.

affecting native predators, scavengers and the entire ecosystem (Monk *et al.*, 2022). This outbreak reinforced the fact that conservation and agriculture sectors can no longer operate independently and that there are serious, potentially irreversible, consequences to pathogen introductions to naïve wildlife populations. In contrast, and outside protected areas, several private initiatives have promoted wildlife-friendly livestock husbandry practices and responsible pet ownership, including adequate health care and disease prevention, albeit with fluctuating continuity and implementation success (Miñarro *et al.*, 2007; Marino *et al.*, 2008). Revitalizing such programs should be encouraged and recommended.

The few health evaluations available for native species in Argentina, such as guanaco (*L. guanicoe*) (Karesh *et al.*, 1998; Marull *et al.*, 2012; Rago *et al.*, 2022), Pampas deer (Fondevila *et al.*, 1999; Uhart *et al.*, 2003), marsh deer (*Blastocerus dichotomus*) (Orozco *et al.*, 2020). Vizcacha (*Lagostomus maximus*) (Ferreyra *et al.*, 2007), mara (*Dolichotis patagonum*) (Marull *et al.*, 2004), Geoffroy's cat (*Leopardus geoffroyi*) (Uhart *et al.*, 2012), maned wolf (*Chrysocyon brachyurus*) (Orozco *et al.*, 2014a), capybara (*Hydrochoerus hydrochaeris*) (Corriale *et al.*, 2013), and wild carnivores and marsupials (Orozco *et al.*, 2014b) show varying degrees of exposure to common domestic animal pathogens, in nearly all cases not obviously linked to disease in the species studied. The major caveat for these surveys is, however, that they are mostly based on antibody detection, which does not allow for recognition of current infection and can produce unreliable results if tests are not validated for the target species or pathogen (Gardner *et al.*, 1996). Nevertheless, wildlife disease surveillance via serological assays is a valuable tool in the absence of other options and allows for assessing the health history of a population. This information is essential to evaluate change over time (especially in relation to human activities and disturbance) and is of particular relevance for conservation strategies requiring animal movements, such as reintroductions and translocations (Gilbert *et al.*, 2013).

There are comparatively more reports on parasites of introduced mammals, in some cases including sympatric native species like mara, huemul and Pampas deer (Marull *et al.*, 2004; Kleiman *et al.*, 2004; Caporossi *et al.*, 2008; Chang Reissig *et al.*, 2010; Flueck and Smith-Flueck, 2012; Flores and Brugni, 2013; Gozzi *et al.*, 2013; Chang Reissig *et al.*, 2016). Several of these studies suffer from limitations like incomplete identification of pathogens (*i.e.*, parasites only identified to genera level from egg taxonomy). This shortcoming restricts interpretation of their significance for the host species' health and/or their likelihood of being shared between native and introduced species. To counteract these problems, in recent years more studies are using molecular diagnostics, which allow deeper understanding of the pathogens found, including genetic proximity between host species, origin, transmission, and evolution (Hernández *et al.*, 2019; see also Lizarralde *et al.*, this volume). Notwithstanding these advances, the majority of the studies referenced above do not report morbidity or mortality associated with parasite findings. Conversely, pathological levels of sheep parasite infestations were found in dead guanaco during a severe mortality event in Chubut province (Beldoménico *et al.*, 2003). Similarly, high loads of likely domestic cat-derived parasites were observed in Geoffroy's cats which died following a prolonged drought and prey decline period in central Argentina (Beldoménico *et al.*, 2005). Likewise, extremely high livestock parasite burdens were documented in marsh deer during several die-offs in Iberá wetlands in Corrientes province and in the Lower Delta of the Paraná River in Buenos Aires province (Orozco *et al.*, 2013; Orozco *et al.*, 2020). These examples underpin that while interaction with introduced species' parasites might be tolerated by native fauna under normal circumstances, introduced pathogens can become significant morbidity and mortality factors when local wildlife is subject to other stressors and adverse environmental conditions.

Considering that introduced animal diseases are listed as one of the main conservation threats for pretty much every threatened native large mammal in Argentina (SAyDS and SAREM, 2019), it is both striking and worrying that so little is known about them. While accessing rare native species is inherently complex and often not an option, indirect assessments are oftentimes possible, yet seldom conducted. In this way, studying pathogens in red deer, wild boar and feral cattle, which are more readily accessible and regularly harvested, would allow for some understanding of risks for overlapping endangered native southern pudu (*Pudu puda*) and Patagonian huemul. Even opportunistic and passive (non-invasive) gathering of samples (*i.e.*, feces, saliva) would fill in current basic knowledge gaps, over time enabling better informed management and conservation decisions. For example, by examining feces from Pampas deer, sheep, cattle and axis deer in Samborombón Bay (Buenos Aires province), Caporossi *et al.* (2008) showed that five parasite genera were shared between the first three, and one by all four species. These data allowed for targeted interventions in livestock to minimize risk for the endangered native deer (Marull and Uhart, 2008), and provided baseline knowledge for future monitoring.

Fortunately, and following methods applied in other countries for wildlife disease surveillance, increasing numbers of investigations are being conducted on samples collected opportunistically via an *ad hoc* network of wildlife researchers reporting to the Argentine national veterinary service (SENASA, A. Marcos personal communication). Moreover, several ongoing studies rely on samples collected by recreational hunters and/or culling and harvest operations, further broadening the reach of disease surveillance in terms of species and geographic coverage (*e.g.*, Tammone *et al.*, 2018, 2021). Importantly as well, there are new examples of participatory surveillance for wildlife disease morbidity and mortality events, such as that implemented by Orozco *et al.* (2020) for marsh deer, which are based on a network of researchers, field partners (veterinarians, park rangers, and local community), and decision-makers.

Opportunities to enhance local conservation by improving disease management

Recently, it has been pointed out that policies to control diseases caused by introduced invasive species that affect wildlife, ecosystems and their services must be enhanced, as they are lagging in comparison to efforts directed towards those diseases directly impacting humans, livestock and plants (Roy *et al.*, 2016). These authors also emphasize that dealing with this threat requires interdisciplinary expertise and inter-agency coordination. Based on the information conveyed in the preceding sections of this chapter, it seems like this is both wise and timely advice.

As previously described, introduced invasive species can change the dynamics of disease in colonized ecosystems in several ways. Rare local pathogens can become more common, if they can be amplified by the new invading host species. Alternatively, introduced species can bring associated introduced pathogens that find naïve hosts and propagate. These changes in the disease landscape can have profound and often costly impacts on native fauna, as well as on livestock, food security and public health (Bright, 1999; Charles and Dukes, 2007; Marbuah *et al.*, 2014; Monk *et al.*, 2022).

Currently, knowledge is scarce about whether or how invasive species pathogens impact and alter ecosystem processes in Argentina. Clearly, more research is needed to diagnose the present situation and assess future risks. Mirroring global priorities highlighted by Roy *et al.* (2016), the top of the list with regards to recommendations would be the collection of baseline information on the distribution and dynamics of introduced pathogens, hosts and vectors. Moreover, efforts should extend to developing methods for predicting host shifts, pathogen-host dynamics and the evolution of introduced pathogens, so that proper prevention, mitigation, and control can be implemented. Acknowledging that many suggestions have been made in earlier segments, below are a few additional summary recommendations specific to introduced and invasive mammals in Argentina:

Research. Many extant reports of disease impacts on native species are anecdotal. Also, risk appraisals are often based on generalizations (*i.e.*, all diseases of cats and dogs can be a threat for native carnivores). While valuable for context, there is a need to pinpoint exactly what the existing problems are so that they can be tackled, recognizing that resources (and oftentimes opportunities) are limited. Therefore, it is suggested that researchers need to:

- Carry out studies to learn if and how introduced pathogens disturb the health dynamics of endangered, indicator or special interest native species.
- Conduct such studies on invasive species, with a focus on pathogens that could pose a threat for sympatric native fauna.
- Create a curated database and sample biobank that can be accessed for research and surveillance, including prospective and long-term investigations.

Monitoring. Too often alarms ring when it is too late to act. Monitoring should allow for the detection of subtle changes, thereby providing an opportunity to react accordingly and in a more timely manner. Following the canary in the coal mine metaphor, researchers and managers could work together to:

- Use proven health indicators (*e.g.*, stress hormones, Alford *et al.*, 2007; hematological parameters and body condition, Beldoménico *et al.*, 2008, 2009) to anticipate declines and/or a collapse in diminishing populations.
- Systematically gather health data to define baseline conditions and learn about the natural history of wild species, particularly for those of highest conservation concern.

Management. Even simple interventions can have deep and long-lasting effects. The task may seem daunting, but starting basic and progressively increasing in complexity can provide a realistic pathway for effective progress and success in the context of logistical and budgetary constraints. Keep in mind that best practices are often enough to greatly reduce risk (Simons and De Poorter, 2009). Some possible actions include:

- Restrict/avoid contact between domestic animals and native fauna to decrease opportunities for pathogen spillover by:
  - Aiming for livestock-free protected areas. If livestock are allowed in protected areas, frequent health controls and mandatory preventive health plans (including vaccines and deworming) should be applied to minimize the possibility of disease transmission to wildlife. This should be extended to working dogs used on farms.
  - Enforcing extant regulations on pet possession in protected areas (*e.g.*, APN, 2013).
  - Encouraging responsible pet ownership and husbandry best practices in communities, particularly in the immediate vicinity of protected areas.
  - Establishing and enforcing plans for dealing with free-roaming and feral dogs.
- Restrict/avoid contact between introduced invasive species and native wildlife to decrease opportunities for pathogen spillover by:
  - Preventing introductions of new species, as well as limiting the geographic spread of invasive species already present in the country (*i.e.*, keeping red deer out of Santa Cruz province).
  - Ensuring good sanitation and effective separation of native wildlife from introduced species kept in enclosures (*i.e.*, those used for trophy hunting in game reserves).
  - Reinforcing regulations on imports of species and/or subproducts (*i.e.*, hunting lure) to avoid inadvertent pathogen introductions.
  - Avoiding supplementary feeding or any similar practice that might favor aggregation and close contact between native and introduced mammals.
- Improve wildlife disease surveillance by:
  - Favoring communication and coordination efforts between institutions and sectors (veterinary service, public health, veterinarians, biologists, national parks administration, wildlife experts) to enable an effective, functional and nation-wide wildlife disease surveillance system (Stephen *et al.*, 2018).
  - Using all ethical and planned culling and harvest opportunities to systematically monitor the health of introduced species and/or feral animals.
  - Setting up mechanisms that allow proper investigations of wildlife morbidity and mortality events (which often go undiagnosed), so that similar events can be prevented in the future (*e.g.*, Orozco *et al.*, 2020).
  - Extending surveillance in the face of climate change to detect introduction or range-expansion of disease vectors (*e.g.*, insects) of concern.
- Avoid accidental human introduction of pathogens by:
  - Implementing simple biosecurity measures in vulnerable protected areas that receive tourism. For example, the installation of footbaths in hiking trails could reduce the risk of tourists accidentally introducing pathogens attached to shoes when visiting an area with Patagonian huemul or other endangered fauna.
  - Following best practices and enforcing biosecurity routines for work/research involving native wildlife (mainly for park rangers and researchers). In general, avoiding unnecessary contact with humans (*e.g.*, restrict visitation to sensitive areas),

maintaining adequate hygiene when handling wild animals, avoiding touching sick or dead animals without suitable protective gear and training, and immediately reporting the finding of dead or sick animals to the authorities.
- Strictly enforcing regulations on garbage and waste removal and avoiding contamination of water sources (*i.e.*, do not feed wildlife).

There is an intentional bias in this list towards actions aimed at prevention. The reason is that preventing the introduction of diseases into susceptible populations is, and has always been, the most effective method of disease management (Wobeser, 2002). Moreover, Argentina is fortunately still mostly free (or blissfully ignorant) of diseases of concern (*i.e.*, those which are harmful to conservation, human health or the livestock trade) in wildlife species. This situation heavily contrasts with that of the USA, for example, where a number of reportable diseases, namely bovine tuberculosis, paratuberculosis, brucellosis, rabies, and cattle fever tick, have a wildlife reservoir; and where the complexities of this wildlife component are a recognized impediment to eradication (Miller *et al.*, 2013). Years of unfruitful trials in many countries (*e.g.*, USA, Canada, South Africa, UK, New Zealand) have shown that while bovine tuberculosis may be controlled when restricted to livestock, it is almost impossible to eradicate once it has spread into ecosystems with free-ranging maintenance hosts (Miller and Sweeney, 2013). Another example is brucellosis, which is expanding among Rocky Mountain elk (*Cervus canadensis nelsoni*) in the USA's Greater Yellowstone Ecosystem and re-emerging in cattle from this area after short-lived nationwide eradication from cattle in 2008. Recent studies have shown that despite billions of US dollars spent in control efforts, there is ongoing interspecific transmission of *Brucella abortus* between elk, bison, and cattle, and contrary to previous assumptions, elk have been the source of several outbreaks in cattle since 2002 (O'Brien *et al.*, 2017).

In closing, the axiom “an ounce of prevention is worth a pound of cure” is at the essence of ensuring healthy wildlife and functional ecosystems, free of introduced invasive species and pathogens. With increased connectivity and globalization, pathogen “pollution” is becoming more prevalent and widespread. Lessons from other parts of the world lend proof to the incalculable value of adequate preparedness and early response. Therefore, this must be among the highest priorities for environmental management and conservation.

Acknowledgements

Hebe Ferreyra collaborated with literature review, references and preparation of the table; A. Marcos provided information on introduced wildlife disease surveillance performed by SENASA.

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9 | EXOTIC SPECIES IN THE FORMAL EDUCATIONAL SPHERE IN ARGENTINA

LAS ESPECIES EXÓTICAS EN EL ÁMBITO EDUCATIVO FORMAL EN ARGENTINA

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Editors' note: *to avoid miscommunication, there was an editorial decision reflected throughout this book to avoid the term "exotic" and instead favor "introduced" to describe these species (see Car* et al.*, this volume). However, in this chapter, "exotic" was retained because it was appropriately part of the analytical framework used to assess formal science education programs that employ ecological definitions of "native" and "exotic."*

Abstract. Education about exotic species is essential for controlling and managing biological invasions and constitutes a part of the environmental knowledge a scientifically literate citizen should have. Scientific information is converted into knowledge "to be taught," as expressed in official curricula, documents and programs, and school textbooks. At the same time, knowledge "to be taught" is adapted to classroom settings as knowledge "actually taught," which results from an interaction among knowledge, teachers and students. Here, we analyze 1) how exotic species are portrayed in formal curricula (national documents and provincial curriculum designs in Córdoba, Buenos Aires and Mendoza) and textbooks, and 2) what are the views and conceptualizations of exotic species held by teachers and students, placing emphasis on the teaching of exotic species as a problem. In curriculum documents, biological invasions are only mentioned as contents in one primary grade level (7th grade) and in the initial cycle of secondary school. However, many contents related to ecosystem dynamics and biodiversity conservation offer the opportunity to include exotic species in the latter curricular cycle of elementary education and throughout secondary school. A variety of terms are used in school textbooks to define biological invasions and exotic species, calling into question the coherence of concepts being taught as compared to scientific knowledge. The examples offered by textbooks are not always accompanied by images, but encompass several species, particularly exotic mammals. Two native mammals were reported as exotic (Patagonian mara, *Dolichotis patagonum*, and Patagonian huemul, *Hippocamelus bisulcus*). Our studies also show that students are more familiar with exotic mammals, particularly domestic or charismatic ones like dogs, horses, etc., than with native species. Indeed, many students even believe that these exotics are native. Nonetheless, in their last years of high school, students can name more native species. Teachers recognized 41 exotic species from Argentina, seven of which were mammals, but almost all teachers surveyed consider that the definition of “exotic species” is instead that of “invasive species.” We recommend that teachers make pedagogical decisions concerning the contents of curricula and school textbooks based on sound science as a dynamic knowledge-construction process.

Resumen. Los saberes se producen, circulan y son apropiados en contextos particulares y mediante procesos complejos de negociación. El saber científico, aquel producido por los investigadores y dado a conocer en el mundo académico, debe adaptarse para ser enseñado en la escuela. En el camino desde su producción hasta la llegada a las aulas ocurren una serie de transposiciones didácticas que dirigen el saber en direcciones definidas, con fines determinados, en contextos históricos y políticos particulares y con una perspectiva ideológica. Un saber científico se transforma en un saber «a enseñar», el cual nuevamente se adecua para llegar al aula como saber «enseñado», producto de la interacción entre saberes, docentes y alumnos.

La educación sobre las especies exóticas es un apoyo imprescindible en el control y la gestión de las invasiones biológicas y ha pasado a formar parte de los conocimientos que debería tener un ciudadano científicamente alfabetizado. En este capítulo revisamos algunos aspectos de la educación sobre especies exóticas en Argentina. Primero, analizamos cómo el tema es abordado en documentos curriculares (nacionales y de las provincias de Córdoba, Buenos Aires y Mendoza) y libros de texto escolares. Luego, analizamos la familiaridad de los alumnos y docentes con saberes acerca de las especies exóticas, haciendo énfasis en la perspectiva de la enseñanza de estas especies como problema.

El análisis de los documentos curriculares muestra que la introducción de especies exóticas solo se menciona como contenido en séptimo grado de la primaria y en el ciclo básico de la educación secundaria. Sin embargo, contenidos relacionados con la dinámica ecosistémica, relaciones tróficas y conservación de la biodiversidad brindan la oportunidad de estudiar las invasiones biológicas en general y de mamíferos exóticos en particular, en el último ciclo de la primaria y a lo largo de la secundaria. Del análisis de los libros de texto concluimos que no todas las editoriales responden adecuadamente a los aprendizajes propuestos en los documentos curriculares. La variedad de términos que se evidenció para definir a las invasiones y a las especies exóticas pone en duda que se alcance una conceptualización coherente con el conocimiento científico, ya que no se revisan los referentes empleados ni se dan oportunidades a los estudiantes para que cuestionen sus conocimientos cotidianos. Con ello se reforzarían concepciones intuitivas de lo que es nativo, exótico, invasor, etc. Los ejemplos que brindan los textos incluyen varias especies, entre las que se destacan los mamíferos exóticos, pero en un par de casos es errónea la información aportada (p.ej., se mencionan a la mara, *Dolichotis patagonum*, y al huemul, *Hippocamelus bisulcus*, como especies exóticas en Argentina). Dado que no siempre la información está acompañada de imágenes, sugerimos a los docentes recuperarlas a partir de fuentes confiables para identificar correctamente a las especies nativas y exóticas.

Indagando acerca de las concepciones de los alumnos, encontramos que los estudiantes están más familiarizados con los mamíferos exóticos domésticos y carismáticos que con las especies nativas, salvo en los últimos años de la secundaria, en que son capaces de nombrar más especies nativas. Algunas especies muy conocidas para los alumnos (como vaca, perro, caballo, burro o gato) son consideradas nativas, porque asumen que todo lo que nace en el país o se observa en la naturaleza tiene

la condición de nativo. Estas conceptualizaciones de los alumnos necesitan ser tenidas en cuenta a la hora de abordar el estudio de la introducción de especies exóticas como problema para la conservación de la biodiversidad. Los docentes encuestados nombraron un total de 41 especies exóticas, de las cuales siete fueron mamíferos: castor (*Castor canadensis*, 40% de las respuestas), liebre europea (*Lepus europaeus*, 20%), jabalí (*Sus scrofa*, 20%), ciervo colorado (*Cervus elaphus*, 12%), «ciervos» (3%), ciervo axis (*Axis axis*, 0.7%), ardilla de vientre rojo (*Callosciurus erythraeus*, 0.7%) y gato doméstico (*Felis sylvestris catus*, 0.7%). Los docentes de casi todos los niveles educativos consideran que una especie exótica es aquella introducida en un ecosistema del cual no es originaria y que logra establecerse y dispersarse produciendo diferentes impactos, definición que corresponde a especie invasora. Cuando los docentes fueron indagados acerca de los problemas causados por las especies exóticas mencionaron principalmente efectos a nivel ecológico. Sin embargo, consideran que el conflicto con especies exóticas es complejo y se necesita desarrollar nuevas estrategias y enfoques que permitan valorar las especies nativas. De esta forma, se puede trabajar el tema de las especies exóticas teniendo en cuenta todos los abordajes posibles, como el conflicto con especies exóticas que resultan beneficiosas o útiles para el ser humano o la protección de ambientes dominados por especies exóticas que aun así brindan bienes y servicios.

Para abordar la educación acerca de las especies exóticas invasoras proponemos a los docentes enseñar sobre biodiversidad y los problemas asociados como un proceso en donde los saberes no constituyan monumentos que el profesor expone a los estudiantes, sino como un conjunto de constructos conceptuales, procedimentales y axiológicos que se ponen en juego para resolver problemáticas. Proponemos trabajar en el contexto social a través del uso de estrategias didácticas que promuevan la argumentación, la toma de posición, la participación y el diálogo de saberes. Este enfoque permite identificar a los actores involucrados, comprender los roles y discursos que tienen respecto a la problemática e interpretar las relaciones de poder que se ponen en juego. Pueden utilizarse diversos recursos, además de los saberes relacionados con las ciencias naturales, como entrevistas, juegos de roles, notas periodísticas, información disponible en la web, interpretación de imágenes, relatos históricos, estudio de casos, etc.

El trabajo didáctico de selección y organización del contenido exige al docente una transposición que adapte los saberes de expertos a las necesidades e intereses del nivel educativo y su contexto particular de enseñanza. El docente debe formarse para ser un mediador calificado en la construcción del conocimiento escolar que incorpora la vigilancia epistemológica a las competencias y saberes profesionales. Como recomendación para la práctica docente, invitamos a los docentes a tomar decisiones sobre los contenidos que figuran en la currícula y en los libros de texto, teniendo en cuenta que la ciencia es dinámica y los saberes están en continua construcción.

Introduction

At the present time, the teaching of science constitutes a field of social action that acknowledges and values the anchoring of scientific activity in complex realities. Thus, science education should (and often does) seek to transcend a positivist position and go beyond the mere development of cognitive activities (Sauvé, 2010). Indeed, education efforts recognize that knowledge is produced, circulates and is appropriated in specific contexts and through complex processes of negotiation. Therefore, scientific knowledge, which is produced by researchers and released into the academic world through publications, journals, reports, congresses, etc., must be adapted and integrated with other knowledges to be taught and incorporated into the broader society.

Along the path from the generation of scientific knowledge through to its incorporation in classrooms, a series of content adaptations and didactic transpositions occurs that drive knowledge in defined directions and for specific purposes, in particular historical and political contexts and ideological perspectives (Cardelli, 2004). Scientific knowledge is converted into knowledge "to be taught," which then is transposed into knowledge "actually taught" in the classroom (Chevallard, 1991). This process depends on the interaction between knowledge, teachers and students. According to a constructivist scientific-pedagogical position, students are active and subjective in the construction of their own knowledge (*e.g.*, Piaget, 1984; Caravita and Halldén, 1994).

Education about invasive and exotic species is essential for controlling and managing biological invasions and has become part of the knowledge that a scientifically-literate citizen should have (Verbrugge *et al.*, 2021). The Convention on Biological Diversity (CBD)'s Article #8, Section h states that the introduction of "…alien species which threaten ecosystems, habitats or species" will be prevented, and those species controlled and eradicated (United Nations, 1992: p. 8). Plus, although it addresses the conservation and sustainable use of biodiversity in a general fashion, when the CBD refers to education and public awareness, it posits the novelty of considering education as a strategy for promoting and encouraging the comprehension of issues related to biological diversity. Years later, it was acknowledged that there is still a need to intensify these efforts through education and dissemination of scientific knowledge (Morgera and Tsioumani, 2010).

In this chapter, we review some aspects of how exotic species are integrated and represented in Argentine educational programs. First, we analyze the way the topic is approached in curricula and school textbooks. Then, we assess the views and conceptualizations of both teachers and students, placing special emphasis on the perspective of teaching about exotic species as a problem.

From scientific knowledge to knowledge to be taught

The role of curricula

A first step in transposing scientific knowledge to pedagogical settings is in the definition of contents in official curricula, documents and programs. In this section, we analyze the presence of exotic species, particularly mammals, and indicators of their study in national and provincial education programs. Specifically, we assess national curriculum documents and the curricular designs in the provinces of Córdoba, Buenos Aires and Mendoza, looking for allusions to specific content (*i.e.*, knowledge "to be taught") related to issues threatening biodiversity, particularly invasions by exotic species.

National Law #26,206, sanctioned in 2006, established that secondary education (SE) is mandatory in Argentina and that it constitutes a pedagogical and organizational unit for those who have completed their elementary education (EE) (Article #29). This regulation allows jurisdictions to choose between two possible structures: six years for EE and six for SE, or seven years for EE and five for SE. For the purposes of this analysis, we delimited the assessment of curricula to both EE and SE.

Priority learning nuclei for Argentina. In the framework of the Consejo Federal de Cultura y Educación, a core set of priority learning objectives and contents were established in 2006 (Ministerio de Educación, Ciencia y Tecnología, 2006). A priority learning nucleus (PLN) encompasses a set of relevant and significant core knowledge, which as content contributes to "developing, constructing and expanding cognitive, expressive and social possibilities that children put into play and recreate daily in their encounter with culture, thus widely enriching their personal and social experience" (Ministerio de Educación, Ciencia y Tecnología, 2006).

In 2011, after a long process of federal cooperation and participation among the provinces, the PLNs developed in 2006 were reorganized, given the differential implementation regarding the number of years for EE and SE established by Law #26,206. Thus, for the seventh year of EE or the first year of SE in a six-year EE program, the standards became "interpretation of trophic actions, their representation in networks and food chains, and recognition of the role of producers, consumers and decomposers" and "explanation of some modifications in ecosystem dynamics caused by disappearance and/or introduction of species into food webs" (Ministerio de Educación, 2011a). Then, for the first year of SE in jurisdictions with a seven-year EE, and for the second year of SE with a six-year EE program, PLNs included the "problematizing around the classification of living beings and identification of some criteria for grouping them, from the perspective of the classical division into five kingdoms" and "explanation of the importance of preserving biodiversity" (Ministerio de Educación, 2011b).

During the three last years of SE (in what is termed the "Oriented Cycle"), Biology can be taught over one to three years, depending on the jurisdiction. Agreed knowledge is organized into axes and as a text without scaling by grade, and contemplates subsequent jurisdictional adaptations (Consejo Federal de Educación, 2012). In this sense, for the axis "in relation to evolutionary processes," the "recognition of current and past biodiversity as a result of changes in living beings over time, highlighting the macro-evolutionary processes (massive extinctions or adaptive radiations) and the interpretation of the impact of human activity on its loss or preservation" are considered a priority nucleus (Consejo Federal de Educación, 2012).

Curriculum designs in Córdoba province. SE is organized into two cycles: a Basic Cycle (BC, first three years) and an Oriented Cycle (OC, last three years). Currently, Biology is a part of two subjects in the BC; one in the 1st grade (called Natural Sciences – Biology) and the other in the 2nd grade (called Biology). In presenting the area of natural sciences for the BC, both "diversity" and "organization, unity, interaction and changes" are acknowledged as being the major structural concepts (Ministerio de Educación de la Provincia de Córdoba, 2011).

For the 1st grade, "identification of material and energy exchanges in ecological systems and interpretation of their inherent trophic relationships" and "manifestation of interest in seeking explanations to some changes in ecosystem dynamics (*e.g.*, consequences of introducing exotic species, or indiscriminate logging, among others)" are listed as contents. For the 2nd grade, one of the objectives shared with Chemistry is that students should interpret "the consequences to environment and health entailed by human decisions and actions." For Biology in particular, students are expected to be able to "recognize diversity as an outcome of the evolution of living beings over time" and are encouraged to "search for explanations to the importance of biodiversity preservation from the ecological and evolutionary viewpoints." In the OC, Natural Sciences orientation for the 5th grade is focused on the "recognition of the consequences of biodiversity loss and their relationship with human health."

Curriculum designs in Buenos Aires province. SE in Buenos Aires province is structured to last 6 years and is divided into Basic Secondary Education (BSE) and Oriented Secondary Education (OSE) cycles. The latter cycle offers the students different modes or "orientations," one of which being in Natural Sciences.

Also, according to the organization of the curriculum design, one of the subjects for the first year of the BSE corresponds to Natural Sciences, structured in four thematic axes with their respective nuclei of contents (Dirección General de Cultura y Educación de la Provincia de Buenos Aires, 2006). Biodiversity-related topics are located on the axis called "interaction and diversity in biological systems," which contains the "life: unity and diversity" and the "living beings as open systems that exchange matter and energy" nucleus of contents. In these PLNs, it is indicated that, through the "analysis of journalistic and outreach texts," the goal is to refine the prior ideas that students have constructed about "biodiversity, its importance and the causes and consequences of its alteration by human activities." At this point, and depending on the didactic orientation of the design, it is recommended that students debate and discuss the effects on ecosystems of the disappearance and/or introduction of species into food webs.

In Biology for the 2nd year of the BSE, the central topic is the origin, evolution and continuity of biological systems (Dirección General de Cultura y Educación de la Provincia de Buenos Aires, 2007). Contents are grouped into units, with the first of these thematic units being "evolution: origin and diversity of biological structures." In the curriculum design, this unit intends to provide opportunities for the treatment and discussion of the value of biodiversity, including issues of economic importance or health issues, and for analyzing the effects of species extinction by the impact of human activities.

In the 6th year of the OSE, the "environment, development and society" subject is specific to the Natural Sciences orientation and provides a broad overview of environmental issues and possible solutions, such as responsible citizen practices (Dirección General de Cultura y Educación de la Provincia de Buenos Aires, 2011). Themes related to biodiversity loss, its consequences and likely risks, as well as conservation strategies, are included in the axis called "air, water, soil and biodiversity" and "responses," presenting examples of case studies relative to current problems in the country, so that the teacher can address the themes put forward.

Curriculum designs in Mendoza province. The provincial curriculum design of EE in Mendoza details the capacities to be developed in the permanent education of youths and adults (Dirección General de Escuelas de la Provincia de Mendoza, 2015a). Among them, it is proposed to "recognize ourselves as subjects of socially productive, politically emancipatory, culturally inclusive and ecologically sustainable practices." Within this capacity, the curriculum mentions "favoring local, national and regional organization for promoting policies that guarantee the life of present and future generations and of the ecosystems into which they are inserted." Among the stated problematizing contexts, which visualize fundamental aspects of contemporary society, we find the "dichotomy between development and care of nature" and the "denaturing of that which is technological: visualizing everyday scientific production." In module 4, the curriculum structure for the 2nd cycle of EE sets forth the development of the problematizing context: "citizenship-emancipation," and for Natural Sciences, it details the following specific learning goals along path 1: "man and nature," "recognition of habitats and different levels of organization of living beings," "participation of man as an environment-modifying agent and importance of prevention;" and along path 2: "analysis and integration of the elements composing the environment," "awareness raising about the importance of caring the environment to attain a better quality of life" and "analysis of the interrelation between human needs and natural resources."

In the 1st year of SE basic formation, in the axis called "in relation to living beings: diversity, unity, interrelations and changes," in the area of Natural Sciences, knowledge is proposed that allows recognizing unity in the diversity of all biological systems, these being acknowledged as open systems, taking into account the classification of diversity. Also highlighted is the value of biodiversity from ecological and economic perspectives, as well as identification of human actions that endanger or protect diversity. On the other hand, within the same axis in the 2nd year of SE basic formation, knowledge is more closely related to biological evolution (Dirección General de Escuelas de la Provincia de Mendoza, 2015b).

In the OC, problematizing contexts and subjects vary depending on orientation. Thus, in the Natural Sciences orientation, in the 4th year, the following axes are detailed in Biology: "population as an ecological system" and "population and evolutionary processes." In the subject Environmental Issues for the 5th year, problems are identified, the factors that put at risk and/or cause biodiversity deterioration and loss are recognized, and conservation strategies are discussed (Dirección General de Escuelas de la Provincia de Mendoza, 2015c).

Synthesis. From the analysis of the knowledge to be taught, as stated in national curriculum documents and in the curriculum designs of the provinces of Córdoba, Buenos Aires and Mendoza, it becomes evident that biological invasions are only mentioned as contents in the 7th grade of EE and the initial cycle of SE. However, there are also diverse objectives and contents related to ecosystem dynamics, trophic relationships, and to the study and conservation of biodiversity that offer the opportunity to study invasions in general and of exotic mammals in particular, in the latter cycle of EE and across SE. The priority status of these contents allows the design of more varied and extensive didactic units that promote in students a better and sustained learning of core contents. This entails a selection and adaptation process on the part of the teacher, who can discard those contents that can be omitted or subsumed, thus generating further opportunities for teaching and learning fundamental and primordial contents.

The role of school textbooks

A second step in didactic transposition is the use of school textbooks, which provide a valid conception of the knowledge to be taught and are an important assistance for the teacher in daily classroom work (Cobo Merino and Batanero, 2004). However, some problems have been described regarding high school textbooks' treatment of different topics. For example, with respect to the study of biological diversity, school textbooks show a lack of axiological and social contextualization and present species richness as the only component of biodiversity (Bermudez *et al.*, 2014; Bermudez and Nolli, 2015). Additionally, children's books show a strong bias toward exotic flora, fauna, and environments with far-reaching implications for conservation efforts and children's appreciation of native biodiversity (Celis-Diez *et al.*, 2016).

In this section, we evaluate how school textbooks for Natural Sciences and Biology present and define the issue of biological invasions and exotic species, placing a particular emphasis on mammals. For this purpose, we identified the textbooks published from 2010 to 2015 by editors of national circulation in Argentina, finding 17 books destined for the BC and six books for the OC (Table 1). We analyzed the inclusion and definition of biological invasions and exotic species, and the examples given by these school textbooks and the images they show of exotic mammal species of Argentina.

It is important to highlight that varied terminology is used in the analyzed textbooks to refer to exotic species and biological invasions (see also Car *et al.*, this volume). We found 12 different ways of mentioning these topics, and even eight different ways in just one of the textbooks. For example, in Balbiano *et al.* (2012a), we found "introduction of exotic species," "exotic species," "rare/odd species," "biological invasion," "invaders," "introduced species," "intruding species," and "bio-invasions" used at different times.

Overall, Argentine textbooks include the treatment of biological invasions, especially for Natural Sciences 1, corresponding to the first year of SE. Notwithstanding the inclusion of these terms, only approximately half of the school textbooks that refer to the issue of biological invasions actually define the concept explicitly (Table 1). For instance, Balbiano *et al.* (2012a) question "what happens in an ecosystem where species from another ecosystem are introduced? The consequences are always unpredictable. They often become invaders, because aside from persisting in the environment where they have been introduced, they proliferate and expand beyond determined limits. These species, called exotic, have neither predators nor parasites […]." Other conceptualizations are less specific, and indicate exotics as typical from another place: "native species are characteristic of an area; exotic ones live in other regions. Introduction of the latter is frequent […]" (Mollerach *et al.*, 2013). In the case of Adragna *et al.* (2013), exotic is defined as synonym with alien: "one of the negative actions of human beings on the environment consists of introducing alien or exotic species, without considering the consequences this may have on a region's native species."

Table 1. Analysis of how school textbooks in Argentina treat the topics of biological invasions and exotic mammal species. Secondary education is divided into a Basic Cycle (**BC**) and Oriented Cycle (**OC**).

Cycle	Publisher	Textbook	Biological invasions		Definition of exotic species	Exotic mammals of Argentina	
			General treatment (pp.)	Definition		Examples	Images
BC	Aique	De Dios *et al.*, 2011	Yes (p. 65)	No	No	No	No
		Mollerach *et al.*, 2013	Yes (p. 259)	Yes	Yes	red deer	red deer, European hare
	Estrada	Adragna *et al.*, 2013	Yes (p.196)	No	No	European hare, red deer	No
		Alberico *et al.*, 2013	Yes (p.172)	No	Yes (p. 228)	North American beaver	No
	Kapelusz / Norma	Antokolec *et al.*, 2012	No	–	–	–	–
		Blaustein *et al.*, 2011	Yes (pp. 59/83)	No	No	North American beaver, red deer	Patagonian huemul*
	Longseller	Mosquera *et al.*, 2010	Yes (pp.131/133/155)	No	No	North American beaver, European hare	–
	Mandioca	Sarazola *et al.*, 2010	Yes (p. 202)	No	No	No	No
	Maipue	Mosso *et al.*, 2013	Yes (p.197)	Yes	No	No	No
	Puerto de Palos	Carmona de Rey *et al.*, 2010	Yes (pp. 89/94)	No	No	European hare	European hare
	Santillana	Balbiano *et al.*, 2012a	Yes (p.186)	Yes	Yes	European hare	Pallas's "beautiful" squirrel
		Balbiano *et al.*, 2012b	No	–	–	–	–
		Balbiano *et al.*, 2015	Yes (pp.185/189)	Yes	No	North American beaver	North American beaver
	SM	Antokolec *et al.*, 2010	No	–	–	–	–
		Carreras *et al.*, 2010	Yes (p.155)	No	No	No	No
		Furriol *et al.*, 2013	Yes (p.120)	No	No	No	No
		Irigoyen *et al.*, 2011	Yes (p. 69)	No	No	No	No
OC	Estrada	Bocalandro *et al.*, 2012	Yes (p.198)	No	No	red deer	red deer
	Kapelusz / Norma	Adami *et al.*, 2010	Yes (pp. 275/9)	Yes	Yes	American mink, Pampa fox, European rabbit, North American beaver, European hare, wild boar, red deer	North American beaver
	Maipue	Tedesco *et al.*, 2012	No	–	–	–	–
	Santillana	Balbiano *et al.*, 2011	Yes (p. 208)	Yes	Yes	mara	mara*
	SM	Basterio *et al.*, 2011	Yes (p.185)	No	Yes	No	No
		Wolovelsky *et al.*, 2013	Yes (pp.180/215)	No	No	European hare	No

*The mara and the Patagonian huemul are native species.

Conversely, one of the most complex conceptualizations is contributed by Mosso *et al.* (2013), who reproduce a segment of a scientific text and make it clear that "for Ecology, a biological invader is a species native to another place (*e.g.*, another land, river or ocean) that arrives in a different ecosystem and colonizes it, becoming a part of the new environment. It reproduces quickly, occupies many places with different characteristics (generally due to the absence of their natural predators, who stayed in their place of origin) and interacts with other species of the same ecosystem […]." Finally, succinctly, De Dios *et al.* (2011) present the issue of invasions, alerting as to likely consequences, but providing no definitions: "introduction of invasive exotic species can be accidental or voluntary. Exotic species compete for resources with native species, or prey on them, or modify environments."

Regarding the consequences of introducing an exotic species, most school textbooks only mention the ecological disturbances it causes, as Blaustein *et al.* (2011) express "[…] introduction of exotic species, such as the sweetbriar, the North American beaver and the red deer, results in extinction of native species as a consequence of competition for food and space." Similarly, Balbiano *et al.* (2015) indicate that "invasive species proliferate and expand swiftly across a particular area, which brings unpredictable and often undesirable impacts, such as displacement of autochthonous species, alteration of food webs or of the original environment." In turn, the economic effects of introducing exotic species are mentioned, to a lesser extent, and always making reference to specific examples, such as the one presented by Balbiano *et al.* (2012a) related to the Pallas's squirrel (*Callosciurus erythraeus*) that "[…] damaged telephone, electric and television wires, peeled the bark off trees, and tore flowers and fruits by biting them."

Regarding the examples of exotic mammals in Argentina that are given by these textbooks, there is a clear predominance of the red deer (*Cervus elaphus*) and the European hare (*Lepus europaeus*). However, it is not always made clear whether or not these exotic species are invasive in Argentina. For example, Mollerach *et al.* (2013) contextualize the invasion of the red deer in our country, clarifying that it was "introduced in Argentina in the 19th century; it is considered one of the 100 most damaging invasive exotic species on the planet." In contrast, other exotic species are not considered in the context of Argentina, such is the case of the European hare, which is mentioned as "[…] introduced in North and South America, in Siberia […]" and the European rabbit (*Oryctolagus cuniculus*), which appears as"[…] taken to Australia, where it became a pest, that is, an invasive species that damages crops." Another text, instead, presents a table describing the continent of origin and the Argentine distribution for species of fish (salmon and trout, *Salmo* spp., and carp, *Cyprinus carpio*), birds (domestic pigeon, *Columba livia*, and sparrow, *Passer domesticus*), and mammals (red deer and European hare) (Adragna *et al.*, 2013). Moreover, this last text describes historical facts about how the hare was introduced and turned into a pest, stating that "towards the end of the 19th century, a German consul incorporated the European hare into Santa Fe province. Its striking ability to adapt to diverse climates and topographies, added to its astonishing reproductive capacity, made it possible for it to currently occur across nearly all of our country. In 1907, it was declared a pest for agriculture by law." Similarly, Alberico *et al.* (2013) present the circumstances under which the North American beaver (*Castor canadensis*) was introduced in Tierra del Fuego.

Several texts give examples of interactions among exotic mammals introduced in Argentina and native species that were directly affected. Such is the case of the European hare and the mara (*Dolichotis patagonum*) (Carmona de Rey *et al.*, 2010; Balbiano *et al.*, 2012a), the North American beaver and the lenga tree (*Nothofagus pumilio*; Mosquera *et al.*, 2010), the red deer and native deer, Patagonian huemul (*Hippocamelus bisulcus*) and southern pudu (*Pudu puda*) (Blaustein *et al.*, 2011). Also mentioned in these textbooks is the "[…] American mink (*Neogale vison*) introduced in the Patagonian forests […] that feeds on birds native to the region" (Mollerach *et al.*, 2013). Some examples may be confusing, because the terms are not correctly used. Such is the case of the example given in Antokolec *et al.* (2010), where it is mentioned that "[…] in Patagonian forests, all Chilean bamboos bloom together every fifteen years and an invasion of mice occurs […];" in this case the term *invasion* is used to refer to an explosive growth in native rodent populations, and not to biological invasions caused by exotic species.

As for the images used to exemplify exotic mammals in Argentina, only four species were found to be represented: Pallas's squirrel, red deer, European hare and North American beaver.

The topic of exotic species is once again dealt with in the textbooks for the OC. Santillana, SM, and Kapelusz/Norma publishers address the concepts with a level of complexity similar to that used in school textbooks for the BC. For instance, Balbiano *et al.* (2011) define biological invasion as the "process of expansion […] of a species mediated by the establishment of new populations which are viable in habitats where they had not been present before. In this context, a species is labeled as exotic when it is found at sites outside its region of origin." The incorporated examples correspond to mammal species introduced in Tierra del Fuego (American mink; Pampa fox, *Lycalopex gymnocercus*, which is native to the Patagonian mainland; European rabbit; North American beaver; European hare, which is not present in Tierra del Fuego; wild boar, *Sus scrofa*; and red deer), including a photograph of an individual beaver (Tedesco *et al.*, 2012). However, when Balbiano *et al.* (2011) describe the consequences of disturbances, including the introduction of exotic species, they erroneously exemplify and present a photograph of the native mara as an introduced species: "different types of disturbances can be observed […] and an introduced species (this is the case of the Patagonian mara)." As found in BC textbooks, in Wolovelsky *et al.* (2013) a non-contextualized example is given for Argentina "when a non-native species is introduced in a natural environment, there may be no predators for such species, and it can become a pest, as happened with European rabbits in Australia."

From the analysis of school textbooks, it is concluded that not all publishers comply appropriately with the learning contents proposed in the PLN regarding ecosystem structure and dynamics (Table 1). In addition, the variety of terms used to define invasions and exotic species calls into question that a coherent conceptualization can be reached with reference to scientific knowledge, since references used are not revised and no opportunities are offered to students for them to question their everyday knowledge. This would reinforce intuitive conceptions of what is native, exotic, invader, etc. (Bermudez *et al.*, 2021). The examples offered by school textbooks include several species, among which exotic mammals stand out, but in one case the information provided is wrong. As information is not always accompanied by images, teachers are suggested to seek drawings, photographs and qualified websites to correctly identify native and exotic species. It is important to build a bridge between the students' own references and antecedents and new academic knowledge. Finally, as OC textbooks do not delve deeper into the treatment of the analyzed contents with respect to the BC (Bermudez and Nolli, 2015), teachers are encouraged to use ecology books for university students, scientific articles and outreach materials to enhance the didactic transposition on these contents into their science classes.

From "knowledge to be taught" to "knowledge actually taught": the role of students and teachers' knowledge about biodiversity and exotic species

Students

During knowledge construction processes, learners handle information by either accommodating (*i.e.*, adapting) their own cognitive structures or assimilating information to make it fit into their current worldview (Piaget, 1984). The existing conceptual structure, built by prior knowledge and ideas, has a tendency to be stable. This condition can be an obstacle for the learning process, especially when prior knowledge is opposed to the content to be learned. Therefore, for teaching processes, it is helpful to consider students' prior associations, concepts, and subjective theories to improve learning interventions and learning process (Meinardi *et al.*, 2010) (*e.g.*, when the aim is a better understanding of biodiversity issues).

Despite the interest in and curiosity of children and young people about living beings, some studies show that many have little knowledge of the species occurring in their surroundings (*e.g.*, Lindemann-Matthies, 2002, 2006; Lindemann-Matthies and Bose, 2008; De Melo *et al.*, 2021). Students, especially those living in urban areas, are often more familiar with species that are not part of local biodiversity, and which they know from sources like books, television or the internet (Paraskevopoulos *et al.*, 1998; Campos *et al.*, 2012). In a study conducted to determine familiarity with biodiversity of students from urban and rural areas of Mendoza province, 1,746 students between seven and 18 years old were asked to mention 10 animals and indicate the source of their knowledge (*e.g.*, experience in the countryside, a home garden, books, television, the Internet, etc.). Overall, students mentioned more exotic than native species and, like elsewhere in the world, they are familiar with domestic and charismatic exotic mammals (Campos *et al.*, 2012). The 10 species students found most familiar were, in order of descending mentions, dog (*Canis lupus familiaris*), cat (*Felis sylvestris catus*), lion (*Panthera leo*), horse (*Equus ferus caballus*), "monkey," cattle (*Bos primigenius taurus*), "birds," tiger (*Panthera tigris*), elephant (Elephantidae) and European rabbit. The students' place of residence (*i.e.*, urban or rural) and gender affected familiarity with species, whereby rural boys recognize more native species and mentioned going outside as their main source of contact with biodiversity. Girls, in turn, were more familiar with exotic species and, due to an aesthetic appreciation, are generally more familiar with pets and charismatic mammals (Badarraco, 1973). This trend is also reflected in adult women, who have been shown to fear or have less interest in native species (Kellert and Berry, 1987).

Similarly, when 865 students of rural schools in Valle Fértil (San Juan province) were asked about their favorite animal, 72% mentioned exotic domestic species (*e.g.*, dog, horse, cat) and 12% mentioned exotic wildlife species (*e.g.*, European hare); exotic domestic mammals were considered to be the most useful species (Nates *et al.*, 2010).

In a study conducted in Córdoba province, 328 students in the three last years of EE with a Natural Sciences orientation were asked to mention 10 animal species native to the province. In this case, half the species mentioned were mammals and 64% of them were species actually native to Argentina (*e.g.*, mountain lion, *Puma concolor*; Geoffroy's cat, *Leopardus geoffroyi*; plains vizcacha, *Lagostomus maximus*; and Pampa fox). But they also again included exotic domestic species as native (*e.g.*, cattle, dog, horse, donkey [*Equus africanus asinus*], cat) and exotic wildlife species (European hare). This confusion between exotic and native species may be explained by the fact students are conceiving these species based on their everyday experience and considering that every animal born in or observed in local nature is native (Bermudez *et al.*, 2015, 2021).

In synthesis, our research showed that students are more familiar with domestic and charismatic exotic mammals than with native species. Many of them even assume that these exotic mammals are native. Our results could be explained by the differences in the students' conception of "native" and by the species with which they are in closer contact or recognize as familiar. Students from the latter years of SE, however, were able to name more native species. In rural areas, domestic mammals, such as dogs and horses, are considered the most useful species.

Teachers

In this section, we attempt to promote an approach that facilitates communication between the scientific community and teachers, based on the exchange of and dialogue about knowledge, assuming that there are different modes of circulation for knowledge, values and beliefs, which are put into play during educational processes in diverse contexts. To better understand the way in which teachers approach the study of exotic species in the classroom, a survey was conducted among Argentine natural science teachers, inquiring whether exotic species are viewed as a problem. Most of the 212 teachers who responded to the survey were between 30 and 50 years of age (64%) and were women (76%). Teachers from 20 provinces participated, mostly from Buenos Aires (22%), Córdoba (18%), Mendoza (15%) and Misiones (9%). Most work in the public sector (81%) and have achieved either master's or doctorate degrees (31%) or specialization or postgraduate certificates (24%). The majority of respondents teach at the secondary level (41%) or higher (tertiary 22% and university 26%).

When teachers were asked to mention an exotic species from Argentina, a total of 41 were named. Only seven of these were mammals, but several were frequently mentioned, including: North American beaver (40% of responses), European hare (20%), wild boar (20%), red deer (12%), "deer" (3%), axis deer (*Axis axis*; 0.7%), Pallas's squirrel (0.7%) and domestic cat (0.7%). When they were asked whether they had had the opportunity to know about the issue of exotic species introductions, 85% of them commented on their experiences, such as "while volunteering in Parque Nacional El Palmar, I observed and knew about the work carried out by the crew of "paradisers," who kept a record of the control tasks for the paradise tree (*Melia azedarach*)," "I got information in college," and "I learned from conferences I attended and from outreach articles throughout life." A minority of respondents explicitly answered that they had not had the opportunity to know about the issue (7%) or did not answer (7%).

To inquire about the conceptualization that teachers have regarding exotic species, they were offered three options: 1) it is an rare or odd species, because of its appearance or because we do not know much about it (*i.e.*, the definition of a little known species), 2) it is a species that has been introduced in an environment that is not its ecosystem of origin (*i.e.*, the definition of exotic or non-native species), and 3) it is a species introduced in an ecosystem of which it is not native and that manages to become established and disperse across extensive areas, causing economic and environmental damage or damage to human health (*i.e.*, the definition of invasive species). Teachers at almost all educational levels consider that the definition of invasive species is the one corresponding to exotic species (see also polysemy for exotic species found in the media, Car *et al.*, this volume) (Table 2).

Table 2. How teachers define exotic species, reported as percentages (%) according to the educational level at which respondents teach.

Respondent teaching level	Responses (n)	Little known species (%)	Exotic or non-native species (%)	Invasive species (%)
Informal	5	0	20	80
Initial-elementary	9	2	4	3
Secondary	110	2	39	59
Tertiary	58	7	46	47
University	71	3	39	58
Total	***253****	***4***	***41***	***55***

*This number is greater than the number of total respondents because some teachers work at more than one educational level.

When required to give an example of the problems caused by introducing exotic species, 31% of teachers referred to particular projects or species, whereas 15% provided no examples or did not answer. Most of the teachers who explained the problems caused by exotic species made reference to exclusively ecological aspects, such as "the introduction of trout (Salmoninae) in Río Negro resulted in it occupying the ecological niche of autochthonous species, causing their disappearance." To a lesser extent, they referred to broader environmental problems, considering historical aspects of how introductions or invasions occur: "the impact of exotic herbivores in colonial times;" economic problems: "they can bring about economic losses through damage to biodiversity or to the machinery man uses to exploit resources;" and health problems: "they cause diseases."

As final comments, teachers considered it necessary to device new strategies and approaches that allow valuing native species and to work on the topic of exotic species, bearing in mind all possible approaches to issues such as the conflict with exotic species that turn out to be beneficial and useful for the human being, or the protection of environments dominated by exotic species which, despite their being introduced, do provide ecological and social goods and services (see Bobadilla *et al.*, this volume).

Conclusions and proposals to educate about exotic mammals

Ecologists have generally placed considerable emphasis on a species being exotic, and many studies on biological invasions use emotional, militaristic, and even manipulative language to discuss the topic. Because of that, some authors have encouraged a critical reflection on whether metaphors currently used to characterize these species may actually contribute to social misinterpretation of invasion biology, thereby interfering with conservation objectives (Larson, 2005; Selge *et al.*, 2011). The use of loaded language in scientific works may have also led to an ambiguous and inconsistent use of terminology (Verbrugge *et al.*, 2021), especially in school textbooks. The confusing use of the terms "native," "exotic" and "invasive" does not do justice to the complexity of the issue. Even though native/exotic is mostly thought of as a dichotomous category (*i.e.*, a species is either native or not), in fact, species considered native for an area can be considered exotic for another, even in the same country (*e.g.*, Pampas fox in mainland Patagonia versus Tierra del Fuego). Therefore, defining nativeness (and non-nativeness) in a more concise manner might prevent a potential "reflexive anti-exotic bias" (Stromberg *et al.*, 2009), which automatically leads to suspecting that a species is problematic as soon as it is identified as exotic. Furthermore, when exotic species are considered useful (*e.g.*, horses in rural areas) or emotionally bonded to humans (*e.g.*, pets), the argument about non-nativeness can be detrimental by producing distrust in scientific knowledge. In this regard, Nuñez *et al.* (2018) suggested five key factors—arrival time, economic impact, aesthetic preferences and phobias, effect on human health, and origin of introduced species and origin of human immigrants—that can profoundly affect whether and when a species is reviled or prized by people. Nonetheless, the perception of the ecological effects of exotic species is often underestimated (Diaz Isenrath and Llano, 2020).

In both the fields of science and education, a more holistic and transparent debate is necessary regarding aspects like the social and historical context of species introductions, impact of invasive species beyond ecosystem disturbances, conflicts based on stakeholder values regarding species, and disagreements over invasive species control (Estévez *et al.*, 2015; Archibald *et al.*, 2020). In addressing the topic of learning about exotic species, teachers and students should be able to recognize the origin, usefulness, reason for being, and the why and wherefore of the knowledge about invasive and exotic species. We propose teachers to work on the social context by using didactic strategies that promote argumentation, taking of positions, participation and dialogue about knowledge. Such an approach allows identifying the stakeholders involved, understanding their roles and discourse about the issue and interpreting the power relations at stake. Different resources can be used, besides the knowledge relative to natural sciences, such as interviews, role playing, journalistic notes, information available on the web, image interpretation, historical narratives, case studies, etc. (Massarini and Schnek, 2015; Bermudez *et al.*, 2021).

The didactic work of selecting and organizing contents demands that teachers be able to affect a transposition that adapts expert knowledge to the needs and interests of the particular educational level and teaching context. The teacher must become trained to be a qualified mediator in the construction of school knowledge that incorporates epistemological vigilance into professional competences and knowledge. As a recommendation for their teaching practice, we invite teachers to make decisions about the contents in the curricula and school textbooks, taking into account that science is dynamic and knowledge is in constant construction.

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10 MEDIA REPRESENTATIONS OF INTRODUCED INVASIVE MAMMALS: A COMPARISON BETWEEN TRENDS IN ARGENTINA AND TIERRA DEL FUEGO PROVINCE

REPRESENTACIONES MEDIÁTICAS DE LOS MAMÍFEROS INTRODUCIDOS INVASORES: UNA COMPARACIÓN ENTRE LAS TENDENCIAS PARA LA ARGENTINA Y LA PROVINCIA DE TIERRA DEL FUEGO

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Abstract. Despite recognizing the need to integrate the ecological and social dimensions of environmental problems, biological invasions research and management still lack broad assessments of their human dimensions. In contemporary Western societies, mass media has become a fundamental social factor in the creation of shared ideas about nature, shaping different stakeholder's values, attitudes and behaviors. However, little attention has been paid to media portrayals of biological invasions. Using communication theories to build a conceptual framework, we studied the media representations of introduced invasive mammals (IIMs) in newspapers, comparing national-level outlets with those from Tierra del Fuego (TDF). Using key words related to IIMs, we identified and selected relevant articles (n=344) that were assessed for 1) importance given to the topic of IIMs (*e.g.*, cover stories, article length, accompanying photographs); 2) the values present and thematic orientation (*e.g.*, negative, positive, neutral); and 3) information sources referenced in articles. Only 13 of Argentina's 23 IIMs were portrayed in newspapers; none were frontpage news. TDF showed a greater frequency of negative-oriented articles, coinciding with the scientific perspective provided by both scientific and political sources, and a lesser degree the agricultural sector. Plus, in TDF these articles were placed mostly in the newspapers' politics section. Nationally, articles were more general, citing both scientists and Non-Governmental Organizations (NGOs). Nationally, there were cases of information errors, and frequently "exotic" had polysemic meanings (*e.g.*, exuberant, desirable, interesting) with an unclear value-orientation regarding biological invasions. IIMs are part of public discourse and part of TDF's public agenda. However, their portrayal in the media is highly conditioned to territorial issues and information sources. We recommend including science communication as

part of professional media training, but biological invasion researchers and managers should also recognize the diversity of values and understandings of IIMs and the way that can affect policies.

Resumen. La forma de estudiar y manejar el ambiente debe basarse no solo en sus dimensiones biofísicas, sino también en la construcción social sobre cómo entendemos y nos relacionamos con esta realidad. Sin embargo, a pesar de ser cada vez más claro que es necesario integrar las dimensiones ecológica y social de los problemas ambientales, temáticas como la investigación y el manejo de las invasiones biológicas aún carecen de evaluaciones integrales. En las sociedades occidentales contemporáneas, los contenidos de prensa gráfica se han convertido en un factor social fundamental, dado que se articulan con la agenda pública, y recortan, jerarquizan e instalan temas que afectan a la construcción de valores y comportamientos de diferentes actores sociales sobre distintas problemáticas, incluyendo las ambientales. Sin embargo, a la fecha este proceso ha recibido poca atención en la literatura de las invasiones biológicas.

Por este motivo, en el presente capítulo se construyó un marco conceptual en base a las teorías de comunicación, con el objetivo de estudiar las representaciones de los mamíferos introducidos invasores en diarios argentinos entre 2013–2015 (ambos inclusive), comparando cuatro principales diarios nacionales (*Clarín*, *La Nación*, *Página/12* y *Crónica*), seleccionados por sus diferentes líneas editoriales, con los tres de mayor circulación de la provincia de Tierra del Fuego, Antártida e Islas del Atlántico Sur (*El Diario del Fin del Mundo*, *El Sureño* y *Provincia 23*), dado que es la que presenta un mayor número de mamíferos introducidos invasores. Se espera que las representaciones de los mamíferos introducidos invasores en los medios del nivel provincial sean más frecuentes y además estén más influenciadas por el discurso científico, teniendo en cuenta que el tópico de las invasiones biológicas ha sido posicionado como un problema ambiental y político en la Patagonia Austral.

Se utilizaron diferentes palabras clave referidas a los mamíferos introducidos invasores (generales: *especie exótica*, *especie introducida*, *especie no nativa*, *especie invasora*; y los nombres científicos y comunes de cada especie de mamífero introducido invasor) para encontrar los artículos de prensa que hicieran mención a la temática en los correspondientes buscadores de cada diario seleccionado durante los años de referencia. Se encontraron un total de 344 artículos relevantes que fueron analizados en términos de importancia (presencia en tapa, extensión del artículo/número de palabras y uso de material fotográfico), orientación (valoración de las invasiones y sección temática dentro del diario), y fuentes de referencia consultadas. Solo 13 de los 23 mamíferos introducidos invasores de Argentina fueron nombrados en los artículos encontrados, y en ninguno de los casos la relevancia dada a estas noticias fue suficiente como para figurar en las tapas de los diarios. Sin embargo, esto se vio atenuado por un tratamiento un poco más profundo dentro del diario, con artículos de mayor extensión y la presencia de fotografías.

Las representaciones en Tierra del Fuego fueron más frecuentes e influenciadas por el discurso científico, con mayor cantidad de artículos brindando información acerca de los impactos negativos de los mamíferos introducidos invasores sobre los ecosistemas nativos y las personas. Además, la mayoría de los artículos se ubicaron en la sección de política de los diarios, indicando que los mamíferos introducidos invasores han sido posicionados como un problema político-ambiental para la provincia. Incluso, las principales fuentes de información para los diarios de Tierra del Fuego incluyeron tanto científicos como políticos y gestores. En particular, a nivel provincial en Tierra del Fuego, los perros asilvestrados (*Canis lupus familiaris*) y los castores (*Castor canadensis*) fueron las especies más

reportadas, y los artículos que las mencionaban tuvieron principalmente una valoración negativa respecto a sus impactos. Estas dos especies probablemente constituyen las más reconocidas entre los mamíferos introducidos invasores en la provincia, los primeros por su impacto sobre la actividad ganadera (*i.e.*, pérdidas por depredación, cambio de ovejas a vacas para evitar pérdidas económicas, etc.), mientras que los segundos por sus impactos en los bosques fueguinos (los castores afectaron el 40% de la superficie de bosque ribereño).

Por su parte, en los diarios nacionales se evidencia que las representaciones fueron más generales y descriptivas, incluso con errores de información, el uso de términos fuertemente polisémicos (por ejemplo, debido al uso de la palabra «exótico» como algo «lindo» y/o «raro») y una valoración dispar hacia las invasiones biológicas. En este caso las principales fuentes de información predominantes fueron los científicos, pero también el sector privado conservacionista representado por las organizaciones no gubernamentales (ONGs).

Concluimos que los mamíferos introducidos invasores en general no han sido priorizados en la agenda pública y que su aparición en la prensa está fuertemente condicionada a problemáticas territoriales y a la experiencia directa de los lectores. Se recomienda incluir la comunicación de la ciencia en la prensa como parte de nuestra formación y quehacer profesional, pero también reconocer la necesidad de incluir la diversidad de valores de diferentes actores para incorporar a las especies introducidas invasoras y sus impactos en la agenda pública-política.

Introduction

We live in a natural world that we represent in concepts, images and words that are the product of a socio-ecological construction built upon our biophysical surroundings and culturally-derived elements, understandings, behaviors and processes (Morin,1998). For example, social imaginaries of nature are constituted by shared ideas that in turn regulate our actions and behaviors. These ideas are acquired through direct experience with nature, but also via formal (*e.g.*, schools, churches) and informal institutions (*e.g.*, the family, celebrities) (Díaz, 1996). As such, the relationship between what is "natural" and what is "social" includes both causes and consequences driven by ecological and human factors.

Increasingly, scientists, authorities and society in general recognize and accept that problems traditionally considered "environmental," such as climate change, habitat fragmentation and biological invasions, should be conceived of not only as biological issues, but also as socio-ecological phenomena (see Anderson and Pizarro, this volume). Nonetheless, the natural sciences, including invasion biology, usually consider humans almost exclusively through the lens of being a disturbance that drives environmental change, as reflected in the increasing prominence of the Anthropocene concept in ecology (Crutzen, 2002). Consequently, it is a theoretical and practical challenge for environmental research and management to fully incorporate the multi-faceted aspects of human subjectivity, including social representations and constructions.

In all societies throughout history, human beings have produced and exchanged information and content in multiple ways, but for contemporary Western culture, mass media has come to fulfill a central role in the production of significances and meaning about the world we inhabit; mass media communication is fundamentally a re-elaboration of the symbolic character of social life and a restructuring of the way in which subjects relate with others, with their own selves and with their surroundings (Thompson, 1988). Today, media are one of the most influential social actors involved in the circulation of images and words and engaged in the dispute of social meanings regarding the world and our shared ideas about it (Schuliaquer, 2014).

Within the body of literature about introduced invasive species there has been little emphasis on media's role in the construction of social imaginaries about biological invasions. Yet, studies about the metaphor of "invasion" (Larson, 2005) and on the diverse stakeholders and values involved in invasive species conflicts (Estévez *et al.*, 2015) indicate that there is a plurality of ways that people understand, value and assess these species and biological invasions in general. In this context, media representations are crucial to understanding this environmental problem as a socio-ecological phenomenon, and communication studies provide conceptual elements to elucidate these complex interactions. For example, the theory of agenda setting (McCombs and Shaw, 1993) explains that the process of topic construction, including the selection and prioritization of newsworthy issues, should influence the ways that invasive species appear and are portrayed in the media. Agenda setting posits that the press may not be successful much of the time in telling people "what to think," but it is stunningly successful in telling its readers "what to think about" (Cohen, 1963).

At the same time, the study of the way that these issues are enunciated (Verón, 2004) provides a qualitative and quantitative analysis of news items, assessing such aspects as their value and thematic orientation (*e.g.*, values can be negative, positive, neutral; news items can be classified as political, scientific, general interest). Within such a theoretical framework, the social imaginary concept (Castoriadis, 1975) is a useful analytical tool to apply to media representations and identify key elements in the social construction of meaning, allowing us to distinguish on the one hand the ideas about invasive species and biological invasions that are shared by social groups, but on the other to determine the institutional structures or processes that promote specific conceptualizations (*e.g.*, sources cited in the media). In particular, the relationship between a newspaper and its readers is a method to study the media setting, and the type of media-reader "contract" is a specific mode that is established between both from discourse analysis (Verón, 1985). Taken together, we constructed an integrated theoretical scaffolding from the social sciences to comprehend the ways that biological invasions are produced, circulated and read in the media.

We evaluated newspaper media's role in the representation of introduced invasive mammals (IIMs) at the national level in Argentina and at the provincial level in Tierra del Fuego (TDF). While there is currently a dynamic reconfiguration of the media due to new technologies, from the possible universe of media sources and outlets (*i.e.*, radio, TV, multi-media platforms, social networks, etc.), we chose to study newspapers because they are still a principal media actor responsible for installing reference points and interest topics, or what is called the "media agenda" (Boczkowski, 2006). Specifically, we sought to elucidate how at national and provincial levels, information about these species and biological invasions in general is mediated. We analyzed: 1) the species that are mentioned in newspapers (*i.e.*, assemblage of taxa reported); 2) the importance given to these news items (*i.e.*, number of publications, placement in the newspaper, photographs, word count);

3) the values and thematic orientation of the articles (*i.e.*, negative, positive, or neutral; section of the newspaper); and 4) the sources cited as references for information in the new items (*i.e.*, stakeholders, institutions). Results found at the national level were compared to findings from TDF because we expected that news about IIMs coming from the Fuegian Archipelago would be heavily influenced by the scientific tradition that has made TDF a "natural laboratory" for this topic and achieved making it part of the political agenda of the province, as well as in adjacent Chile (Anderson *et al.*, 2011; Valenzuela *et al.*, 2014). Additionally, the Magellanic subpolar forest is the biogeographic unit with the most IIMs in southern South America, and in TDF these species represent more than the 60% of the terrestrial mammal species assemblage in the province (Valenzuela *et al.*, 2014; Ballari *et al.*, 2016). Finally, we anticipated that the media representations of biological invasions in a territory associated with virgin and pristine nature, like TDF and Patagonia more generally (Moss, 2008), would create a different level of importance and valuation of the topic compared to the national social imaginary.

Methodology

An integrated methodological strategy was used by bringing together different types of data and knowledge production by way of triangulation between quantitative and qualitative sources (see Creswell, 2014). First, we chose to study the most important newspapers at two spatio-political levels: i) national in Argentina—*Clarín*, *La Nación*, *Página/12*, *Crónica*; and ii) provincial in Tierra del Fuego (TDF)—*El Diario del Fin del Mundo*, *El Sureño*, *Provincia 23*. National newspapers were selected to cover a spectrum of types of readers and political orientation. In the provincial context, the media-reader contract (Verón, 1985) does not have major differences, given that these outlets are mostly conditioned by the production of local news and links to territorial references. As a result, for TDF, the selected media were those with the greatest circulation in the province's major cities (Ushuaia and Río Grande). Using each of these newspapers' online database, we searched for articles published between 2013–2015, using keywords in Spanish that included general terms for biological invasions (*especie exótica*, *especie introducida*, *especie no nativa*, *especie invasora*) and the names of the IIMs, including their scientific and common names (Table 1). The possible assemblage of IIMs in Argentina was taken from Ballari *et al.* (2016) and SAyDS and SAREM (2019), and included 23 species.

To quantify and describe the importance of the representation of these general and specific terms about IIMs in newspapers, we used agenda setting (McCombs and Shaw, 1993), which is a positivist approach that seeks to understand not only the news that are produced, but also their hierarchy and classification within the newspaper. Two units of analysis were used to obtain these data: 1) the news item itself, and 2) the placement and categorization of the article inside the newspaper. This dual standard was designed because frequently multiple key words appeared in the same article. Importance was assessed by considering whether 1) the article appeared as a headline or cover story on the newspaper's front page; 2) it had accompanying photographs; and 3) the overall length of the article measured as word count (small: <300 words, medium: 300–600 words, large: 600–1,100 words, very large: >1,100 words).

Table 1. List of Spanish keywords used for the search of articles about introduced invasive species in Argentine and Tierra del Fuego newspapers.

especie exótica	*rattus*	*Lepus europaeus*	zorro gris
especie introducida	ratón doméstico	ciervo dama	*Lycalopex griseus*
especie no nativa	*Mus musculus*	*Dama dama*	*Lycalopex gymnocercus*
especie invasora	ganado exótico	perros asilvestrados	*Pseudalopex griseus*
visón	ganado silvestre	perros baguales	rata almizclera
Neovison vison	conejo	*Canis lupus familiaris*	*Ondatra zibethica*
Mustela vison	*Oryctolagus cuniculus*	*Canis familiaris*	ciervo axis
castor	jabalí	gatos silvestres	*Axis axis*
Castor canadensis	*Sus scrofa*	gatos asilvestrados	peludo
ciervo colorado	chanchos salvajes	*Felis sylvestris*	*Chaetophractus villosus*
Cervus elaphus	chanchos silvestres	ardilla de vientre rojo	antílope
ratas	liebre	*Callosciurus erythraeus*	*cervicapra*

Then, we applied a qualitative interpretive strategy for content analysis of these articles. The social imaginary concept allowed us to understand the mechanisms at play in the construction of these news articles' communicational setting and analyze the production, circulation and reception of these terms in different enunciation contexts. The articles' values and thematic orientation were assessed as being negative, positive or neutral. The assessment of the news values was carried out based on the ways that the enunciator (the editorial line of each newspaper) established evaluative referential frameworks. If from its positioning, the article conceived the introduction of invasive species to be incorrect or having negative impacts on native ecosystems and species, then it was classified as negative. If it was not possible to identify a valuation in the discourse, either for or against, it was classified as neutral. Finally, if the newspaper detracted attention from the biological invasion aspects or directly supported introducing invasive species, then it was categorized as positive. To restrict the polysemic dimension of the keywords in the assessment of news values, only the news articles that name the targeted species were used. In addition to orientation, we categorized the article by the section in which it appeared, constructing four categories: 1) Science, 2) General Information, 3) Tourism and 4) Politics.

Finally, information sources referenced in the article were identified, including individual stakeholders and institutions. These sources were categorized as Political, Private Citizen, Private Sector, Protected Area and Science. The categories of Private Sector and Science were sub-divided to determine Private Sector sources related to agriculture and conservation, and Science references coming from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and all other institutions, including museums, universities and zoos. A category of Other was used to group remaining articles.

Results and discussion

The species and concept assemblage represented by newspapers

Of the 53 terms used in each newspaper's search engine, only 17 were found in 344 articles (Table 2). At the national level, the majority (73.5%) of the 222 news items used general terms. However, at the provincial level there was more attention given to particular species; only 38.6% of the 122 mentions in TDF were of general terms. Furthermore, overall, the search discovered that only 13 IIM species were mentioned in the media: 12 at the national level and seven at the provincial level. Although the media IIM assemblage was more speciose in the national press, their frequency was less, and no species was in more than 4.1% of these articles about biological invasions and exotic species. In contrast, in

Table 2. Newspaper articles (number and percentage) that mention general biological invasion or specific introduced invasive mammals' terms from newspapers at national level in Argentina and the provincial level in Tierra del Fuego.

Search keywords*		# of articles		% of articles	
		National	**Provincial**	**National**	**Provincial**
General terms	exotic species	55	11	24.8	9
	non-native species	75	8	33.8	6.6
	introduced species	23	5	10.4	4.1
	invasive species	10	23	4.5	18.9
	Subtotal	***163***	***47***	***73.5***	***38.6***
Common names	beaver	9	23	4.1	18.9
	red deer	7	1	3.2	0.8
	mink	6	2	2.7	1.6
	grey fox	6	0	2.7	0
	wild hog	3	0	1.4	0
	rabbit	4	2	1.8	1.6
	hare	8	0	3.6	0
	rat	3	2	1.4	1.6
	boar	8	0	3.6	0
	antelope	1	0	0.5	0
	feral livestock	0	1	0	0.8
	feral dog	2	44	0.9	36.1
	Subtotal	***57***	***75***	***25.6***	***61.2***
Scientific names	*Dama dama*	2	0	0.9	0
	Subtotal	***2***	***0***	***0.9***	***0***
	Total	***222***	***122***	***100***	***100***

***Search terms were in Spanish; see **Methods** for full list.

TDF, feral dogs (*Canis lupus familiaris*) and the North American beaver (*Castor canadensis*) were responsible for 36.1% and 18.9% of the newspaper articles, respectively. At the national level, these same species were treated in only 0.9% and 4.1% of the assessed articles.

Regarding the use and portrayal of these terms and concepts in the media, it is important to note that we detected a frequent polysemy of the term *especie exótica* ('exotic species' in Spanish). Almost half of the time it was used at the national level, it was as a synonym of rare, strange, exuberant. It was also often associated with articles about travel, tourism and zoos, referring positively to rare or beautiful species (Table 3).

Table 3. Ways that newspaper articles use the term *especie exótica* (exotic species in Spanish) at the national and provincial levels.

Use	National	Provincial	Total
Ecological meaning	27 (49%)	11 (100%)	38 (57%)
Other uses, like rare, exhuberant	28 (51%)	0 (0%)	28 (43%)
Total	***55 (100%)***	***11 (100%)***	***66 (100%)***

Overall, the representation of biological invasions in TDF's provincial newspapers has been influenced by the position of these species as a socio-territorial problem, which has become important politically. For example, in 2017 a provincial law was approved regarding the control of feral dogs in rural settings, and in 2008 a binational agreement was signed between Argentina and Chile for beaver eradication (Menvielle *et al.*, 2010). Plus, it is noteworthy that at the provincial level the term exotic species was only used with its scientific-ecological meaning, and polysemy with other definitions was only observed at the national level (Table 3). Plus, regarding terminology, it is evident from these database searches of national and provincial print media that while scientific names for species are a common discursive form in academia, their use in newspapers is almost non-existent.

The importance of IIMs in newspapers

Of the total 344 newspaper articles found at the national and provincial levels, none appeared on the front page. The fact that during a 3-year period of news coverage there were no cover stories or headlines on biological invasions or IIMs indicates that the problem has less social resonance than other topics that appear with frequency, including security, economics, and others environmental issues that might be more immediately relevant to broader sectors of these largely urban societies, such as floods, earthquakes, mining, etc. However, at the same time, we found results that would attenuate this apparent thematic invisibility. Based on the extent and graphic support of the news, we found that articles about IIMs were treated and developed within the interior sections of the newspaper, which enhances the importance of articles. Specifically, 67% of national and 55% of provincial articles were large (600–1,100 words). Medium-sized news stories (300–600 words) constituted 22% and 36%, respectively, and small articles (< 300) were the least, with 10% and

7%. Also, the majority at both levels (69% of national, 87% of provincial) of stories built their representation with at least one photo. Additionally, national news on this topic only appeared every 6.4 days on average during the 3-year period studied, while in TDF it was only once every 11.4 days.

In synthesis, these data indicate that while newspaper articles about IIMs and biological invasions are not important enough to merit a headline, they were consistently treated in some depth in the interior of the newspaper, considering both length and graphic material. Plus, it is of note that their treatment was not drastically different between national and provincial levels.

Value and thematic orientation

More than 95% of provincial news items construct their story about introduced invasive species, and mammals in particular, generally from a critical or negative perspective (Table 4). However, at the national level, most articles were classified as presenting the topic from a neutral stance (51.7%), and only 38% were explicitly negative. Plus, we only found positively oriented articles at the national level. Given the largely negative assessment of invasive species, particularly in TDF, we can argue that these value systems transcend the media-reader contract of specific newspapers and affect the overall social representation of environmental issues, where in this case the newspapers agree with and re-enforce this specific value, which appears to be upheld by broader social forces as well. At the same time, we can observe some variation that would affect the way readers understand this issue, related to the polysemy previously described for "exotic species," which can also mean different, far away or even desirable.

Table 4. Value orientation of articles referring to introduced invasive mammals in Argentine and Tierra del Fuego newspaper items.

Values orientation	National (%)	Provincial (%)	Total (%)
Negative	37.9	95.9	74.2
Positive	10.4	0	3.9
Neutral	51.7	4.1	21.9

Regarding the construction of the thematic orientation of these reports, most were published in sections that deal with General Interest (51.7% and 53.2% respectively for national and provincial news; Table 5). Science sections contained 20.8% and 25.3% of national and provincial news, respectively. However, a difference between the two levels was that in national media 26.7% of articles were published in sections that dealt with Tourism. In this case, though, a large portion of the articles used the term "exotic species," but had a different meaning (see above on polysemy). In TDF, 20.3% of articles were published in sections related to Politics, again demonstrating the insertion of this topic into the public/political agenda, particularly surrounding the specific issues of feral dogs and beavers that are explicitly part of the provincial government's environmental agenda.

In particular, besides impacts to native biodiversity, feral dogs are being recognized as a major threat to sheep production in the ranches located in northern TDF, where there are reports of high economic losses and even some ranches are transitioning from sheep to cattle production as a result (Zanini *et al.*, 2008; Valenzuela *et al.*, 2014; Lartigau *et al.*, 2019; Barbe *et al.*, this volume). Furthermore, beavers were introduced in TDF in 1946, and since then, they have spread throughout the entire archipelago and reached the mainland, affecting more than 40% of all riparian forests in TDF (Anderson and Roulier, this volume).

Table 5. Percentage of articles about introduced invasive species categorized by newspaper section.

Section categories	National (%)	Provincial (%)
General information	51.7	53.2
Tourism	26.7	1.3
Science	20.8	25.3
Politics	0.8	20.3

News sources

Overall, specific sources were cited in 27.1% and 89.4% of national and provincial news articles, respectively. At the national level, the principal sources were Science (47.8%) and Private Sector (26.1%), which included representatives from agricultural, hunting and industrial associations. At the provincial level, in TDF, we observed a dominance of Political sources (51.2%), but also an important contribution from scientific experts and institutions (39.3%) (Fig. 1a). At both national and provincial levels, within the scientific sources, the CONICET was the specific institution with a highest contribution to newspaper articles about this topic (21.7% and 22.6%, respectively), followed by the Universidad Nacional de Tierra del Fuego (UNTDF). In contrast, at the national level, the private sector contribution was driven largely by conservation non-governmental organizations (NGOs), while in TDF we found a high citation of sources from the agricultural sector, particularly the Rural Association's opposition to feral dogs (Fig.1b).

In general, it is striking to see the general lack of specific sources being cited in the national media, but the fact that scientists and politicians are driving the discourse in TDF coincided with the hypothesis that this "natural laboratory" of invasion biology (*sensu* Valenzuela *et al.*, 2014) has led the topic to be not only of high scientific interest, but also part of the political agenda. Indeed, the provincial governor and other authorities were often cited in these news items, as well as scientists from CONICET's Centro Austral de Investigaciones Científicas (CADIC) and UNTDF's Instituto de Ciencias Polares, Ambiente y Recursos Naturales (ICPA), the UNTDF's school of the environment. Other social actors that had prominent roles included both traditional environmental organizations, such as conservation NGOs at the national level and also protected areas, such as provincial and national parks administrations. However, it is remarkable to note the inclusion of specific private sector actors, including the agricultural sector in TDF. Yet, among all the news articles found in this search, only three interviewed private citizens. Therefore, the full diversity, breadth and depth of the issue has yet to be addressed in the representation of these species and the issue in general.

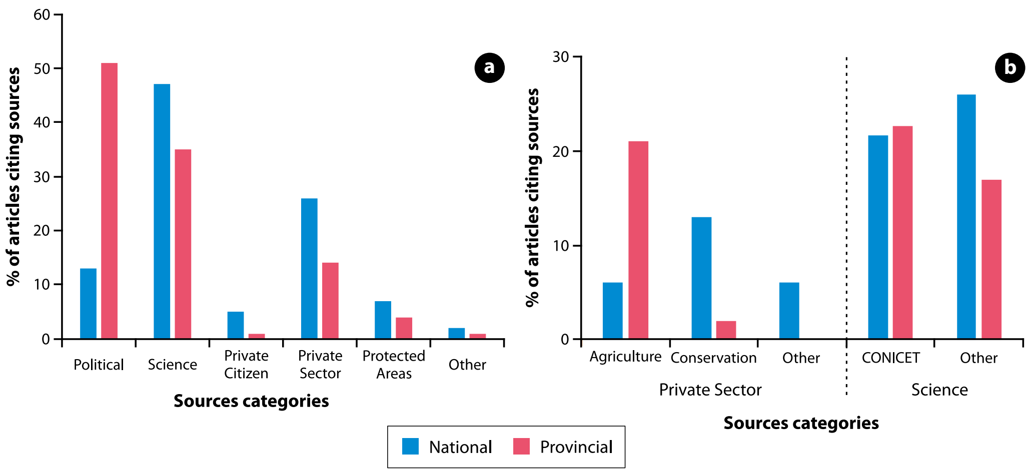

Figure 1a. Percentage of news articles that cited information from different source types; **1b.** percentage of articles citing sources from a subdivision of Private Sector and Science categories.

Conclusions

A total of 23 IIMs have been described for Argentina and 18 for TDF (Valenzuela *et al.*, 2014; Ballari *et al.*, 2016), but this study found that only 13 of these are portrayed in newspapers. Furthermore, since none one of the 344 newspaper articles found were a cover story, the overall position of topic has not been a priority, as is reflected by the news items' relegation to interior pages of the newspaper. This finding leads us to conclude that introduced invasive species are not a priority public issue at both national and provincial levels, which contradicts our expectation that the topic would be more prominent in the provincial media. In TDF, we had expected that the positioning of biological invasions by local scientists would give it greater prominence in the media. Nonetheless, despite not being "front page" news, when presented the articles were frequently well developed (in length and graphic support), and particularly in TDF reports dealt with specific issues surrounding the management of two problematic taxa: North American beaver and feral dogs.

At the same time, it is important to point out that a high percentage of articles in national newspapers use the term "exotic species" in a way that is different than its technical and scientific meaning in invasion biology. Indeed, a high number of publications dealt with "rare" and "beautiful" species that were attractive from a tourism perspective. This polysemy is crucial to take into account, given the contested and potentially contentious nature of invasive species management, which if not addressed can lead to conflicts. Indeed, if large segments of society understand these terms differently, effective communication will be difficult, and invasion scientists and managers should consider other ways of describing the issue. Overall, there is a need to strength the social comprehension of the consequences of species introduction and the impacts of biological invasions, but communication is not a unidirectional activity. Indeed, there is much room for researchers and practitioners to incorporate new metaphors and terms, rather than simply "educate" the public.

At the same time, though, 100% of provincial news in TDF used the term "exotic" related to the term's ecological meaning. Regarding news classification, even when these issues are not in the front page, the politics section of newspapers became key to give importance to them in the public agenda, and also to legitimize the negative perception of species introductions as a harmful practice that not only affects the environment, but also human well-being. The provincial news highlighted the main socio-environmental issues in TDF, which are feral dogs and their impacts on sheep ranching, and the North American beaver that affects riparian forest and the freshwater bodies. This finding indicated that media representations are more important when there are direct experiences that involve the general public in a socio-ecological territorial problem with concrete and visible consequences. We suggest that future communication strategies regarding biological invasions focus media articles in regional/local newspapers to better contextualize each species with its territorial situation, rather than general national-level articles.

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Fact sheets on the Introduced Invasive Mammals of Argentina

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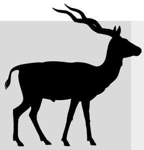

Antilope cervicapra

blackbuck, antílope negro

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Resumen. El antílope negro es originario del continente asiático y su distribución incluye Pakistán, Nepal e India. Posee dimorfismo sexual en adultos por la coloración del pelaje y machos con astas anilladas y en espiral. Especie principalmente diurna, muy veloces y ágiles, y gregarios, excepto los machos que son territoriales en época de apareamiento. Habita en planicies, bosques abiertos, pastizales y áreas de cultivo. Son herbívoros que se alimentan de pastos bajos, hojas, arbustos y cereales de cultivo. *A. cervicapra* fue introducido en Argentina a principios del siglo XX para cazarlo deportivamente. Actualmente, por los escapes de las áreas de confinamiento, por el movimiento de animales y las actividades de caza ilegales, esta especie tiene poblaciones confirmadas en silvestría y/o confinamiento en las provincias de La Pampa, Córdoba, Buenos Aires, Neuquén, Río Negro, San Luis, Santa Fe, Entre Ríos, Corrientes y Santiago del Estero. En su rango nativo hay escasos reportes de sus impactos, indicando principalmente daños sobre cultivos, mientras que en Argentina no se han indicado daños agrícolas hasta el momento. Los cambios en la vegetación nativa por el antílope podrían provocar alteraciones en la dinámica de los depredadores tope y competencia con herbívoros nativos. El Parque Nacional El Palmar, donde ocasionalmente se ha observado la presencia de la especie, ha incluido al antílope dentro de un plan de control de mamíferos exóticos que controla sus poblaciones a través de la caza. Sin embargo, ningún individuo ha sido cazado hasta el momento dentro del área protegida.

General description of the species

Blackbucks are a medium-sized antelope with a graceful and slender build (Fig. 1). They stand about 81 cm at the shoulder and weigh about 40–45 kg. With pronounced sexual dimorphism, sex is readily distinguishable by color differences. Albinos are fairly common. In mature males, the upper part of the body is black with a white belly and eye rings, while subadults are dark brown above and white below with a prominent white circular patch around the eye. Males also have ringed and coiled horns (45–81 cm long), that are sharply pointed and form a "V" above the head. Females are a yellowish fawn color and lack horns (Nowak, 1991; Long, 2003). Blackbuck are mainly diurnal. They are very fast runners and jumpers, crossing high fences. They are largely herd-living, except territorial males that defend mating arenas in open areas. Gregarious, their herds can range from fifteen to hundreds. Their habitats include plains, open woodlands, wet coastal areas, steppe, dry deciduous forest, riverbanks, scrub and grassland, salty flatlands, undulating, stony hills with bushes and cultivated areas. Blackbucks are grazers, preferring to feed on short to mid-length grasses, leaves, forbs, and they browse on common bush species and various cultivated cereals. Antelopes generally have one and rarely two calves per year. The normal lifespan is 10–12 years, and rarely they can reach 18 years in the wild or 15–16 in captivity (Canevari and Vaccaro, 2007; Long, 2003; Mahato *et al.*, 2010; Jadeja *et al.*, 2013).

Figure 1. *Antilope cervicapra* in Argentina. Photo: Gabriel Rojo.

History of the invasion

The blackbuck is native to Asia, mainly found in India, but also present in Pakistan and Nepal. Its distribution is discontinuous, with very sparse populations (Long, 2003; Mallon, 2008; Mahato *et al.*, 2010). This antelope was introduced in Argentina between 1906 and 1912 for sport hunting in game reserves in southeastern La Pampa, Córdoba, southwestern Buenos Aires, Chaco and San Luis provinces. Subsequently, other introductions were conducted in eastern Entre Ríos, southern Santa Fe and Buenos Aires between 1940 and 1960 (Petrides, 1975; Navas, 1987; Long, 2003; Canevari and Vaccaro, 2007). More recently, blackbuck is also known to be present in Neuquén, Río Negro, Corrientes, and Santiago del Estero provinces (Ballari *et al.*, 2019).

Patterns of expansion and current distribution

The antelope is currently found in the central and northeastern region of Argentina (Fig. 2). The main vector for its movement to new locations is people and their activities

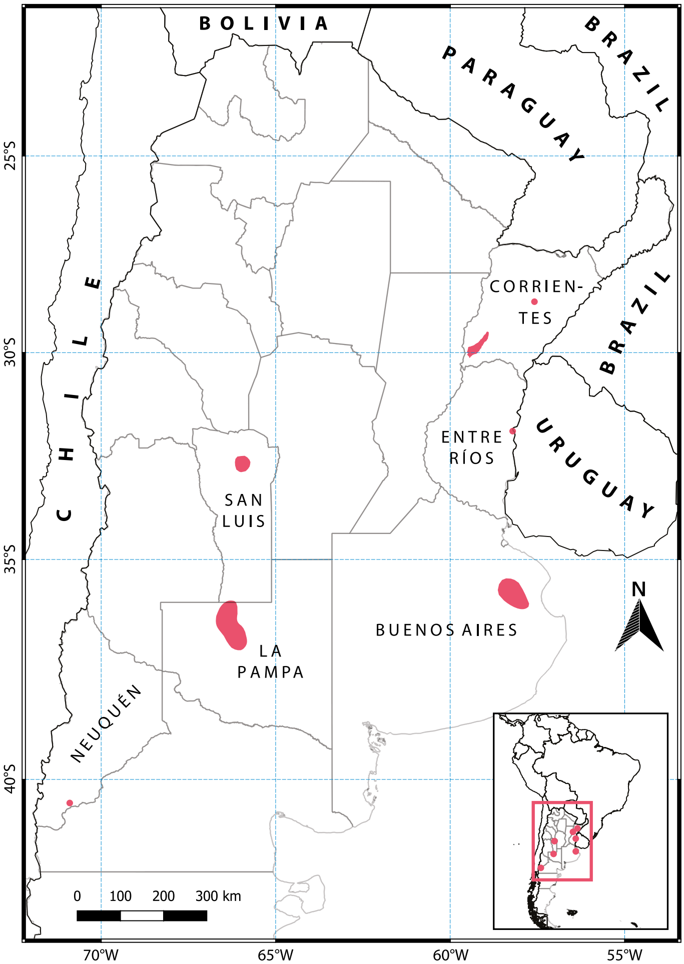

Figure 2. Distribution of *Antilope cervicapra* in Argentina. Modified from Ballari *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

related to legal and illegal hunting. The unregulated transport of animals and the presence of illegal hunting reserves seem to be the current sources of dispersion of this species in Argentina (Ballari *et al.*, 2019). Additionally, there are numerous legal hunting reserves in central and northeastern Argentina, where the species can be found and represent potential sources for new escapes (Ballari *et al.*, 2016). The species' wide and continuous dispersal for hunting purposes and the scarcity of natural predators mean that antelope populations are abundant and increasing (Ballari *et al.*, 2019).

Impacts

There are no studies of this species' impacts in Argentina. In its native range, blackbucks can damage agricultural crops, but overall their effects are not significant (Chauhan and Singh, 1990; Jhala, 1993). On the other hand, antelopes do host internal and external parasites (Thornton *et al.*, 1973; Mertins *et al.*, 1992) that may harbor diseases that endanger native wildlife. In particular, this could affect native deer that coexist with antelopes, such as brown brocket (*Mazama gouazoubira*) and marsh deer (*Blastocerus dichotomus*). In their native range, blackbucks are important seed dispersers, including seeds of invasive weeds that mostly depend of the large behavioral differences between individuals of a species, arising from extreme male mating strategies (Jadeja *et al.*, 2013). In Argentina, studies have indicated that antelope modifying plant communities could alter the population dynamics of predators (*e.g.*, cougar *Puma concolor*) and compete with native herbivore species (*e.g.*, patagonian mara *Dolichotis patagonum*, greater rhea *Rhea americana*) (Cabrera, 2015; Sánchez, 2015).

Management

In Argentina, no national management strategy has been implemented. Parque Nacional El Palmar in Entre Ríos included *A. cervicapra* in the list of potential targets in its controlled hunting plan since 2006. However, no individuals were hunted because their presence inside the protected areas is circumstantial (Gürtler *et al.*, 2018).

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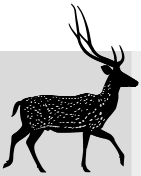

Axis axis
chital, ciervo axis

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Resumen. El ciervo axis o chital es nativo del subcontinente indio. Es una especie generalista de hábitat que evita ambientes extremos. Su sistema digestivo es de un consumidor intermedio y se alimenta de gran variedad de plantas, principalmente pasturas. Puede formar grupos de más de 150 individuos y alcanzar altas densidades en áreas protegidas libres de ganado y depredadores. Fue introducido en Uruguay con fines cinegéticos y desde allí se translocaron individuos a la provincia de Buenos Aires, donde se expandió asociado a montes de tala (*Celtis ehrenbergiana*) próximos a la Bahía Samborombón. Desde Uruguay habrían cruzado a Entre Ríos (Argentina), y se expandieron por prácticamente toda de la provincia llegando a la provincia de Corrientes y al bajo delta bonaerense del Río Paraná. También se translocaron individuos a la provincia de Santa Fe y a los Esteros del Iberá en Corrientes, desde donde se han expandido y formado poblaciones silvestres. En Argentina se ha observado que producen daño sobre la flora nativa y plantaciones forestales. Puede competir con el ganado, tanto de forma comportamental como por el uso de recursos alimenticios. A su vez es vector de enfermedades bovinas como la Diarrea Viral Bovina. Posee además parásitos que podrían afectar a la fauna nativa y a la salud humana. Las medidas de control han sido escasas hasta el momento y focalizadas en áreas protegidas, principalmente en el Parque Nacional El Palmar.

General description of the species

Chital, axis deer or spotted deer is one of the most common and widely distributed native cervid in the Indian subcontinent. It originally inhabits India, Nepal, Bhutan, Bangladesh and Sri Lanka (Duckworth *et al.*, 2015). It is a medium-sized deer. Males are usually larger, reaching a weight of up to 113 kg; nevertheless, the average adult males weigh 75 kg and the females 45 kg (Long, 2003). Their coat is reddish brown, darker at the top, with well-defined white spots on the back and flanks; a black stripe runs down the spine from the nape to the tip of the tail (Fig. 1). The abdomen, chest, throat, insides of legs and ears, and underside of tail are white. The head is brown and the muzzle blackish. Only males have antlers, which usually have three ends, with a brow tine (found just above the base) and a forked main beam. Chital is a habitat generalist species. In its natural environment it avoids extremes, such as dense moist (evergreen) forests and open semi-deserts or deserts. Moist and dry deciduous forest areas, especially adjoining dry thorn scrub or grasslands, appear to be optimal for it, and highest densities of chital are reported from these habitats (Duckworth *et al.*, 2015). It eats a wide variety of plants. Being an intermediate feeder, the gastrointestinal system is similar in morphological characteristics to both types of ruminants: browsers and grazers (Pérez *et al.*, 2015). It usually feeds on grasses, but it also consumes leaves, flowers and fruits, mainly in seasons where forage quality decreases (Johnsingh and Sankar, 1991). Groups may number up to 150 or more individuals, with a composition that changes frequently during feeding periods and in flight from potential predators (Dinerstein, 1980). In their natural distribution they can be found at densities ranging up to 200 animals per km^2 in protected areas practically free of predators and livestock (Raman *et al.*, 1996). In a day, the periods when they are most active are usually during dawn and dusk, which are characterized by peaks in feeding activity (Álvarez-Romero *et al.*, 2008). Reproductive patterns in India show a clear seasonality; however, deer with hardened antlers and in rutting condition may be found throughout the year. Only one fawn (rarely two) is produced per pregnancy after a gestation period of 210–238 days (Mishra, 1982).

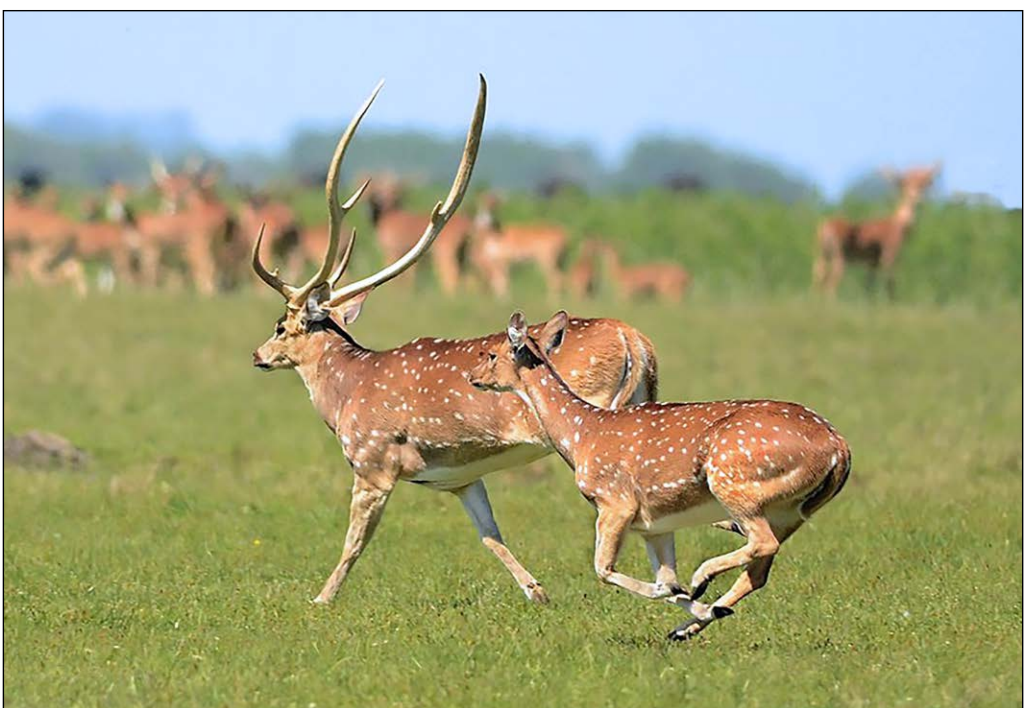

Figure 1. *Axis axis* in Argentina. Photo: Horacio Patrone.

History of the invasion

The first specimens in South America were introduced for hunting purposes by Aarón de Anchorena, in his farm in Barra de San Juan in Colonia department, Uruguay (González and Lanfranco, 2010). As for Argentina, chital were introduced sometime between 1928 and 1930, sent by Anchorena from Uruguay to Punta Indio, Buenos Aires province (Navas, 1987). Specimens from this region were later introduced to the mountain range systems of Ventania and Tandilia, and to central provinces such as La Pampa, Córdoba and Santa Fe (Abba *et al.*, 2009). The Santa Fe introduction in particular is reported to have been at least 30 years ago, in the vicinity of San Javier (Pautasso, 2008). Chital specimens were also taken to the provinces of Neuquén and Río Negro (Navas, 1987). In 1973, they are thought to have been introduced in Tucumán, in the Yastay hunting club (Grau *et al.*, 1995). In the early 1980s, 12 specimens were released in the area of Sayuque Viejo, San Luis province (Jackson, 1986). From Uruguay, crossing the homonym river, the species would have entered to Entre Ríos province (Muzzachiodi, 2007). In Corrientes province, chital would have entered from the south, coming from Entre Ríos; and also, it would have been introduced in the Esteros del Iberá (Fabri *et al.*, 2003). It has been observed in the Buenos Aires portion of the lower delta of the Paraná River since 2008 (Fracassi *et al.*, 2010).

An earlier introduction of chital in Argentina is proposed by Novillo and Ojeda (2008), following Lever (1985). It would have been introduced in 1906, in La Pampa province, at about the same time when red deer specimens (*Cervus elaphus*) were introduced in the farm San Huberto (future nature reserve Parque Luro). However, a close examination of the data from the reserve does not support this proposal: the introduction of chital on that date is not mentioned in the reserve's history, neither is its presence when the farm was bought in 1939 (Amieva, 1992), and no specimens have been recorded in that location up to the present.

Patterns of expansion and current distribution

In Argentine territory, chital specimens have undergone numerous translocations because of their hunting importance. Subsequently, this species has expanded from the hunting grounds and formed wild populations (Fig. 2). However, not all the sites where the species is reported to have been introduced correspond to areas where wild population can be found in the present: for some of them, the number of individuals has declined or even disappeared; for others, they remain restricted to farms or hunting grounds; lastly, there are some specific sites where they may have not been introduced.

In Buenos Aires province they have proliferated in association with natural tala (*Celtis ehrenbergiana*) forests close to Bahía Samborombón (Navas, 1987), extending in General Lavalle, Magdalena, Tordillo, Punta Indio, Chascomús, Berisso and Castelli departments. Wild populations have also been recorded in Gral. Madariaga and Gral. Pueyrredón. Individuals have been registered in Tornquist, Bahía Blanca, Balcarce, Guaminí, Gral. Belgrano and Coronel Suárez (Carpinetti and Merino, 2000); however, we cannot ensure that wild populations exist in those departments. In the Buenos Aires portion of the lower delta of

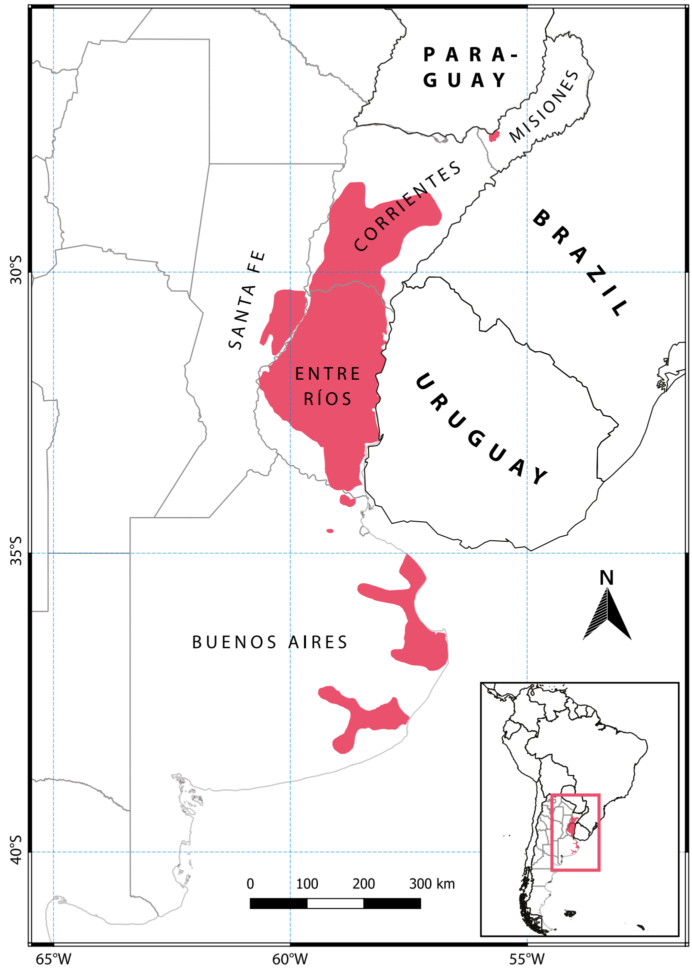

Figure 2. Distribution of *Axis axis* in Argentina. Modified from Tellarini *et al*. (2019). (Mapping: Ian Barbe and Alfredo Claverie).

the Paraná River, chital is found on a reduced area, due to the recent nature of the invasion, but records from the last few years suggest that it is expanding (Tellarini, pers. obs.).

In Entre Ríos, it has expanded practically all over the province, and presence has been documented for the protected areas of Parque Nacional El Palmar, Parque Nacional Predelta and the El Potrero private reserve (Muzzachiodi, 2007). In Santa Fe, the species seems to be scattered over a large area that includes the entire zone between Saladillo Dulce and Saladillo Amargo streams and the surroundings of the provincial route 39 (San Javier and San Justo departments), it has also been recorded a little north of Fortín Olmos in Vera department (Pautasso, 2008). In Corrientes, it is distributed mainly in the center and south of the province, and in the south-east area of the Iberá reserve, occupying mainly the Espinal environments; even though it seems to be beginning to expand into patches of hygrophilous forests surrounded by grasslands (Cirignoli, pers. comm.). In Neuquén there are no wild populations; it is confined to private farms (Guichón *et al.*, 2016). The same may have occurred in Córdoba and Río Negro: in the latter, the wild population of Victoria Island could not prosper due to the cold weather and the competition with red deer and fallow deer (*Dama dama*) (Navas, 1987). In Tucumán, it may have never been introduced (Juliá, pers. comm.), and the notion of chital in that province could be attributed to a miscitation of red deer presence. In San Luis, the only available report is of an individual that was found dead on Route 27, 80 km south to Villa Mercedes. In Misiones, there are recent records in the south of the province as well as in the center-east, in El Soberbio locality. In La Pampa province, it is present in numerous hunting grounds, where it probably remains confined.

Impacts

No studies on the impacts of chital on native and implanted flora have been performed in Argentina. Nevertheless, damage to trees has already been observed in native trees in Parque Nacional El Palmar (Sobral Zotta, pers. comm.), as well as in forest production in Entre Ríos (Tellarini, pers. obs.) and ornamental trees in Uruguay (González and Seal, 1997). These effects are greatest during the reproductive season, when bucks rub their antlers on bark.

It has been shown that chital compete with other deer species such as white-tailed deer in Texas, USA (Faas and Weckerly, 2010). In Argentina, it shares territory and could compete with the pampas deer (*Ozotoceros bezoarticus*) in Bahía Samborombón and Corrientes, with marsh deer (*Blastocerus dichotomus*) in Paraná River delta and Corrientes, and with gray brocket (*Mazama gouazoubira*) in Corrientes, Santa Fe and Entre Ríos; agonistic behaviors towards the latter have been observed in Iberá (Cirignoli, pers. comm).

Chital presence can also be linked to an increase in parasites and illnesses affecting local mammals. Research from Iberá marshlands shows that chital and native fauna are both infected with the same tick species, resulting in a population increase of ticks and their associated parasites (Debárbora, 2012). Bovine Viral Diarrhea antibodies have been detected in blood tests performed on chital individuals hunted in Iberá (Sciocia *et al.*, 2011). In Parque Nacional El Palmar, 22% of the analyzed individuals showed positive seroprevalence for leptospirosis (Tammone *et al.*, 2018). The presence of *Mycobacterium bovis*, the main agent of tuberculosis in cattle, was observed in deer from Buenos Aires, Entre Ríos and Corrientes (Barandiaran, pers. comm.).

A known effect of chital in its native distribution is the competition with livestock, both behavioral and through the use of food resources (Madhusudan, 2004). A survey of field enclosures with winter pastures for cattle performed in Gral. Lavalle (Buenos Aires) showed that chital consumed 60% of the greenery (Mc Loughlin, pers. comm.).

Management

Chital is included in the introduced invasive species management plan of Parque Nacional Campos del Tuyú. Although the species is not established within the park, isolated individuals are occasionally hunted in it (Beade, pers. comm.). In Parque Nacional

Iberá, in Estancia El Socorro, individuals have been hunted as part of a control program in order to reduce its quantity and mitigate its possible impacts (Cirignoli, pers. comm.). In Parque Nacional El Palmar, chital hunting began in 1996. Since 2006, a formal introduced invasive mammal control plan has been applied. Several methods of hunting are used, the most common being the elevated hunting platforms with firearms using salt baiting. From 2006 to 2015, the number of deer hunted per year has grown, reaching 513 deer hunted in 2015 (Gürtler *et al.*, 2018).

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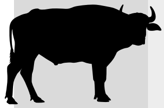

Bubalus arnee bubalis

wild water buffalo, búfalo asiático

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Resumen. El búfalo de agua o búfalo asiático es un bóvido grande originario de Asia, con grandes cuernos y coloración oscura. Herbívoro y gregario, habita ambientes húmedos e inundables. En su distribución nativa las formas silvestres se encuentran amenazadas y en declinación. Las formas domésticas han sido introducidas en casi todo el mundo para la producción de carne, leche y cuero, y para la caza deportiva. Escapes y sueltas de cautiverio han permitido que se establezcan poblaciones silvestres. En Argentina se introdujo para fines productivos en la década de 1970 y hoy la presencia de búfalo de agua confinado atraviesa prácticamente todo el país. Las poblaciones asilvestradas detectadas representan puntos del espacio donde los individuos han sido soltados deliberadamente o han escapado del confinamiento. Los principales impactos de la especie se asocian al sobrepastoreo y pisoteo en suelos poco consolidados, típicos de los ambientes inundables que suele habitar, lo que deriva en impactos potenciales a la fauna, que ya han sido probados en otros países aunque todavía no en Argentina. Si bien algunas provincias poseen marcos legales que habilitan la caza de control y el consumo de su carne, no existen a la fecha planes de manejo que aborden las problemáticas asociadas a las poblaciones asilvestradas.

General description of the species

The wild water buffalo (*Bubalus arnee bubalis*) is a large bovid with a body mass up to 800 kg for females and up to 1,200 kg for males (Fig. 1; Rodríguez Planes *et al.*, 2019). Its height at the shoulder can reach about 2 m. Both sexes carry half-moon shaped horns that can span 2 m wide from tip to tip. It also has a distinctive white "V" below the neck.

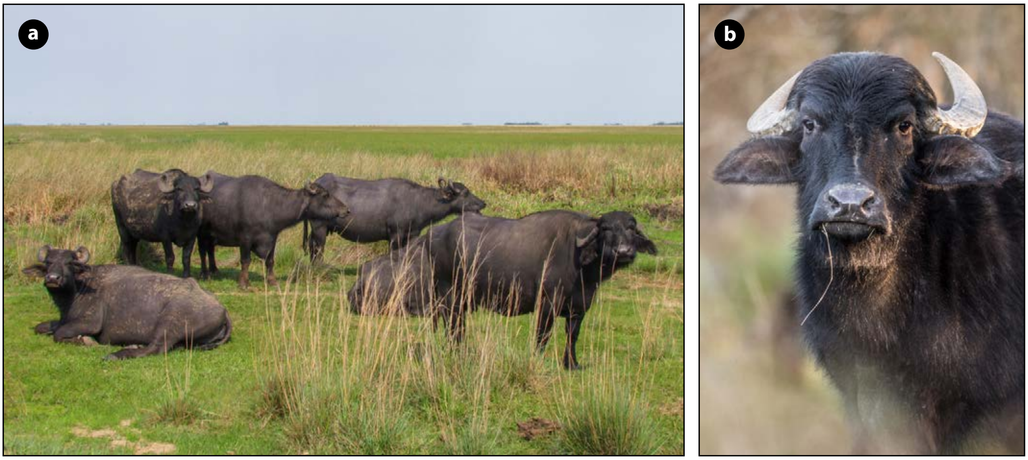

Figure 1. a. *Bubalus arnee bubalis* in Parque Nacional Iberá, Argentina. (Photo: Sebastián Cirignoli). **b.** Detail of a buffalo individual. (Photo: Carlos Carubia).

Its hide is covered by sparse, long gray to black hairs with gray "socks" below knees. Its tail is long and hairy at the tip.

The water buffalo is strongly associated with wet environments, such as forested rivers and wetlands, including swamps and flooded grasslands. It is generally found at low altitudes, except in Nepal, where it inhabits swamps at 2,800 or more meters over sea-level.

The species is a generalist herbivore that is mainly terrestrial and cathemeral. They live in groups of about 10–30 individuals, but occasionally may aggregate in herds of over 100 individuals.

Buffalos have a polygynic mating system. Seasonality may occur only in some areas of its native distribution range. Females reach sexual maturity at about one and half years and males at three. Gestation extends for 312 to 334 days, and cows have one calf every two years (Tulloch, 1979).

Remnant wild populations persist in India, Bhutan, southern Nepal, Thailand, Myanmar, and Cambodia. It is considered extinct in Bangladesh, Vietnam, parts of Malaysia, some islands around Sumatra, Java and Borneo, and probably Lao. *Bubalus arnee* is considered Endangered by the IUCN, and with a decreasing population trend (Hedges *et al.*, 2008).

History of the invasion

While the water buffalo is native to Asia, they were imported from Romania to southern Entre Ríos province in Argentina for meat production in the early 20th century (Crudeli *et al.*, 2004). After the intended crossbreeding with *Bos taurus* failed, a few individuals were released for hunting (Crudeli *et al.*, 2014). Earlier introduction events have been mentioned in the literature, mainly for hunting purposes, around 1900 in Corrientes province, but these apparently did not establish viable feral populations (Petrides, 1975).

Spread pattern and current distribution

Spread of water buffalo is spatially associated with its main productive use: cattle raising and sport hunting. The current free-ranging distribution is mostly based on escapes from captivity, either from pastures or game reserves (Fig. 2). Such events have occurred re-

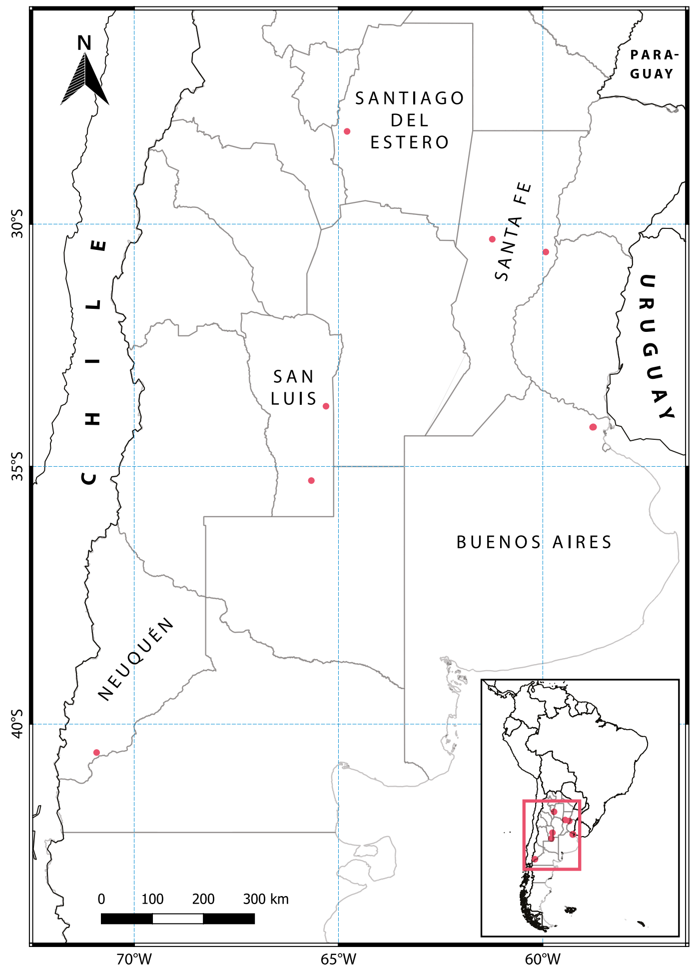

Figure 2. Distribution of *Bubalus arnee bubalis* in Argentina. Modified from Rodríguez Planes *et al*. (2019). Mapping: Alfredo Claverie and Ian Barbe.

cently on some islands in the Paraná River delta (Buenos Aires province) and also in Parque Nacional El Palmar (Entre Ríos province), were they have been controlled. Individuals from an illegal game reserve in central-western Argentina (Santiago del Estero province) were released near Guampacha after a legal intervention in January of 2018. Raising water buffalo is an emerging productive activity in Argentina, promoted by the Asociación Argentina de Criadores de Búfalos and has been considered "the new livestock revolution," which is driving the proliferation of pastures with captive buffalos throughout Argentina. These and the numerous hunting reserves where the species can be found represent potential sources for new escapes (Petrides, 1975).

Impacts

Ecological impact

Environmental impacts have been documented outside of Argentina, including overgrazing that significantly modifies vegetation structure and composition (Skeat *et al.*, 1996; Alho *et al.*, 2011; Michels *et al.*, 2012; Bisaggio *et al.*, 2014), trampling that entails compacting soil and generating wallows and accelerated erosion, affecting the quality of water and wetlands (Skeat *et al.*, 1996), and favoring the spread of introduced weeds (Cowie and Werner, 1993). These changes in turn may negatively affect the associated fauna, as it was seen for caimans and storks in Brazil (Campos, 1993; de Moraes *et al.*, 2016) and geese in Australia (Corbett *et al.*, 1996). The buffalo's spread throughout the Paraná River delta may also affect native deer populations (*Blastocerus dichotomus*), as has already occurred in Brazil (Rodríguez-Planes *et al.*, 2019). Mixed buffalo-cattle pastures in Venezuela have discouraged the attack of big predators, such as jaguar *Panthera onca* and cougar *Puma concolor*, diminishing human-fauna conflicts, which may be considered a positive effect of well-managed buffalo herds (Hoogesteijn and Hoogesteijn, 2008). Environmental impacts have not yet been assessed in Argentina, where no extant literature is available.

Economic impact

Bubaline husbandry produces mainly meat, but also milk and leather. Bubaline milk accounts for 7% of global milk production, but this amount rises to 70% in India. Bubaline milk is less allergenic than cattle milk (Plana, 2005). Currently almost every Argentine province has this kind of productive activity, especially Formosa and Corrientes, which have over 30,000 head of livestock each. Meat has been exported to Brazil and Chile since December 2017, and recently, also to Italy and Vietnam, consolidating the water buffalo as a true livestock revolution. Sport hunting tourism has developed numerous game reserves in La Pampa, Neuquén and Santa Fe provinces (see Ballari *et al.*, this volume).

Health impact

Water buffalo may host some pathogens shared with cattle and fauna (see also Uhart *et al.*, this volume). Pathogens isolated from water buffalo in Argentina include the following: *Brucella abortus*, *Mycobacterium bovis*, *Neospora caninum*, *Toxoplasma gondii* and *Leptospira* in Corrientes, Chaco and Formosa (Campero *et al.*, 2007; Crudeli *et al.*, 2007; Guanziroli Stefani *et al.*, 2008; Konrad *et al.*, 2013), and *Fasciola hepatica* in Corrientes (Racioppi *et al.*, 2009) and Misiones (Lobayan *et al.*, 2016). Antibodies against bovine viral diarrhea (BVDV-1 and BVDV-2) have also been found at north-eastern Argentina (Craig *et al.*, 2015, Pecora *et al.*, 2017). In addition, virus isolated from buffalo encompass bovine parainfluenza 3 virus (Maidana *et al.*, 2012), Herpesvirus bubaline 1 (BuHV1) (Maidana *et al.*, 2014), shared with cattle (Maidana *et al.*, 2016), and rabies virus (Delpietro *et al.*, 1997).

In addition, water buffalo milk experimentally decreased the development of bowel cancer on rats (Ramírez *et al.*, 2012), which may be considered as a potential positive effect for healthcare industry.

Management

Programs promoting the breeding of water buffalo exist throughout Argentina, especially in marginal and less productive areas like wetlands on Paraná River islands (Steverlynck, 2014). In contrast, 50 feral buffalos were successfully eradicated from the Esteros del Iberá wetland (Corrientes province) after four years of exhaustive control and monitoring of introduced species (Cirignoli, 2010a, b). Santa Fe and Entre Ríos provinces have regulation policies that enable hunting for control and meat consumption. Only Corrientes, Neuquén and San Luis provinces have some kind of policy to regulate sport hunting, despite game reserves occurring in many other provinces (see Ballari *et al.*, this volume). No national management strategy has been conducted so far.

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Callosciurus erythraeus

Pallas's squirrel, ardilla de vientre rojo

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Resumen. La ardilla de vientre rojo, *Callosciurus erythraeus* (Pallas, 1778), es una ardilla arborícola y diurna originaria del sudeste Asiático que fue introducida en varios países de Europa, en Japón y en Argentina, logrando establecerse exitosamente. En Argentina fue introducida en la localidad de Jáuregui, partido de Luján, provincia de Buenos Aires en 1970 y hasta el momento se han registrado 28 eventos independientes de escapes o liberaciones de individuos, dando lugar a la presencia de ardillas en al menos 20 partidos o departamentos en las provincias de Buenos Aires, Santa Fe, Córdoba, Mendoza y en la Ciudad Autónoma de Buenos Aires (CABA). El traslado mediado por el ser humano debido a su atractivo ornamental y como mascota es la principal causa del origen de nuevos focos. Habita ambientes arbolados continuos o fragmentados, en zonas rurales, semiurbanas, residenciales y urbanas. Consume principalmente frutos, semillas y hojas de árboles y arbustos y construye nidos en los árboles usando hojas, ramas y corteza. El mayor daño registrado en Argentina es el descortezamiento de árboles, ya sea en plantaciones comerciales, ornamentales, en parques urbanos o en propiedades privadas, junto con los daños ocasionados en distinto tipo de infraestructuras, en el tendido eléctrico, en el cableado telefónico y en sistemas de riego. En relación a la salud pública y animal, esta especie es portadora renal de la bacteria *Leptospira interrogans* y posee parásitos adquiridos en el nuevo ambiente. Hasta el momento no existen planes sistemáticos orientados al control de las poblaciones, si bien se ha realizado un piloto de control en la población del foco de Cañada de Gómez, provincia de Santa Fe, que permitió disminuir su abundancia, y recientemente, se ha llevado a cabo un plan de control en una estancia privada en el foco de Tupungato, Mendoza. Existe un avance en lo que se refiere a las normativas orientadas a regular la captura, tenencia, traslado, comercialización y control de esta especie a nivel Nacional, Provincial y Municipal, pero es necesario seguir trabajando para generar nuevas normativas y asegurarse que las normativas ya existentes sean cumplidas.

General description of the species

General characters

Callosciurus erythraeus is a medium-sized diurnal tree squirrel (Fig. 1). It is native to southeast Asia, and it has been introduced in Argentina, as well as in France, Belgium, Japan, Hong Kong, Italy and the Netherlands (Lurz *et al.*, 2013). It inhabits different types of both continuous and fragmented arboreal habitats in natural and human-made forested patches. In Argentina, it occurs mainly in rural, urban, suburban and residential areas, including within or near protected areas, urban parks and commercial plantations for wood and fruit production (Guichón and Doncaster, 2008; Benitez *et al.*, 2013; Hertzriken, 2021).

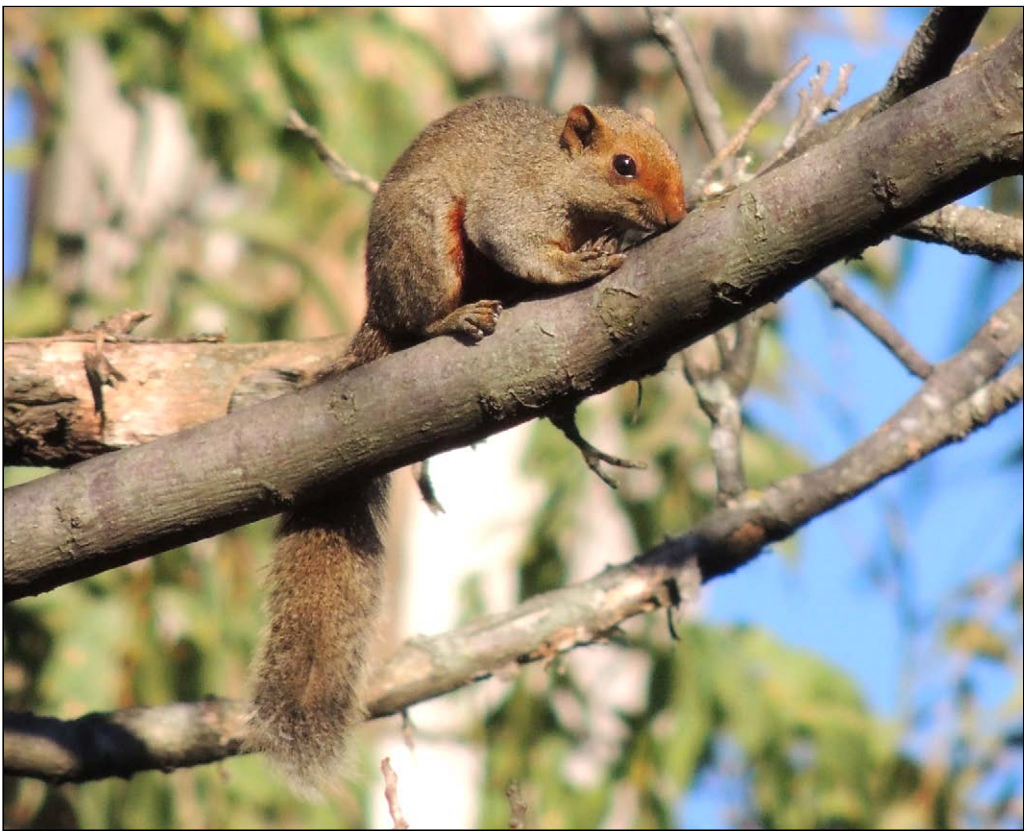

Figure 1. Adult of *Callosciurus erythraeus* in Buenos Aires province, Argentina. (Photo: Marina Hertzriken).

Body measurements obtained in Argentina are smaller than those reported in other countries. The range of adult weight of individuals measured in the main invasion focus (Luján, Buenos Aires province) is 262–270 g (Cassini and Guichón, 2009; Benitez, 2017), while in Taiwan and Japan adults reach 309–467 g (Yo *et al.*, 1992; Chakraborty, 1985; Tamura and Tereauchi, 1994). The mean total length of 32 specimens captured in Luján was 388.5 ± 24.8 mm (Cassini and Guichón, 2009).

This species has an agouti dorsal pelage (described as olive brown to grayish olive) and a black dorsal strip that can be present or absent (Cassini and Guichón, 2009). Ventral pelage varies from an intense red—which is the typical coloration—to a yellowish/orange color, giving different color patterns: from red bellies with yellowish/orange areas in some ventral parts (armpits, groin and chest) or yellowish/orange bellies with other ventral areas more reddish (Cassini and Guichón, 2009). The face from the nose up to the base of the ears is golden orange.

Diet

C. erythraeus in Argentina eats mainly fruits, seeds and leaves. Fruits and seeds represented the bulk of the diet in all seasons (feces analysis: >44%; behavioral observations: >38%) in two invasion foci studied in Argentina (Zarco *et al.*, 2018). Squirrels also consume epiphytic and climbing plants, flowers, bark, ferns, invertebrates, fungi, lichens, mosses and bird eggs in lesser proportions (Lurz *et al.*, 2013; Zarco *et al.*, 2018). Although squirrels feed on several tree and shrub species, only six species dominated their diet: *Cupressus* sp., *Cotoneaster* sp., *Pyracantha* sp., *Ligustrum lucidum*, and *Melia azederach* (Zarco *et al.*, 2018). Bark consumption was recorded from feces analyses throughout the year and included the genus *Cedrus*, *Cupressus*, *Eucalyptus*, *Fraxinus*, *Ligustrum*, *Melia*, *Morus*, *Pinus*, *Platanus*, *Polylepis*, *Prunus*, and *Robinia* (Zarco *et al.*, 2018). The consumption of flowers, seeds and fruits recorded in Argentina is similar to the diet composition described in its native range and in other countries where it has been introduced, such as Japan (Setoguchi, 1990; Lurz *et al.*, 2013). Diet composition varies throughout the year and among sites according to food availability (Lurz *et al.*, 2013; Zarco *et al.*, 2018).

Reproduction and population characteristics

Squirrels reproduce throughout the year in Luján, where reproductively active females, immature individuals and a high proportion of mature males can be found in every season (Benitez, 2017). Squirrels build nests in trees using bark and leaves to raise their offspring (Fig. 2). Preliminary results indicated an annual survival rate of 0.37–0.58 (Benitez, 2017), and a seasonal survival rate similar to those described in other introduced ranges, but higher than in their native range (Benitez, 2017). The lowest survival rates were found in winter, and there were no differences between males and females (Benitez, 2017).

Males have larger home ranges than females (Tamura *et al.*, 1987; Dozières *et al.*, 2015). Mean home range in Luján was 0.38 ha for females (n=12), almost an order of magnitude smaller than that of males (3.29 ha, n=3) (Benitez, 2017). These home ranges are smaller than those reported in other countries, where this species has been introduced, such as Japan (females: 0.48–0.72 ha) and France (females: 2.4–4.3 ha) (Tamura *et al.* 1987, 1988; Dozières *et al.*, 2015; Benitez, 2017).

Diseases and parasites

In Argentina, *C. erythraeus* has not been found to host novel parasites, but has acquired parasites from the recipient community (Gozzi *et al.*, 2013a, 2014). Ectoparasites

Figure 2. Nest of *Callosciurus erythraeus* covered by leaves. (Photo: Borja Baguette Pereiro).

include the flea *Polygenis* (*Polygenis*) *rimatus*, the mites *Androlaelaps fahrenholzi* and *Ornithonyssus* cf. *bacoti*, and the botfly *Cuterebra* sp. Mites of the genus *Cheyletus* that are not considered parasites were also found (Gozzi *et al.*, 2013a). Endoparasites were represented by nematodes of the genus *Stylestrongylus* and *Pterygodermatites* (Gozzi *et al.*, 2014). Regarding zoonotic diseases, *C. erythraeus* was found to be a renal carrier of *Leptospira interrogans* (samples obtained in Cañada de Gómez, Santa Fe province) and could be involved in the epidemiology of leptospirosis (Gozzi *et al.*, 2013b). In addition, feces and serum of squirrels from the main invasion foci were studied for detection of *Salmonella* spp. and *Toxoplasma gondii* respectively, finding negative results (Gozzi, 2015).

In its native range *C. erythraeus* is host of different ectoparasite and endoparasite species. In France, Belgium and Italy, where it has been introduced, this species harbors parasites acquired locally, but also species that have been introduced into the new environment with the founder squirrels (Asakawa, 2005; Sato *et al.*, 2007; Shinozaki *et al.*, 2004; Dozières *et al.*, 2010; Lurz *et al.*, 2013; Mazzamuto *et al.*, 2016; Eguchi *et al.*, 2022).

Genetics

A genetic study conducted in Argentina supported the hypothesis of a single introduction event, followed by subsequent translocations within the country (Gabrielli *et al.*, 2014; Guichón *et al.*, 2015). The genetic characterization of sequences from squirrels captured in Argentina was related to *Callosciurus finlaysonii* according to D-loop and Cytochrome b mitochondrial markers (Gabrielli *et al.*, 2014). Anyway, due to the intraspecific variation among sequences of *Callosciurus* belonging to different subspecies or collected from different regions, further research taking into account diagnostic morphological characters and genetic markers are needed to elucidate the complex taxonomy of the genus *Callosciurus* and the phylogeny of *C. erythraeus* and *C. finlaynsonii* (Gabrielli *et al.*, 2014).

History of the invasion

C. erythraeus was intentionally introduced into Argentina in 1970 in the locality of Jáuregui, Luján district, Buenos Aires province (Aprile and Chicco, 1999). The introduced squirrels were obtained from a pet shop in the Netherlands and taken to a ranch near the town of Jáuregui for ornamental purposes by an European family longing for squirrels. Then, by 1973 about five out of the 10 individuals introduced had been released or escaped from the cage and originated the first wild population of this species in Argentina (Aprile and Chicco, 1999; Guichón *et al.*, 2005). Since then, this original wild population has expanded (Guichón and Doncaster, 2008) and intentional human transport and release have given rise to several other invasion foci (Benitez *et al.*, 2013; Borgnia *et al.*, 2013, 2019; Guichón *et al.*, 2015, 2020).

Patterns of expansion and current distribution

C. erythraeus inhabits natural, urban and rural environments in association with the presence of trees; both the establishment and the natural spread of this species are favored by the presence of arboreal patches. Squirrels can use fragmented woodland patches, such as tree lines along roads and railways, as well as arboreal patches in parks in urban and residential areas both for its establishment and its expansion (Guichón *et al.*, 2005; Benitez *et al.*, 2013). For example, the presence of riparian vegetation along the Luján River favored its dispersal and resulted in a concentric expansion from the original release site (Guichón and Doncaster, 2008; Benitez *et al.*, 2013). This species uses suitable arboreal habitats that offer food and nesting resources for their establishment and avoid open habitat. In highly fragmented urban-rural landscapes, they also use cables, roofs and wire fences, among other human-made pathways, to reach suitable habitat. To date, 28 independent escape or release events of *C. erythraeus* (including the original introduction of the species) have been recorded in Argentina (see Guichón *et al.*, this volume). At present, this species is found in more than 20 districts or departments in the autonomous city of Buenos Aires (CABA) and four provinces: Buenos Aires, Córdoba, Santa Fe and Mendoza (Coniglione and Zalba, 2018; Guichón *et al.*, 2020) (Fig. 3, Tab. 1). Buenos Aires province has the largest area occupied by squirrels (> 180,000 ha), with the main invasion focus (Luján) encompassing several districts (Table 1). The number of released or escaped squirrels in each recorded event varies from two to 30 individuals (Table 1). Squirrel density in the main invasion focus is higher than recorded in its native range and in other sites where it has been introduced, although low and intermediate densities were recorded in other foci initiated more recently (Benitez *et al.*, 2013) (Table 1). The main reason that led to the introduction of this species is related to its charisma and attractive appeal to humans, who release individuals in parks and ranches to enrich wildlife and for ornamental purposes, and in some cases to keep (temporarily) as a pet (Benitez *et al.*, 2013; Borgnia *et al.*, 2013; Guichón *et al.*, 2015).

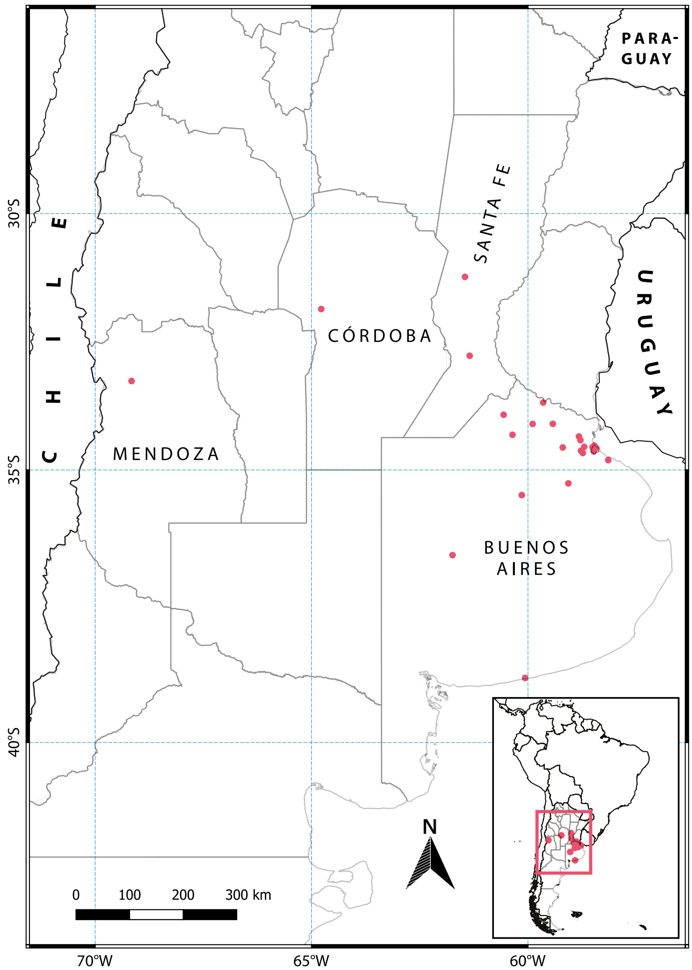

Figure 3. Distribution of *Callosciurus erythraeus* in Argentina showing the sites that represent independent releases/escapes in Argentina. Modified from Guichón *et al.* (2019). (Mapping: Alfredo Claverie and Ian Barbe).

Impacts

C. erythraeus causes different changes and damage to natural and productive systems (Fig. 4). Debarking of commercial plantations and ornamental trees is among the most widespread impacts reported (Bertolino and Lurz, 2013; Lurz *et al.*, 2013). In Argentina, this squirrel species damages a large number of tree species by debarking, many of which are of economic importance, such as *Eucalyptus dunni* and *Pinus elliotti* (Pedreira *et al.*, 2017; 2020). The damage to urban services, such as gnawing cables used for lighting, telephone and television (see Fig. 4), was also reported, and the consumption of grains in storage silos and damage to irrigation systems have been recorded in suburban and rural environments (Guichón *et al.*, 2005). Damage to natural systems involves potential modification of plant reproduction due to the consumption of flowers, fruits and seeds, and the dispersal

Table 1. List of sites where independent release or escape events of *Callosciurus erythraeus* have been recorded in Argentina. We indicate the year of introduction or date of the first observation of squirrels in the area, the invaded area (year of estimation), spread rate since liberation, relative abundance [95% confidence interval] (year of estimation), and estimated relative density [95% confidence interval]. Arrecifes and Capitán Sarmiento are considered a single invasion focus resultant from two independent releases (Source: Benitez *et al.*, 2013; Guichón *et al.*, 2015; Coniglione and Zalba, 2018; Guichón *et al.*, 2020; Borgnia *et al.*, 2019).

Release/escape site	Year	Number of squirrels released/ escaped	Invaded area (km^2)	Districts/ Departments per province included in the invaded area	Spread rate (km/year)	Relative abundance (squirrel/point)	Relative density (squirrel/ha)
Luján[1]	1973	25	1336 (2009)	Luján, Mercedes, San Andrés de Giles, Exaltación de la Cruz, Pilar, Gral. Rodríguez	0.61	1.89 [1.58–2.24] (2007)	15.3 [12.0–19.5]
Escobar[1]	1995	Unknown	34 (2008)	Escobar	0.39	0.41 [0.22–0.69] (2008)	3.23 [1.72–5.53]
Arrecifes[1]	1995	30	317 (2014)	Arrecifes	0.53	1.90 [0.6–3.0] (2014)	14.8 [4.5–23.8]
25 de Mayo[1]	1997	Unknown	122 (2012)	25 de Mayo	0.66	0.90 [0.5–1.2] (2012)	6.7 [3.9–9.4]
Cañada de Gómez[2]	1999	8	33 (2009)	Iriondo	0.44	0.61 [0.31–1.09] (2009)	4.86 [2.43–8.70]
La Cumbrecita[3]	2000	30	0.42 (2010)	Calamuchita	0.05	0.42 [0.18–0.83] (2010)	3.35 [1.45–6.60]
Capitán Sarmiento[1]	2001	2	*See Arrecifes*	Capitán Sarmiento	*See Arrecifes*	0.90 [0.5–1.5] (2014)	7.3 [3.9–12.2]
Lobos[1]	2002	2	6 (2017)	Lobos	0.18	–	–
Plaza San Martín[4]	2004[a]	Unknown	Not established	*	–	–	–
Fac. Agronomía UBA[4]	2005[a]	Unknown	Not established	*	–	–	–
Salto[1]	2005[a]	4	16 (2014)	Salto	0.41	0.30 [0.1–0.8] (2014)	2.3 [0.5–6.3]
San Miguel[1]	2007[a]	Unknown	7 (2012)	San Miguel	0.53	0.60 [0.2–1.3] (2012)	4.9 [1.9–10.2]
Parque Gral. Paz[4]	2007	Unknown	–	*	–	–	–
Rafaela[2]	2008	20	3 (2014)	Castellanos	0.33	0.80 [0.5–1.5] (2014)	6.2 [3.6–11.6]
Parque Avellaneda[4]	2010[a]	Unknown	–	*	–	–	–
Del Viso[1]	2011[a]	Unknown	–	Pilar	–	–	–
Claromecó[1]	2011[a]	–	–	Tres Arroyos	–	–	–
Tupungato[5]	2011	10	–	Tupungato	–	–	–
Daireaux[1]	2012	Unknown	0.2 (2014)	Daireaux	0.12	–	–
Moreno[1]	2013[a]	–	–	Moreno	–	–	–
San Pedro[1]	2013[a]	Unknown	–	San Pedro	–	–	–
San Cristóbal[4]	2014[a]	Unknown	Not established	*	–	–	–
Merlo[1]	2015[a]	Unknown	0.12 (2018)	Merlo	–	–	–
Villa Lía[1]	2015[a]	–	–	San Antonio de Areco	–	–	–
Botánico Thays[4]	2015[a]	–	–	*	–	–	–
Berazategui[1]	2016[a]	–	–	Berazategui	–	–	–
EMyDDHH[4,A]	2017[a]	–	–	*	–	–	–
Pergamino[1]	2018[a]	–	–	Pergamino	–	–	–

[a] Provisional data corresponding to the first observation of squirrels in the area; ***** sites belonging to Ciudad Autónoma de Buenos Aires (CABA); **–** insufficient data/under study. [A] Espacio de la memoria y de los Derechos Humanos (ex ESMA), [1] Buenos Aires province, [2] Santa Fe province, [3] Córdoba province, [4] CABA, [5] Mendoza province.

Figure 4. a. Damage caused by *Callosciurus erythraeus* on a tree by debarking; **b.** a squirrel with a ball of bark in its mouth; **c-d.** fruits (orange and nuts) damaged by squirrels; **e-f.** gnawed cables and irrigation hoses. (Photos: Adrián Gorrindo, Mariela Borgnia).

of introduced species (Bobadilla *et al.*, 2016; Zarco *et al.*, 2018). These squirrels also could decrease native bird abundance and richness although more studies are needed (Pereira *et al.*, 2003; Messetta *et al.*, 2005). The species close proximity to protected areas, such as the Parque Nacional Ciervo de los Pantanos which offers suitable habitat conditions for this squirrel, must raise an alert of conservation concern because its spread may threaten sensitive native species protected in this reserve.

As mentioned above, we found that *C. erythraeus* is a renal carrier of *Leptospira interrogans*. So, it might be involved in the epidemiology of the transmission of leptospirosis. Studies about the zoonotic potential of this species in its native range and in other introduced areas is still scarce; therefore, more studies would provide new insight into the role of this species as a reservoir of zoonotic pathogens.

Finally, a cultural impact of squirrels should also be considered since *C. erythraeus* is a charismatic species, which can lead to local communities undervaluing native fauna and even changing their cultural identity (Borgnia *et al.*, 2103). For example, in the original introduction site (Jáuregui, Luján, Buenos Aires province) this introduced and invasive squirrel species has become a local icon.

Management

In Argentina, systematic control programs for this species are mainly isolated and driven by independent actions of local producers to temporarily reduce squirrel numbers on their properties to mitigate squirrel damage. As an example, control actions using live-trapping and euthanasia were conducted in a private ranch located in Cañada de Gómez, Santa Fe province in 2010 (Benitez, 2017). Both the capture success and time-area counts, the two estimators of population density employed, showed that the number of individuals decreased due to control actions conducted in a six-month period (Fig. 5).

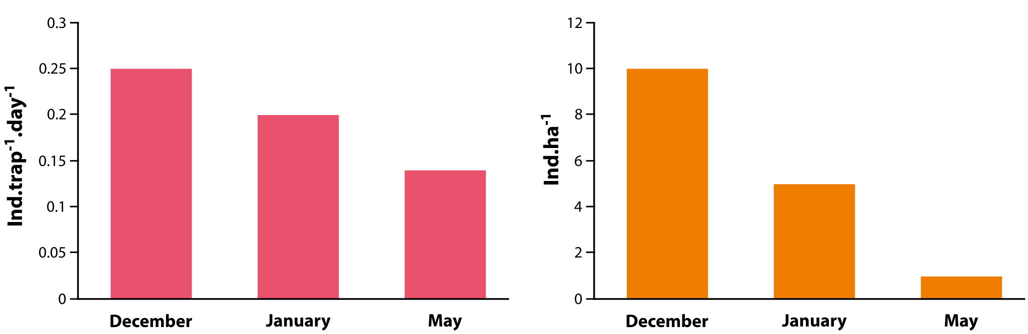

Figure 5. Reduction of squirrel population density based on capture success (**left**) and time-area counts (**right**) during a pilot control plan conducted in December 2009, January 2010 and May 2010 in Cañada de Gómez, Santa Fe province. Trapping effort: 22.5 traps/day (16 days). Squirrels captured: 72.

Recently, control actions organized by the Mendoza provincial government in coordination with national and local authorities were implemented in a private farm in the locality of Tupungato (DRNR, 2021; Benitez, V., unpublished data; Guichón *et al.*, this volume).

Regarding the legal framework, the GEF project entitled "Strengthening Governance for the Protection of Biodiversity through the Formulation and Implementation of the National Invasive Exotic Species Strategy" (GCP/ARG/023/GFF), coordinated by the national ministry of environment (Ministerio de Ambiente y Desarrollo Sostenible) in association with the UN's Food and Agriculture Organization, has recently come into force. This program intends to integrate various actions related to the problem associated with the invasion of this squirrel and other introduced species in the country. At a national level, the red bellied squirrel was recently categorized as a restricted and required control species (Resolution #109/2021, Ministerio de Ambiente y Desarrollo Sostenible). In the province of Buenos Aires, the Rural Code includes *C. erythraeus* in the category of "harmful" or "injurious" species that can be hunted with poison (Decree #2018-279 GDEBA GPBA). To date, there are three Municipality Ordinances in Buenos Aires province that include the prevention of the expansion of this species: Luján (#5996/11), Capitán Sarmiento (#2125/13), and Daireaux (#2262/18).

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Canis lupus familiaris
domestic feral dog, perro doméstico asilvestrado

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Resumen. El perro doméstico asilvestrado tiene una gran diversidad de formas y tamaños. Tiene una flexibilidad muy alta y un nicho amplio que le permite sobrevivir y reproducirse en una enorme gama de hábitats. De hábitos terrestres, hábitat generalista y actividad catemeral, es una especie que forma jaurías en su estado en silvestría y su dieta es omnívora y generalista. El promedio de crías por camada es de 6 cachorros y excepcionalmente pueden tener hasta 15 crías. La población de perros domésticos, asilvestrados o semi-asilvestrados en Argentina ha ido aumentando en casi todas las localidades y áreas rurales del país. Su gran adaptabilidad la convierte en una de las especies invasoras más exitosas en el mundo. Proviene de los perros de caza que arribaron con los colonizadores europeos y su introducción también tuvo que ver con fines recreativos. Progresivamente se produjo una transformación hacia la silvestría a partir de escapes, abandono de ejemplares, mala gestión o tenencia no responsable de perros criados en el campo, en zonas urbanas y suburbanas. Según registros de individuos o poblaciones, los perros domésticos y asilvestrados se encuentran distribuidos en prácticamente toda Argentina. El acoso y la depredación de los perros sobre los mamíferos salvajes es el impacto más importante, afectando a varias especies. Además de provocar accidentes de tráfico y agresiones a las personas, los perros están implicados en la propagación de enfermedades zoonóticas y parásitos graves como hidatidosis, leptospirosis, toxocariasis, brucelosis, toxoplasmosis, etc. Hay algunas provincias con planes de manejo para la especie.

General description of the species

Domestic dogs (*Canis lupus familiaris*), even feral ones, come in a great diversity of shapes and sizes. Its external morphological characteristics are extremely variable, with different and varied coats; individuals can range from a few kg to more than 45 kg, and even reaching up to 95 kg in some breeds (Fig. 1; Lartigau *et al.*, 2019). In general, this species relies on food supply and shelter from humans; however, feral dogs could be absolutely human independent (Butler and Du Toit, 2002).

Habitat

The dog has colonized forests, tundra, jungles, steppes and mountains. They have very high ecological flexibility and a wide niche that allows them to survive and reproduce in a huge range of habitats. They occupy practically all environments, particularly where urban and rural human populations are established (Lartigau *et al.*, 2019). The dog is a social species that forms packs, and it has a generalist, omnivore diet and terrestrial and cathemeral activity (Long, 2003).

Figure 1. *Canis lupus familiaris* in Parque Nacional Tierra del Fuego, Argentina. (Photo: Proyecto Huillín TDF).

Reproduction

Feral dogs can display reproductive behaviors comparable to those of wolves, with the presence of well-established and organized social groups. So the rearing of pups is usually shared between members of the group (Lartigau *et al.*, 2019). The average of young per litter is 6; exceptionally, they can reach 15 offspring.

Native range distribution

The dog derived from the Eurasian wolf, but since its domestication, it has been introduced practically around the entire globe, even in polar regions (Long, 2003). Currently, the dog is the world's most abundant and widely distributed carnivore (Doherty *et al.*, 2016).

History of the invasion

Its great adaptability makes *Canis lupus familiaris* one of the world's most successful invasive species (Young et al., 2011; Paschoal, 2016; Doherty et al., 2017). Genetic studies indicate that the dog arrived to the Americas with *Homo sapiens*, around 11,000 years ago, crossing through the Bering Strait (Leonard *et al.*, 2002), and there is evidence suggesting the existence of domestic dogs in various places in the Americas in pre-European times (Valadez *et al.*, 2003). In particular, pre-European records exist for domestic dogs in Argentina (Acosta *et al.*, 2011), but genetics indicates that today's feral dogs, which are invading the country and the continent, originated from the hunting dogs brought by early European colonizers (Cabrera, 1932). Since then, the dog's introduction has been mostly related to recreational purposes and as a pet (Lartigau *et al.*, 2019).

Patterns of expansion and current distribution

The spread of feral or semi-feral dogs is mainly associated with humans, mostly due to abandoned or mismanaged domestic individuals. Despite not having national studies, it is estimated that the population of domestic, feral or semi-feral dogs in Argentina is

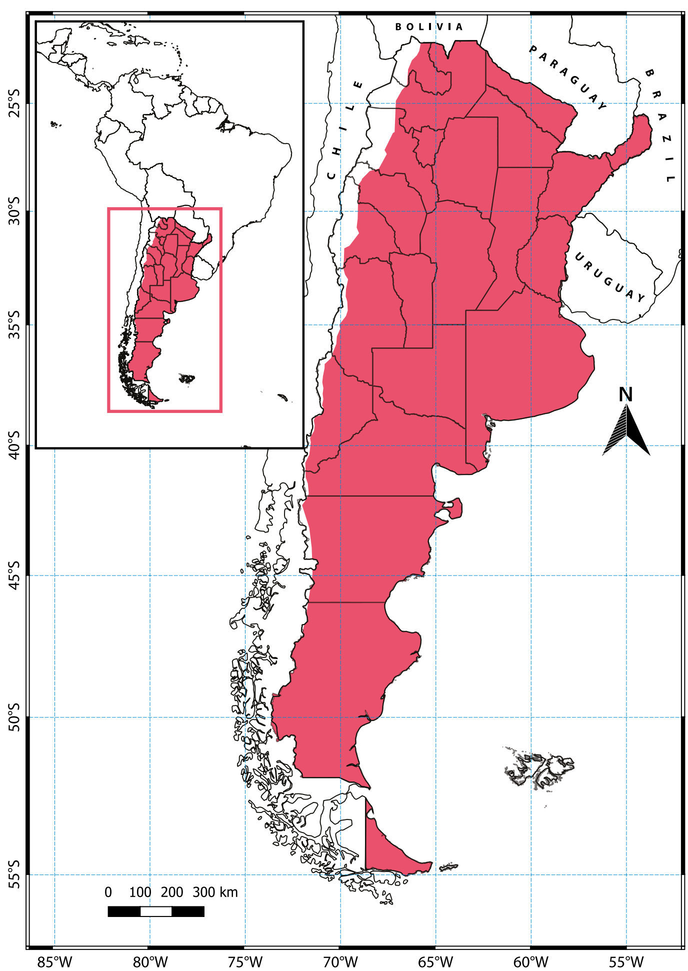

Figure 2. Distribution of *Canis lupus familiaris* in Argentina. Modified from Lartigau *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

increasing, occupying the entire country, with presence in almost all protected areas (Fig. 2; Lartigau *et al.*, 2019). Additionally, urban centers often function as sources of new individuals to feral populations, or sometimes domestic or street dogs leave the cities temporarily, with potential impacts on the native fauna (Lartigau *et al.*, 2019).

Impacts

Ecological impact

The impact of dogs on native biodiversity in Argentina has not been properly evaluated (Lartigau *et al.*, 2019). Globally, this carnivore species is known to threaten native species by predation (Doherty *et al.*, 2017). In addition to predation, harassment, bird nests disturbance, competition with native predators and scavengers, and transmission or introduction of pathogens (*e.g.*, distemper, leishmaniasis, bovine neosporosis, parvovirus, rabies, hydatidosis) have been reported (Echaide, 2000; Fiorello *et al.*, 2004; Zanini *et al.*, 2009; Orozco *et al.*, 2014; Czupryna *et al.*, 2016; Feng *et al.*, 2016).

Economic impact

In Patagonia, mainly in Tierra del Fuego province, feral dogs affect livestock by attacking sheep, forcing some ranchers to change their production system to cattle (Zanini *et al.*, 2008). In Santa Cruz province, damage from dogs to sheep farming was described as even greater than that of puma (*Puma concolor*; Lartigau *et al.*, 2019). Additionally, the transmission of bovine neosporosis, caused by *Neospora caninum*, a protozoan that mainly affects cattle and dogs, is of international importance for cattle production (Echaide, 2000). As with American mink (*Neogale vison*; Claverie *et al.*, this volume), feral dogs also affect nature-based tourism economic activities (Lartigau *et al.*, 2019).

Health impact

Feral dog populations have been known to directly attack people, as well as cause traffic accidents (Zanini *et al.*, 2008). On the other hand, dogs are implicated in the spread of zoonotic diseases and serious parasites, such as hydatid disease, leptospirosis, toxocariasis, brucellosis, toxoplasmosis, etc. (Milano and Oscherov, 2002).

Management

To date, there is no national management plan for feral dogs (Lartigau *et al.*, 2019). Due to its cultural status as a pet, the perception of the species and its impacts in general does not correspond to the ecological reality, favoring the support of animal protectionist laws that prevent the application of feral dog removal measures, generating a conflict regarding the management of feral or semi-feral populations (Lartigau *et al.*, 2019). The effective management of an introduced invasive charismatic species needs social as well as political support (Guichón *et al.*, this volume), not only through responsible ownership but also by supporting ethical feral populations reduction and control actions. Since 2011, a "National Program for Responsible Ownership and Health of Dogs and Cats" has been implemented with the dual goal of preserving native biodiversity and avoiding cruelty to these species (National Decree #1088/2011). Several feral dog management plans at local level are applied in different protected areas (mostly related to responsible ownership) and in livestock production ranches by eliminating problem individuals (Lartigau and Preliasco, 2015; Lartigau and Carminati, 2016; Lartigau and Schiaffino, 2016; Mezzabotta, 2018).

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Castor canadensis

North American beaver, castor americano

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Resumen. El castor norteamericano (*Castor canadensis*) fue introducido en Tierra del Fuego (Argentina) en 1946. Mediante su rápida expansión, colonizó casi todas las cuencas del archipiélago antes de los años 1990, llegando a cruzar el Estrecho de Magallanes y actualmente ocupar sectores del continente hasta Puerto Natales (Chile). Sus impactos ecológicos son profundos, provocando cambios que duran décadas y constituyéndose en uno de los mayores factores de cambio a nivel de paisaje en Tierra del Fuego durante el Holoceno. En términos sociales, los efectos producidos por el castor están siendo estudiados recientemente, pero se sabe que pueden ser no solo negativos, sino también positivos o neutros. El manejo de este «ingeniero de ecosistemas» en la Patagonia tanto argentina como chilena ha sido poco efectivo, con esfuerzos aislados de ambos países por varias décadas. Sin embargo, en 2008 se empezó a abordar el conflicto como un problema binacional y en los últimos años se contó con dos proyectos del *Global Environment Facility* para ensayar la erradicación de la especie y la restauración de los ecosistemas afectados.

General description of the species

The North American beaver (*Castor canadensis* Kuhl) is a semi-aquatic rodent that ranges in size from about 14 to 30 kg (Fig. 1). It reaches sexual maturity at approximately two years of age and gives birth to a typical litter of two to three kits in spring. In their native distribution, *C. canadensis* inhabits a broad diversity of freshwater ecosystems, including lakes, rivers, streams, bogs and wetlands, found in forest, grassland, tundra and desert biomes from northern Mexico to northern Canada. They consume herbaceous vegetation and woody plants' leaves and phloem. Beavers also use their large, powerful incisors to cut trees and shrubs that they use to construct dams and lodges, which in turn create, modify and destroy existing habitats, making them the quintessential ecosystem engineer (*sensu* Jones *et al.*, 1994). In their native range, they face predation from medium-sized and large carnivores, such as bears, wolves, alligators, raptors, mustelids and coyotes.

Figure 1. *Castor canadensis* in Tierra del Fuego province, Argentina. (Photo: Sergio Anselmino).

History of the invasion

Primary historical sources, including a government newsreel (Anonymous, 1946) and a personal letter from trapper Tom Lamb (Lamb, 1969), document that the Argentine government purchased 20 beavers trapped near Moose Lake in Manitoba, Canada to "enrich" Tierra del Fuego's fauna with ostensibly valuable furbearers. In 1946, these were introduced to a site on the north shore of Lake Fagnano. In the same newsreel, the government also reports its simultaneous Patagonian projects, including farmland expansion in the north and petroleum exploration around the city of Comodoro Rivadavia. The imposition of this development mentality on Tierra del Fuego also lead the government to successfully introduce muskrats (see Deferrari, this volume), but they failed in a plan to establish a reindeer population with individuals from South Georgia Island (Archibald *et al.*, 2020). While the reason for this introduction was to promote a fur industry, there was never a significant commercial venture for pelts.

Patterns of expansion and current distribution

As an invasive ecosystem engineer, the beaver rapidly expanded across most of the Tierra del Fuego Archipelago (Fig. 2), colonizing the neighboring islands of Navarino, Dawson, Nueva, Lennox, Picton and Hoste (all in Chile); currently, there are no confirmed reports from the Wollaston Islands (Chile) or Staten Island (Argentina) (Anderson *et al.*, 2009; Valenzuela *et al.*, 2014). After the initial introduction in 1946, reports indicate the expansion first occurred in the forest biome, crossing south of the Beagle Channel to

Navarino Island (Chile) by the mid-1960s. Subsequently, beavers achieved relatively high densities in nearly all watersheds in the archipelago by the 1990s (Lizarralde, 1993). Despite the fact that steppe and grassland ecosystems were colonized later than forests (Anderson *et al.*, 2009; Pietrek *et al.*, 2015), a recent demographic study suggests that these are not sub-optimal habitats (Pietrek *et al.*, 2017). The invasion of the mainland was confirmed south of Punta Arenas (Chile) in the mid-1990s (Lizarralde, 1993; Wallem *et al.*, 2007), but a recent dendrochronology study indicates that this arrival to the continent may have been as early as 1968 (Graells *et al.*, 2015). In 2013, beavers were found near the town of Puerto Natales (Chile) (Sanguinetti *et al.*, 2014). Overall, this successful biological invasion has been attributed to ecological conditions (*i.e.*, favorable habitat, lack of predators or competitors) and the beaver's autecology (*i.e.*, relatively fast population growth, the ability to engineer its own trophic and habitat niche) (Wallem *et al.*, 2007). Habitat suitability

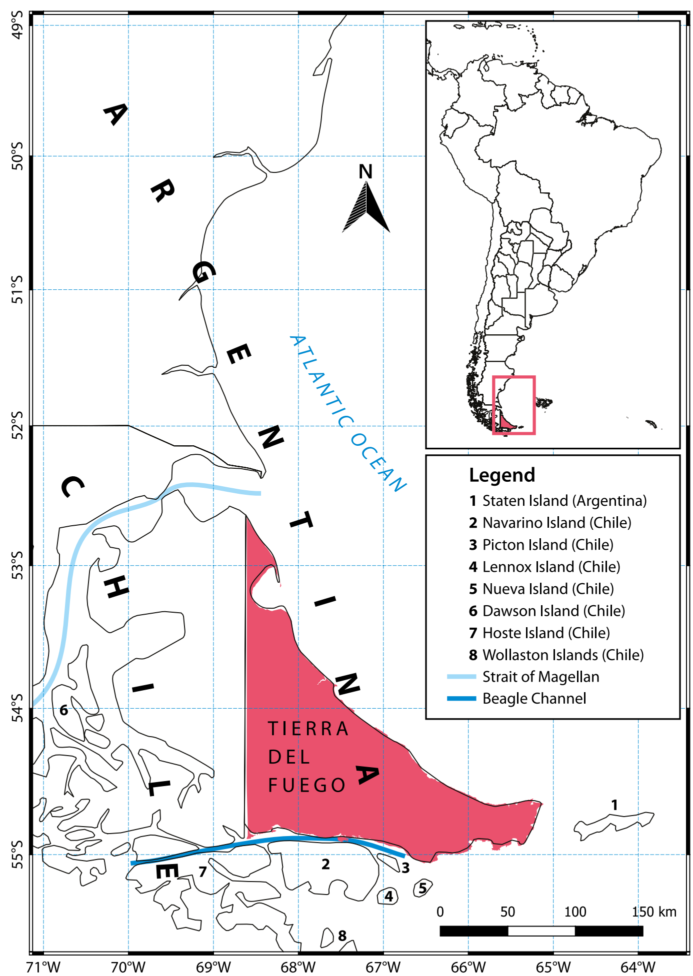

Figure 2. Distribution of *Castor canadensis* in Argentina. Modified from Anderson *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

models also suggest that site occupation patterns are not only affected by ecological conditions *per se*, but also the time since first invasion (Davis *et al.*, 2016). Furthermore, it is increasingly recognized that social aspects, including the absence of effective control measures and the incorporation of beavers into local-regional cultural and symbols, have combined to make this a socio-ecological phenomenon (see Anderson and Pizarro, this volume).

Impacts

Beavers provoke a wide range of ecological alterations from the species- to landscape-levels, causing some of the largest impacts to Tierra del Fuego in the Holocene (Anderson *et al.*, 2014; Henn *et al.*, 2016). For example, beavers increase the secondary production and dependence on allochthonous organic matter of stream benthic food webs (*e.g.*, Anderson and Rosemond, 2010), convert riparian forests to meadows (*e.g.*, Wallem *et al.*, 2010), and enhance some ecosystem-level processes, such as higher decomposition rates and greater organic matter retention (Anderson *et al.*, 2014). Their overall effect to the landscape includes direct transformation of approximately 30,000 ha in the Argentine portion of Tierra del Fuego (Henn *et al.*, 2016). To date, most research has addressed the beaver as a negative "biological" invasion, but new social science and humanities studies show that while most local residents know that the beaver is negative ecologically, their valuation of this species can be either positive or negative (Berghoefer *et al.*, 2010).

Management

In Argentine Tierra del Fuego, the government has declared beavers as a "harmful species" (Provincial Law #696/2006), which complements an earlier designation in Chile (National Law #19,473/1996 and Executive Order #5/1998). These legal instruments provide the basis for management of this species, but neither country has a specific law or regulations for biological invasions. Parque Nacional Tierra del Fuego (Argentina) has carried out the only systematic control program since 2001, which has successfully returned the beaver population in the southern portion of the park to the early 1980s levels (Sanguinetti *et al.*, 2014). Beginning in the 1990s, Argentina and Chile conducted separate beaver control efforts, focusing on paying hunters a bounty for trapping (Anderson *et al.*, 2011). In 2008, the two governments signed a binational agreement that modified their approach towards the eradication of the species in Patagonia and to promote action to restore the ecosystems affected (Malmierca *et al.*, 2011). In the past few years, a pilot phase of this program was implemented via funding from Global Environment Facility grants to each. Beaver eradication is an extremely ambitious goal whose feasibility is questionable, but internationally, this case has become an extremely high profile example of invasion biology and conservation in southern Patagonia (Choi, 2008). Nonetheless, there are significant obstacles that may hinder such an effort, including explicit social rejection by some stakeholders (see Urbano, 2015), while others, like ranchers in both Chile and Argentina, view such a program favorably (Santo *et al.*, 2015).

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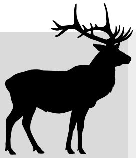

Cervus elaphus

red deer, ciervo colorado

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Resumen. El ciervo colorado europeo, un cérvido de gran tamaño, fue introducido por primera vez en Argentina entre 1902 y 1906. Actualmente se ha confirmado su presencia en al menos 14 provincias, con más de 150.000 ejemplares silvestres. Se organizan en grupos familiares, formados por una hembra y sus descendientes de los últimos dos o tres años, o en grupos de machos, cuyos tamaños dependen del tipo de hábitat, perturbaciones, densidad poblacional y la estación del año. Machos y hembras permanecen separados la mayor parte del año, hasta la época de celo (marzo-abril), seguida de un período de gestación de 235 días, y el nacimiento de una cría por año. Presentan un sistema de apareamiento flexible: los machos dominantes muestran territorialidad y los subordinados exhiben otras estrategias. Su dieta es mixta y varía según el hábitat, la estación y la competencia interespecífica; son muy adaptables a una amplia gama de condiciones ambientales, lo que facilita su dispersión, que en Patagonia se ve acelerada por las grandes extensiones de terreno con baja densidad humana, las plantaciones de pinos, las introducciones (legales o ilegales) de ciervos en nuevos lugares, y los escapes de cotos. Pueden ser residentes todo el año o migrantes estacionales. Se estima que en un futuro podrían ocupar toda el área cordillerana de Patagonia, desde Mendoza hasta Santa Cruz, incluyendo una variedad de hábitats, desde bosques húmedos valdivianos hasta la estepa patagónica. Adicionalmente a los impactos ecológicos ocasionados por el ciervo colorado, es importante tener en cuenta su papel epidemiológico en relación con las especies autóctonas y el ganado. Además, su presencia ha provocado la caza furtiva dentro de las áreas protegidas. Se presentan opciones de gestión para mantener/reducir el tamaño poblacional, que tienen en cuenta a todos los grupos sociales interesados y utilizan estrategias científicas de gestión adaptativa.

General description of the species

The red deer (*Cervus elaphus*) is a large cervid, with stags reaching shoulder heights up to 150 cm. Only males possess antlers, 5 tines or more on one antler in prime stags, which are cast each year in late winter. The adult coat is basically solid, reddish-chestnut in summer and greyish-brown in winter; calves are born with spots.

Biology

Adult females at Parque Nacional Nahuel Huapi (PNNH) averaged 119.2 kg while the five largest males averaged 291.6 kg (Smith-Flueck and Flueck, unpublished data). Dental formula is 0.1.3.3 / 3.1.3.3. The Patagonian rutting season is March to April. Females are seasonally polyestrous; a cycle lasts 18 days with one to two days of receptivity. Gestation lasts 235 days with one calf per year. Females reach sexual maturity at approximately 16 months of age, but this can vary considerably depending on local conditions. The males can begin reproducing at two years of age, but generally begin much later due to competition with older males. Males reach their maximum development at 12–14 years of age (Fig. 1). In Patagonia, free-ranging males and females have reached 25 and 20 years of age, respectively (Smith-Flueck and Flueck, unpublished data).

Behavioral ecology

A mixed feeder, the red deer diet varies considerably according to habitat, season, and competition with other herbivores. They are most active foraging during dawn and dusk. In disturbance-free areas, they can be seen resting and foraging in the open during

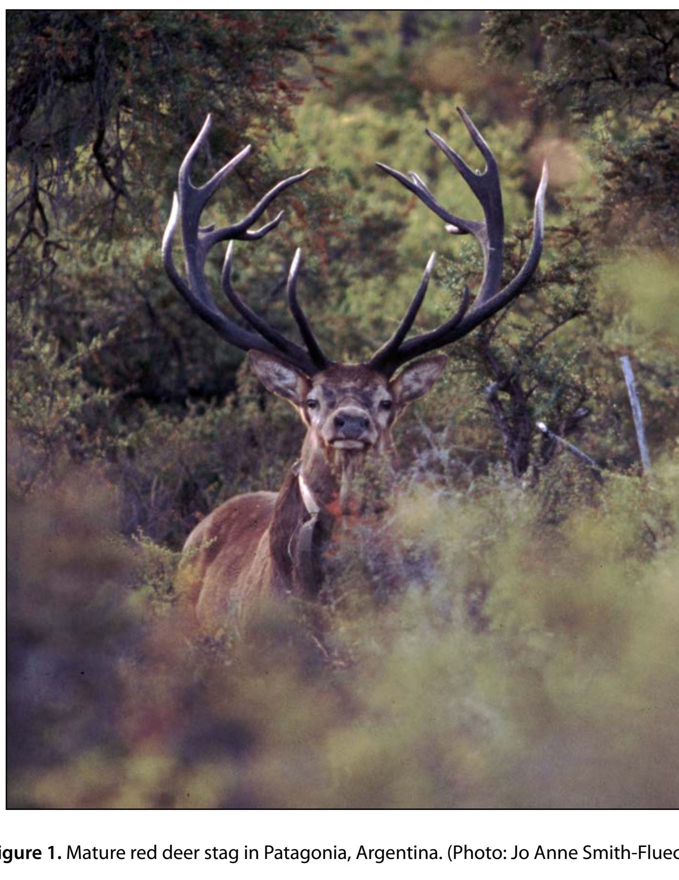

Figure 1. Mature red deer stag in Patagonia, Argentina. (Photo: Jo Anne Smith-Flueck).

daylight hours. The basic social unit is a family group formed by one female and her descendants of the last two to three years. Young males disperse to then form groups with similar aged males. The sexes remain apart most the year. During the rut, the stags vocalize frequently with loud deep bellows that signal their status (Hurtado *et al.*, 2012). The mating system in Patagonia is flexible, with prime males being territorial while non-prime males exhibit various other semblances of mating strategies. Mobile harem defense, as described in Europe, was not observed (Smith-Flueck and Flueck, 2006). The social organization of the stags during the rut determines the frequency and severity of male fights. Inappropriate hunting practice can result in injuries and deaths by a modified social structure. Group size depends on habitat type, disturbance, population density, and season. A gregarious species, their numbers can reach hundreds in open areas. In contrast, in forest habitat, group size is commonly three to five animals. They can be year-round residents or seasonal migrants, sometimes migrating long distances between summer and winter ranges. They easily jump fences, run quickly from predators, and are also exceptional swimmers.

History of the invasion, patterns of expansion and current distribution

The first individuals arrived to Argentina from Europe between 1902–1906 at Reserva Provincial Parque Luro in La Pampa province. In 1922 a few from this stock were brought to the Andean pre-cordillera in Neuquén province. By 1952, deer were culled from this population to reduce competition with livestock. By 1959, this deer was officially declared a "pest" species in Neuquén (Flueck and Smith-Flueck, 1993).

In 1926, red deer were liberated in southern Neuquén province on Huemul Peninsula inside PNNH (Hurtado *et al.*, 2012). The expansion was then aided by further liberations (Flueck and Smith-Flueck, 1993). Three principal ones were at: 45° S (1945); 44° S (1966) (Smith-Flueck and Flueck); and 42°53' S (1979) (Smith-Flueck, 2003). By April 1995, the deer from the latter liberation site had spread a minimum of 15 km further northeast, entering Parque Nacional Los Alerces. It was estimated they would join the population expanding south from Río Negro by 1996 (Smith-Flueck, 2003). The estimated distribution of red deer in Patagonia by 2002 was 51,500 km²; using known rates of dispersal, the range was predicted to reach 206,500 km² by 2050 (Flueck *et al.*, 2003) (Fig. 2). This estimate did not consider further introductions, escapees, nor the influence of introduced pine plantations as corridors.

The highly adaptable behavior of red deer facilitates their dispersal over a large range of environmental conditions. Their expansion in Patagonia is further accelerated by the vast tracts of land with low human density, the pine plantations, the introductions (legal or illegal) of deer to new sites, and escapees from enclosures. In New Zealand, the distribution of red deer recently expanded due to illegal translocations (26%) and escapees (38%) (Nugent *et al.*, 2001).

Red deer will eventually inhabit the entire western cordillera of Patagonia, from Mendoza to Tierra del Fuego (Flueck *et al.*, 2003), and could reasonably extend east to where the precipitation gradient falls to 150mm/yr or less. Today, the North Patagonian population extends continuously along the western portion of the provinces of Neuquén, Río

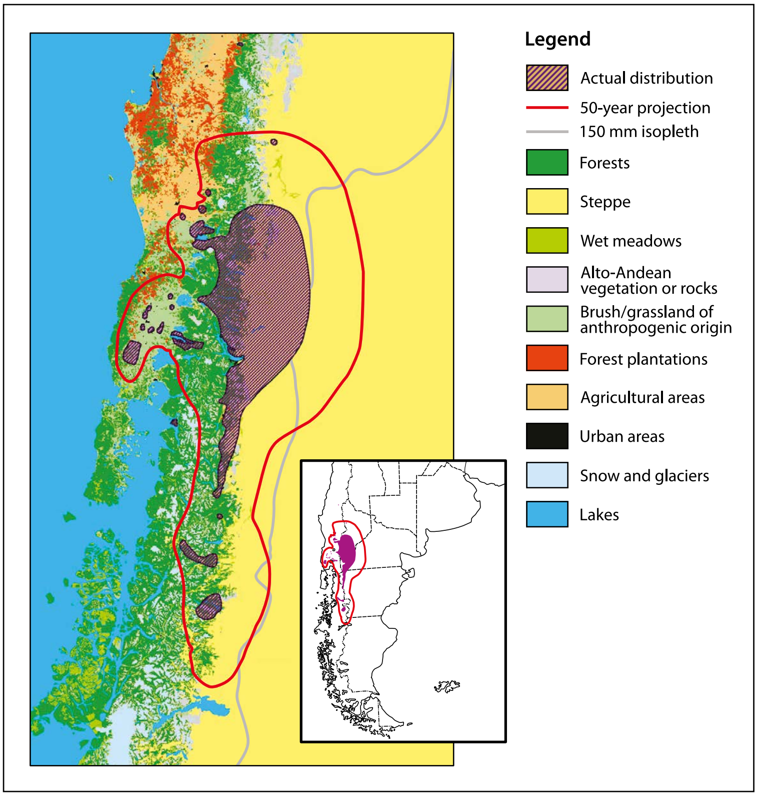

Figure 2. Red deer distribution in Patagonia (as of 2002), including Chile, is 37°42' S – 54°55' S and 73°36' W – 69°50' W (not contiguous). Provinces confirmed to have free-ranging red deer are the following nine: La Pampa, Neuquén, Río Negro, Chubut, Mendoza, San Luis, Tucumán, Salta, and Jujuy. Provinces with red deer in captive and/or semi-captive centers (deer farms or hunting reserves) include: Buenos Aires, Entre Ríos, Corrientes, Santa Fe, La Rioja, and Córdoba. Additionally, they were introduced in 1973 to Staten Island (AR) and in 2000 to Tierra del Fuego, Chile, for farming and hunting. Although not confirmed, red deer may also already be in Catamarca, Chaco, CABA, Formosa, San Juan, Santa Cruz, Santiago del Estero and Tierra del Fuego.

Negro and northern Chubut, including portions of three large national parks (Nugent *et al.*, 2011). North of Patagonia, they recently escaped two enclosed hunting reserves in the district of La Carrera, Tupungato, in Mendoza province, and are now free-ranging (F. Cuevas, pers. comm.). Currently, they are found in 14 continental provinces (Fig. 3), by way of introductions, deer farms, and hunting reserves, with six of these possibly having animals still only in captive facilities (Flueck, 2010). Lastly, they were introduced in 1973 to Staten Island and in 2000 to the Chilean side of Tierra del Fuego Island for farming and hunting (Flueck and Smith-Flueck, 2012a).

Impacts

There is no evidence in New Zealand, Chile or Argentina that an equilibrium has been reached between deer and the host ecosystems they inhabit (GISD, 2015). In

Argentina, they inhabit a variety of habitats from dense rain forest to ecotone to grassland steppe. Within this habitat gradient, they have altered the floristic composition, forest understory and stand structure, and impaired tree regeneration (Veblen *et al.*, 1992). Evidence of extensive dietary overlap between red deer, livestock, native guanaco (*Lama guanicoe*) and endangered native huemul (*Hippocamelus bisulcus*) suggests these herbivores might compete under limiting environmental conditions (Bahamonde *et al.*, 1986; Smith-Flueck, 2003; GISD, 2015). Regardless, several populations of huemul disappeared before red deer occupancy or while founding populations of the introduced were still at very low densities, despite the red deer being blamed as one of the main causes of the huemul's current endangered status (Smith-Flueck, 2003; Smith *et al.*, in press). The potential epidemiological role for various diseases of red deer is important to consider in conservation and the livestock industry (Flueck and Smith-Flueck, 2012b; Smith-Flueck and Flueck, 2017).

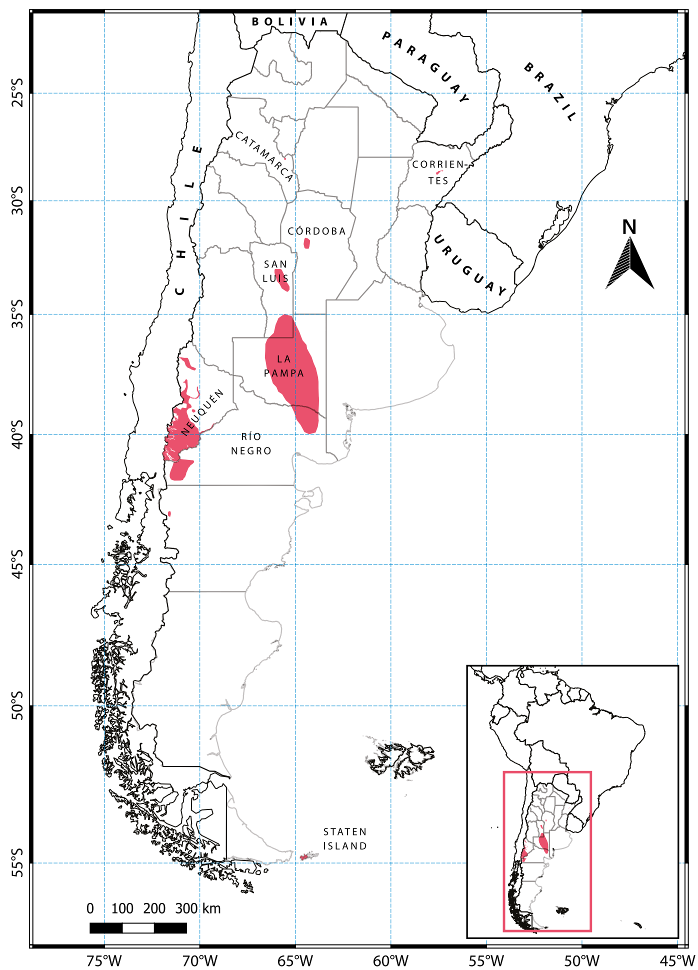

Figure 3. Feral distribution of *Cervus elaphus* in Argentina. Modified from Relva *et al.* (2019). (Mapping: Alfredo Claverie and Ian Barbe).

Management

History of management in Argentine National Parks (APN)

Well-established red deer populations, if appropriately managed, can provide a sustainable economic asset for humans (Flueck *et al.*, 1995). Several provinces and national parks have established hunting regulations for red deer, but not based on population ecology (GISD, 2015). Red deer are often considered a pest, at least in national parks, yet, ironically, there are strict hunting-focused regulations in most jurisdictions limiting the hunting season and restricting the number, sex, and antler size of animals (Nugent *et al.*, in press). Red deer in protected areas are mainly under the jurisdiction of APN. Recreational sport hunting of red deer, principally implemented as a means to control poaching, has been practiced in Parque Nacional Lanín (PNL) and PNNH since 1955 and 1987, respectively. Basic guidelines for red deer management in the parks were first outlined in Resolution #454/1986, where the importance to reduce the density and avoid an expansion were recognized. In 2004, these same guidelines were incorporated into the APN management strategies for red deer (Res. HD #18/04), where they recognized the impossibility to maintain a sport hunting program without population management, and considered sport hunting the tool of choice by which to accomplish this.

Social-cultural aspects

Many landowners and inhabitants inside the parks perceive red deer as competing with traditional livestock activities. Deer do not produce a secure financial income for these stakeholders, and instead have introduced problematic poaching. For social and economic reasons, they cannot justify investing in some form of management, and thus only take opportunistic advantage of hunting mature trophy males for profit. Only where densities have reached high levels on some private lands have red deer been culled.

Of all national parks, PNNH and PNL have the greatest presence of red deer. The zonification of “national reserve,” where people live and some own land legally, makes up 46% of the surfice of these two protected areas. These lands, mostly in the lower elevations of the parks, are winter range for the red deer. These inhabitants can play an important role as the lower zone is most suitable for managing the population (Flueck and Smith-Flueck, 1993), given its importance as winter range, road infrastructure, and high conservation value. Although density reduction is the most important objective to achieve (*e.g.*, Res. HD #18/04), populations regrow regularly beyond carrying capacity due to various factors. For one, harvest of females and young animals has been discouraged (Relva and Sanguinetti, 2016), even prohibited in NPNH (Mendez, 2007). PNL, recognizing this, initiated a control hunting program in cooperation with hunting clubs, resulting in reducing deer density more effectively (Sanguinetti *et al.*, 2014), but only lasting five years. Recreational sport hunting alone achieves little in the way of conservation and benefits only a small sector of the society. Like in New Zealand, it does not control population size, and to the contrary, contributes to higher densities (Flueck *et al.*, 2005; Nugent *et al.*, 2011). Even commercial trophy hunting cannot be maintained, as it is self-limiting, unless scientific population management is part of the program (Nugent *et al.*, 2011). A promising option would be to incorporate landowners in a control program, adopting an integrated approach, whereby APN works with all interest groups. In New Zealand, a consortium of landowners joined forces to develop the successful "Regional Strategy for Managing."

The current hunting system of national parks

When analyzing stags on private lands bordering APN, 69% were misclassified and shot too young (Smith-Flueck and Flueck, unpublished data). The average age for stags hunted in national parks was 7.99 years (SE=0.21, n=255), and the most frequently hunted age class was 6.5 years. Given that stags reached their maximum body size between 12–16 years of age, most of the hunted stags never got to reach their full-antler potential.

Population size in Patagonia overall was estimated at 100,000 red deer, based on a conservative estimate of 2 deer/km^2, given that densities in the ecotone have reached 100 deer/km^2 and 40–50 deer/km^2 in the steppe habitat (Flueck *et al.*, 2003). In APN, few deer get culled compared to New Zealand. With 250,000 deer on 65,000 km^2, the New Zealand government provided 65,000 hunting permits (free of charge): 42,000 deer were harvested. Meanwhile, by 2007 our estimation had increased to 150,000 deer on 51,500 km^2 in Patagonia, but only 600 permits were issued, mostly sold through an auction. Such low levels of harvests explain die-offs occurring due to various dry years, which had reduced carrying capacity (Flueck, 2001a,b).

Adaptive management

To maintain a constant population density, when recruitment rate is high and sustained by an adequate food base, an annual population harvest of 30–35% is required (Challies, 1989). Adaptive management is then used, which involves annual monitoring and measurements of various parameters to identify dynamics in population density, body condition, and vegetational cover. Harvest numbers should be adjusted accordingly. If density, environmental impact and physical condition are shown to have responded as anticipated, one can then assume the harvest figures used for that season were adequate. The main priority is to maintain the deer density at a certain level below the current carrying capacity. The acceptable density for red deer in a particular environment will also depend on sympatric introduced herbivores, whose densities will influence model parameters, and thus, the amount to harvest.

Management options available:

1. ***Recreational sport hunting.*** Studies have shown in New Zealand and Patagonia that such hunting does not control density. The funds generated from the sale of hunting rights through public auction need to be reinvested in deer management (Nugent *et al.*, 2011).
2. ***Recreational public hunting.*** This cannot be carried out on fiscal park nor private lands.

3. ***Commercial hunting.*** Properly designed this would be viable (*e.g.*, New Zealand), pending on public acceptance, and would require harvesting female deer.
4. ***Laisser-faire.*** This does not address conservation, nor does it optimize the current sport hunt by not allowing stags to reach their full potential with well-developed antlers. Practiced when long-term costs of control programs to reduce perceived deer impacts may not be practical.
5. ***Integrated management.*** Landowners would be provided with an incentive to implement management strategies—preferably as a collective—by having access to general funds generated from the recreational sport hunting that is now practiced in the fiscal zones.
6. ***Private concession.*** A report elaborated for APN included a design of hunting units for a concession and successful examples from Europe (Flueck and Smith-Flueck, 2001).
7. ***Professional control hunting.*** This provides results if the deers' activity patterns and social behavior are not modified. Thus, the Judas method was recommended to APN (Flueck,1991), as being feasible, less expensive than other options and with minimal collateral impact. Ideally, implementing this strategy would be combined with scientific studies to monitor the effects on deer population dynamics and social behavior, as well as the effects on the ecosystem (Flueck *et al.*, 1995).
8. ***Stricter enforcement of illegal poaching activities.***

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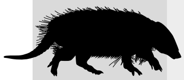

Chaetophractus villosus
large hairy armadillo, peludo

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Resumen. *Chaetophractus villosus* o «peludo» (Xenarthra – Chlamyphoridae) es una especie de armadillo cuya distribución se extiende desde el Gran Chaco de Bolivia y Paraguay hasta el sur de la provincia argentina de Santa Cruz y las provincias chilenas de Bío Bío y Magallanes. Presenta hábitos cavadores, es omnívoro generalista y puede ocupar una gran variedad de ambientes: pastizales, sabanas, bosques e incluso campos degradados por la actividad agropecuaria. Es una especie claramente favorecida por la actividad del hombre dado que puede aprovechar ambientes modificados, alimentarse de ganado y en basurales, y ha ampliado su distribución hacia el sur gracias a ello y a los puentes sobre los ríos. Es la especie más ampliamente distribuida en Argentina; en tiempos recientes ha ocupado toda la Patagonia y en 1982 fue introducida en la Isla Grande de Tierra del Fuego, en la zona de la Bahía San Sebastián, cruzando así el Estrecho de Magallanes. Estudios genéticos determinaron que todos los individuos de esta única ola de colonización pertenecen al mismo linaje mitocondrial, es decir que poseen una gran reducción de la variabilidad genética en la población. Sin embargo su viabilidad y éxito son innegables. Para 2005 la especie ocupaba unos 484 km^2 en una zona de explotación petrolera en la costa de la mencionada bahía, con tuberías calientes soterradas para el transporte de los hidrocarburos extraídos (una ventaja dado el clima fueguino y los hábitos cavadores del peludo). Actualmente ocupa una superficie aproximada de 8000 km^2 que incluye grandes zonas sin tuberías calientes, lo que evidencia su definitiva aclimatación a las condiciones de la región. *C. villosus* no posee depredadores conocidos en Tierra del Fuego y se presume que su presencia allí podría tener impacto sobre varias especies nativas de roedores, aves y el único reptil. Esto tiene sentido dado que en su distribución continental preda sobre anfibios, reptiles, y pichones y huevos de aves, por la distribución que presenta en la Isla Grande y por evidencias indirectas de sus hábitos de forrajeo en el suelo y uso de hábitat en dicha isla. Aunque el peludo *C. villosus* debe ser considerado una especie exótica establecida en Tierra del Fuego, es necesario realizar estudios dirigidos a evaluar su impacto ecológico y económico en el delicado ambiente insular fueguino.

General description of the species

Armadillos are native and typical components of Neotropical faunas associated with temperate climates, historically grouped into the family Dasypodidae. According to a proposal based on mitochondrial DNA, this family should only include long-nosed armadillos or mulitas (*Dasypus*), while the other armadillo species would be part of the family Chlamyphoridae (Gibb *et al.*, 2016), including the large hairy armadillo or peludo (*Chaetophractus villosus*; Fig. 1). This case brings up a classic, but enriching disagreement between genetic versus morphological evidence, both of which have contributed to develop scientific knowledge about phylogenetic relationships of many species.

Figure 1. *Chaetophractus villosus*. (Photo: Leopoldo Soibelzon).

The armadillo's diversity decreases toward higher latitudes; only two species have colonized the Patagonia region: the pichi (*Zaedyus pichiy*) and *C. villosus*. The distribution of the latter in Argentina extends from the Gran Chaco of Bolivia and Paraguay to the southern part of Santa Cruz province, while in Chile it is found from Bío Bío to Magallanes provinces (Atalah, 1975; Wilson and Reeder, 1993). It is the armadillo with the broadest distribution in Argentina, and also includes Tierra del Fuego province (TDF), where it was introduced in 1982 (Poljak *et al.*, 2007). *C. villosus* inhabits diverse environments, such as grasslands, savannas and forests, and also cultivated and degraded fields, such as those used for cattle pasture (Abba and Superina, 2010). Large hairy armadillo individuals reach sexual maturity at an age of one year old, breed during spring, and females give birth to one to three young per litter once a year, after about 10 weeks of gestation. Among the human uses of this species, in a large part of its distribution it is captured for food and in some regions as material to build string instruments (*charangos*) (Aguiar and Fonseca, 2008). In addition, it can be hunted as a pest species in agricultural areas and may also be killed on roads and by dogs (Abba and Cassini, 2008).

Armadillos have a low body temperature and low basal metabolic rate in relation to their body mass, which are adaptations for burrowing habits (McNab, 1979, 1980, 1985). Burrows provide more stable thermal conditions to cope with environmental temperature fluctuations, and in the case of *C. villosus*, this advantage is combined with a low degree of diet specialization (Redford, 1985) that gives it a remarkable plasticity to inhabit regions with diverse climates and food resources. This plasticity is clearly evidenced by the species' distribution range, including TDF where the average annual temperature is 2–3 °C lower than the continent. The presence of large hairy armadillo on this island again raises questions related to the colonization strategies and impact of introduced species on TDF. Thus, the climate would not be an impediment to the distribution of *C. villosus* to the south, but water barriers, such as the Magellan Strait, could be sufficient obstacles to stop its dispersal (Deferrari *et al.*, 2002; Poljak *et al.*, 2007). This hypothesis would explain why this species colonized Patagonia so recently and quickly, crossing the main rivers due to growing anthropic activity, as proposed by Abba *et al.* (2014), and having an increased home range due to a shortage of food resources (Poljak *et al.*, 2010).

History of the invasion

This armadillo species was introduced to the southern part of San Sebastián Bay in 1982. This is an area of intense oil and gas exploitation. Eight individuals brought from Buenos Aires province were introduced for aesthetic reasons in a ranch located to the northwest of Río Grande city, and an unknown number of animals were introduced by an oil drilling crew from Santa Cruz province for consumption as food (Poljak *et al.*, 2007). Subsequent phylogeographic study revealed the genetic relationship between the TDF population with individuals from the Pampean ecoregion (Buenos Aires and La Pampa provinces) and Santa Cruz province (Poljak *et al.*, 2010), which agrees with the purported origins. This study also revealed that a single mitochondrial lineage colonized all of Argentinean Patagonia and the Argentine portion of TDF. A subsequent study suggested that the same single mitochondrial lineage may have also invaded Chilean TDF (Poljak *et al.*, 2020).

Patterns of expansion and current distribution

To facilitate the transport of extracted hydrocarbons to storage tanks, oil pipelines in TDF are heated at 70 °C, even 90 °C during winter, given the low prevailing temperatures in the archipelago. This could have helped the initial establishment and expansion of the large hairy armadillo on the coast of San Sebastián Bay, since almost all the burrows are exactly located on the lines where the above-mentioned pipes are buried (Poljak *et al.*, 2007). Since its introduction in 1982, the distribution of the species increased to 484 km^2 until 2006 (Poljak *et al.*, 2007). Recent studies revealed that the current distribution is of 8,527 km^2, seventeen times larger (Poljak *et al.*, 2020). Expansions of the distribution range were mainly to the west and in a northwest /southeast direction, along the marine coast, probably due to the predominance of loose sandy soils.

The same Patagonian steppe environment where the grasslands of *coirón* (*Festuca* sp.) are abundant, extends about 6,000 km² to the north of the current known invasive distribution of *C. villosus* in TDF. Therefore, it is reasonable to assume that the species is also present there or will be in a short time. Of note, no oil exploitation is in areas where this species expanded its distribution (Poljak *et al.*, 2020). This strongly suggests that the species exceeded the initial obstacles of its biological invasion on the island (see Lizarralde *et al.*, this volume). Predation on newborn lambs and the use of middens by peludos as a source of food in the region (Abba and Cassini, 2008) are undoubtedly also causes of the settlement and expansion of the species. Currently, the large hairy armadillo's distribution in TDF is growing and given the outdated records of its presence in the south of Chile (Fig. 2;

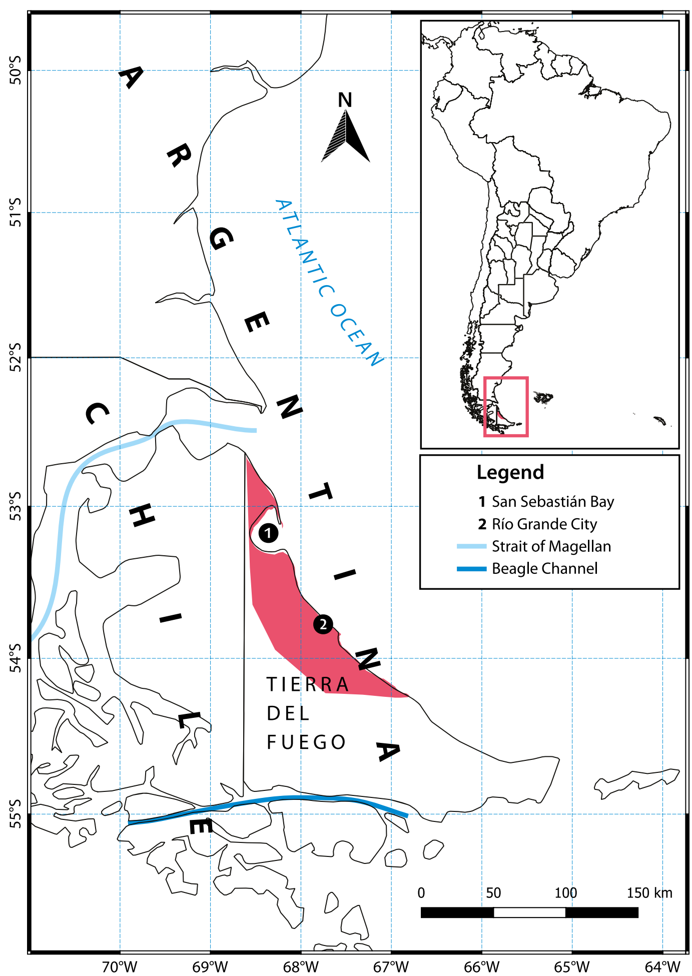

Figure 2. Distribution of *Chaetophractus villosus* in Argentina. Modified from Gallo *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

Cabello *et al.*, 2017; Poljak *et al.*, 2020), new explorations would be important to deepen the understanding of biogeographical studies, including the Chilean portion of TDF. In addition, these studies would complete the distribution map of the large hairy armadillo; and clarify the patterns of expansion and genetic relationships of the TDF population with the continental populations on both sides of the Andes mountains.

Impacts

Poljak *et al.* (2007) mention that the life history traits of *C. villosus* overlap with those of native species in the area of San Sebastián Bay, particularly related to the choice of spaces to build its burrows that coincide with *Ctenomys magellanicus*, also called the *tuco-tuco*. This is particularly concerning because this native rodent is considered vulnerable (Lizarralde and Escobar, 2000). On TDF, the armadillo's foraging area also overlaps with that of the migratory buff-necked ibis (*Theristicus caudatus*), which digs holes in the ground to feed at similar depths as the large hairy armadilllo. In spite of these potential impacts, there are no specific studies that have quantified competition or interactions between or other species. Preliminary data obtained in the areas around heated oil pipelines indicate that *C. villosus*' diet includes roots, beetles and other insect larvae and *calafate* fruits (Poljak *et al.*, 2007). In its continental range, this species also feeds on small vertebrates (*e.g.*, amphibians, reptiles and pigeons) and eggs (Redford, 1985).

It should also be noted that coastal area of San Sebastián Bay is part of an internationally recognized Ramsar wetland (Provincial Law #415/98 TDF, Argentina), which includes the protection of waterfowl habitat. Plus, it is the natural habitat of the Magellanic lizard (*Liolaemus magellanicus*), a lizard species which is the only reptile native to TDF (Úbeda and Grigera, 1995; Lavilla *et al.*, 2000). Therefore, it is reasonable to consider that *C. villosus* presence in the area is a potential risk for the conservation of these species. It should also be noted that Cossa *et al.* (2021) reported the predation of a large hairy armadillo on an upland goose (*Chloephaga picta*) nest in Santa Cruz province, indicating its ability to impact this species which is also native to TDF and nests on the ground.

In its native range, the large hairy armadillo is a very low frequency diet item for fox species found on the continental steppe. However, there is no evidence that invasive Pampa fox (*Lycalopex gymnocercus*), which is the only species that inhabits TDF grasslands, feeds on it (Medel and Jaksic, 1988). On the other hand, in contrast to the cultural, social and economic values that *C. villosus* has along its continental distribution, it is not a species used by the inhabitants of the Fuegian steppe, perhaps for being a new component in the region. Both situations could be favoring the establishment of this species on TDF: from an ecological point of view, due to the fact that there is apparently a lack of predator pressure, and from a socio-cultural one, because it is not a species exploited as a resource.

Management

C. villosus has acclimatized and settled in TDF. Its geographical distribution has increased from 484 km² in 2005 to 8,527 km² in 2020 and must be considered as an established introduced species for TDF (Poljak *et al.*, 2020). This shows that the species can survive without specific conditions created by anthropic activities (*e.g.*, associated with gas pipelines) and supports the claim that the species is in an "expansion phase" of its biological invasion (as proposed by Cabello *et al.*, 2017). To date, there are not systematic management plans.

Additionally, although there is evidence of predation over birds and mammals in other parts of the large hairy armadillo's distribution, there is no direct evidence of this kind of interactions with native species of TDF. Therefore, studies to assess the ecological and economic impact of *C. villosus* in TDF's environment are needed.

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Rodentia: Muridae

commensal rodents, roedores comensales

Mus musculus

house mouse, ratón doméstico

Rattus norvegicus

Norway rat, rata parda o noruega

Rattus rattus

black rat, rata negra o de los tejados

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Resumen. *Mus musculus*, *Rattus norvegicus* y *R. rattus* son roedores invasores de la familia Muridae y se encuentran entre las especies invasoras más importantes del mundo. Estas especies son originarias de Asia y Europa y se han expandido siguiendo al hombre, teniendo actualmente una distribución cosmopolita. Su introducción en nuestro país fue accidental y ocurrió en sucesivos momentos desde la colonización europea como polizón en los barcos, aunque se cree que *R. rattus* habitaba el Nuevo Mundo antes de la llegada de los españoles, posiblemente acompañando las distintas corrientes de asiáticos que llegaron a América. Su alimentación es omnívora y tienen hábitos principalmente nocturnos. Habitan una gran variedad de ambientes, especialmente en estrecha relación con el hombre (comensal), prefiriendo sus viviendas, comercios, industrias y granjas de cría de animales a los ambientes naturales o cultivos. *R. norvegicus* y *R. rattus* también forman colonias en ambientes naturales como en el archipiélago fueguino e Islas Malvinas, donde afectan la fauna nativa. Su actividad reproductiva depende de las condiciones ambientales; en climas templados pueden reproducirse durante todo el año y en climas rigurosos son marcadamente estacionales, con un máximo reproductivo en los meses estivales. Estos roedores producen daños estructurales, consumen y contaminan el alimento, provocando pérdidas productivas, y hospedan y dispersan agentes patógenos. En Argentina se los ha encontrado portando los agentes de la triquinosis, teniasis, rodentolepiasis, criptosporidiosis, toxoplasmosis, leptospirosis, salmonelosis, coriomeningitis linfocitaria y síndrome renal por hantavirus, entre otros. Debido a los daños que producen estos roedores es muy común en la actividad privada la aplicación de medidas de control, principalmente químicas y mecánicas. A nivel programático, es evidente la falta de continuidad de programas y de formación de recursos humanos capacitados, transformándose esto en parte del problema.

***Mus musculus*, Schwarz and Schwarz, 1953**

Familia	Muridae Illiger, 1815
Subfamilia	Murinae Illiger, 1815
Género	*Mus* Linnaeus, 1766

General description of the species

This species has a small, thin body; a small, slightly pointed snout; small black protruding eyes; moderately large, round ears; relatively short legs; and a dark, almost hairless tail with scales distributed like rings (Fig. 1). The tail length is about the same as the body and head length together. The hair is short, soft, and glossy. The back is light brown with ocher dyes to dark grey-brown. The belly fur is lighter. It has five pairs of teats (one pectoral, two postaxillary and two inguinal). The total adult length ranges from 148 to 205 mm; the body-head is 65 to 90 mm; the body is 69 to 85 mm; and the hind foot is 16 to 20 mm. The mouse's weight is 11 to 30 g. This rodent has a dental formula of 1/1 0/0 0/0 3/3. It is omnivorous, but prefers grains and seeds.

Figure 1. *Mus musculus*. (Photo: Gerardo Cueto).

The average life expectancy is about one year. Reproductive strategies change according to environmental characteristics. In temperate rural environments, it reproduces throughout the year with peaks in spring and summer (Gómez *et al.*, 2008; Vadell *et al.*, 2010; León *et al.*, 2013; Vadell *et al.*, 2014). It is reproductively active at 6-to-10-weeks of age. Five to six young are born after 19–21 days of gestation (Timm, 1994a; Vadell *et al.*, 2014). They have postpartum estrous. The population can grow rapidly when the climatic conditions are favorable, but survival and reproduction of young individuals declines when abundance is high.

This species is nocturnal, but it can have diurnal activity, not necessarily associated to a high abundance. It climbs, jumps and swims well, and it enters buildings by gnawing through materials.

It builds burrows in the soil or under wood floors when other places are not available (Timm, 1994a).

The nests are sloppy, and they look like a ball of 10 to 15 cm in diameter. Mice inhabit a great variety of environments. This species is closely associated with humans (*i.e.*, is commensal), preferring houses and other dwellings, commercial buildings, and farms over natural environments and croplands (León *et al.*, 2013; Lovera *et. al.*, 2019). Mice are also common in shanty towns and urban vacant lots where there is a lack of public sanitation services (Cavia *et al.*, 2009; Gomez *et al.*, 2009; Cavia *et al.*, 2015).

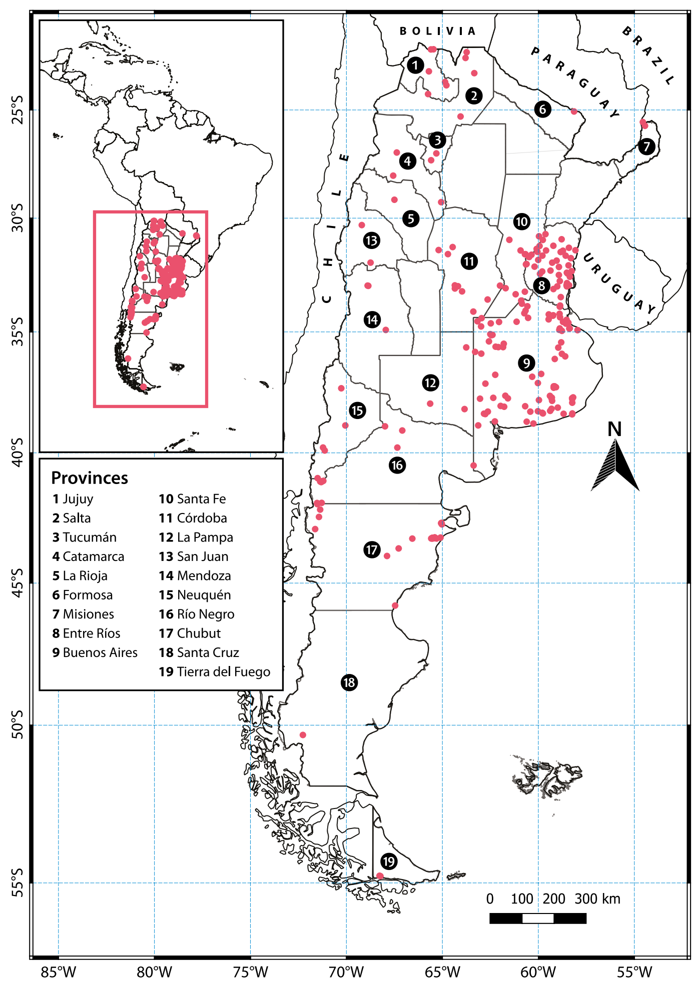

Figure 2. Distribution of *Mus musculus* in Argentina. Modified from Cavia *et al.* (2019a). (Mapping: Ian Barbe and Alfredo Claverie).

History of the invasion

Original from Central Asia, the house mouse introduction in Argentina was accidental and probably occurred multiple times since European colonization. It is among the most detrimental invasive species in the world together with *Rattus norvegicus* and *R. rattus* (Lizarralde, 2016).

Patterns of expansion and current distribution

Mus musculus has been accidentally spread by humans, having today a worldwide distribution (Fig. 2).

Impacts

House mice damage structural, components and equipment buildings, and they consume and contaminate animal and human food, promoting production loss and spread of diseases and ectoparasites (Timm, 1987; Timm, 1994a; Pratt, 1991; Villa and Velasco, 1994).

This species is involved in the transmission of the pathogen agents of teniasis, trichinosis, babesiosis, rodentolepiasis, capillariasis, brachylatmiasis, cryptosporidiosis, chagas, leptospirosis, salmonellosis, campylobacteriosis, rat-bite fever, hemolytic uremic syndrome, cholera, hepatitis, typhoid fever, toxoplasma, cowpox and lymphocytic choriomeningitis to human and livestock (Meerburg *et al.*, 2009; Gürtler and Cardinal, 2015; Cavia *et al.*, 2019a). It is also involved in the transmission of bubonic plague, murine typhus, scrub typhus and vesicular rickettsiosis, transmitted by their ectoparasites (mites, fleas and lice; Meerburg *et al.*, 2009; Bitam *et al.*, 2010; Eisen and Gager, 2012; Lareschi *et al.*, 2016). In Argentina, mice have been found that were infected by various pathogenic agents, including taeniasis, trichinosis, rodentolepiasis, toxoplasma, cryptosporidiosis, leptospirosis and the virus of lymphocytic choriomeningitis (Castillo *et al.*, 2003; Lovera *et al.*, 2017; Hancke and Suárez, 2017, 2018a, 2018b; Fitte *et al.*, 2021).

Management

Due the magnitude of damage *Mus musculus* and other rat species (*Rattus norvegicus* and *R. rattus*) cause to in farming activities (*i.e.*, in cereal storage silos, livestock production, meat industry, food industry, fruit and vegetable markets), extensive management actions have been implemented. Nevertheless, potential contamination of livestock with pathogens of rodents is not yet seen as a problem by farmers (Meerburg, 2010). Mechanical and chemical control measures are the most common methods, which are implemented in various ways. At the institutional level, a lack of program continuity, technical skills and training have been linked to problems in effectively managing rodent problems (Coto, 2015). Some areas have or have had rodent prevention and control programs, such as the Ciudad Autónoma de Buenos Aires and Río Cuarto. Also, in Argentina, rodents are prohibited in pig farms since they are involved in the transmission of *Trichinella spiralis* (see SENASA resolutions #834-2002, #555-2006, #819/2011 in http://www.senasa.gob.ar/normativas).

Figure 3. *Rattus norvegicus*. (Photo: Gustavo Ramos).

***Rattus norvegicus*, Berkenhout, 1758**

Familia	Muridae Illiger, 1815
Subfamilia	Murinae Illiger, 1815
Género	*Rattus* Fischer, 1803

General description of the species

Norway rats have a thick, flat and heavy body (more robust than that of *R. rattus*) and strong legs. Their head is flat and has an obtuse snout. Their eyes are small, and it has small, rounded, almost bare ears. The tail is shorter than the body and head length together. The rings of scales are less marked than in *R. rattus.* Short and stiff fur, but not as rigid as *R. rattus*. The color of the dorsal fur is grey–brown to brown interspersed with black hairs (Fig. 3). Belly fur is pale gray or pale brown. Six pairs of teats (one pectoral, two postaxillary and three inguinal).

The total adult length can range from 320 to 480 mm; the body-head is 150 to 225 mm; the body is 130 to 215 mm; and the hind foot is 37 to 44 mm. The Norway rat weighs from 300 to 500 g. This rodent has a dental formula of 1/1 0/0 0/0 3/3. It is omnivorous, preferring cereals, meat, fish meat and garbage. It especially seeks high fat foods. It needs daily between 20 to 30 g of food and about 30 ml of water.

The average life expectancy is one year. Reproductive strategies change according to environmental conditions (Vadell *et al.*, 2014). In sylvan areas, where animals are more exposed to seasonal changes in weather conditions, changes in reproductive investment are more evident than in rural or urban areas. In temperate climates, it reproduces throughout the year with peaks in spring and summer. Six to twelve young are born after 21 to 23 days of gestation. It can be sexually mature at the age of three to five months.

This species is nocturnal, but high abundances can lead it to also present diurnal activity. Rats typically construct nests in below-ground burrows, but also at ground level or with different materials.

It has poor eyesight, but their senses of smell, taste and touch are well-developed.

It is not a good climber, moving principally at ground level (being more terrestrial than *R. rattus*). It is good at swimming, jumping and gaining entry to structures by gnawing (Timm, 1994b). Its home range is about 36 m in diameter (range from 4 to 45 m in diameter; Timm, 1994b; Gómez Villafañe *et al.*, 2008a; Montes de Oca *et al.*, 2017). It can travel farther than 100 m to obtain food or water.

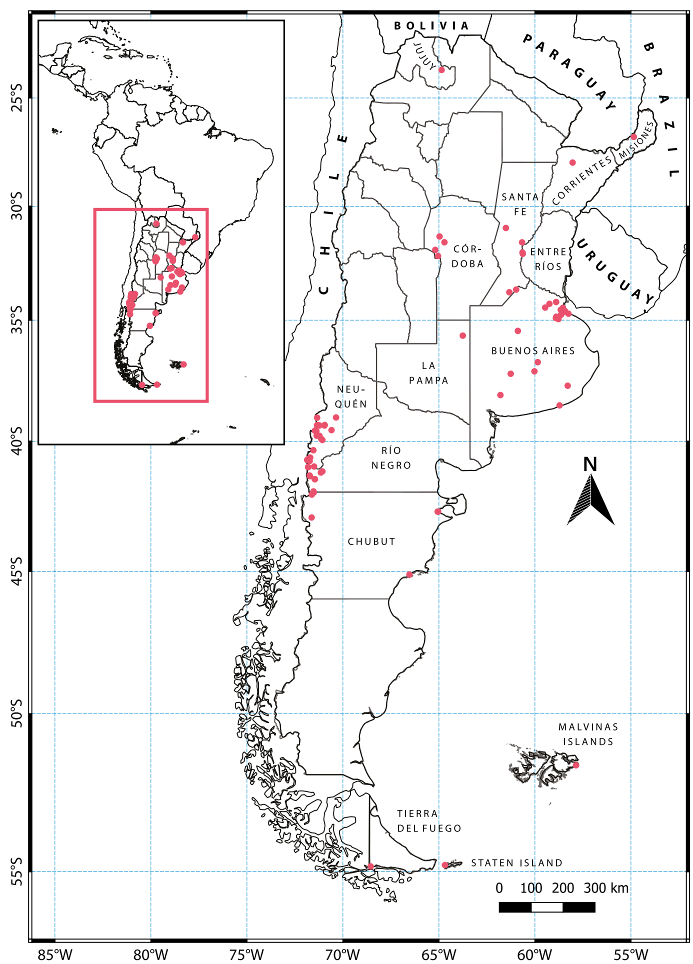

Figure 4. Distribution of *Rattus norvegicus* in Argentina. It also occurs in the South Georgia Islands. Modified from Cavia *et al.* (2019b). (Mapping: Ian Barbe and Alfredo Claverie).

It inhabits a great variety of environments. This species reaches the highest abundances in urban, periurban and rural ecosystems. In this last area, it is associated with livestock production (Coto, 2015; Gómez Villafañe and Busch, 2007; Lovera *et al.*, 2015; Montes de Oca *et al.*, 2020). In urban areas, it prefers sites like garbage dumps, sewer systems and river and channel banks; usually related to socioeconomic conditions differences within the urban areas (Castillo *et al.*, 2003; Traweger *et al.*, 2006; Cavia *et al.*, 2009; Masi *et al.*, 2010; Feng and Himsworth, 2014). These sites provide food and water resources and would provide suitable conditions for the construction of ground burrows. In the Ciudad Autónoma de Buenos Aires, captures occurred in different environments and the highest abundances were registered in shanty towns (Cavia *et al.*, 2009; Cavia *et al.*, 2015), and in Río Cuarto it was only captured along stream and railway banks (Castillo *et al.*, 2003). However, it also can live in natural environments, such as in the Fuegian Archipelago and the Malvinas Islands (Hilton and Cuthbert, 2010; Coto, 2015).

History of the invasion

The Norway rat had its origin in the East, probably in Mongolian China or Russia. In the 18th century it arrived to Europe and by 1775 was in the United States, being brought aboard merchant ships (Coto, 1997). Its introduction in Argentina was accidental and occurred probably in successive times since European colonization. Between 1899 and 1913 bubonic plague, associated to the presence of rats (although species was not specified), was reported in many Argentine cities, such as Tucumán in 1900, Córdoba in 1907, and Bahía Blanca in 1913.

Patterns of expansion and current distribution

Today, this species has a worldwide distribution, principally associated to human activities. But also, it has dispersed to natural environments of the Fuegian Archipelago, Malvinas Islands and South Georgia Islands, living in sylvan colonies. In Argentina, there are many provinces without published data or collected specimens (Fig. 4). The lack of interest by museums to collect this common pest species and differential characters in the jaws with *R. rattus* may contribute to this lack of data. Records from raptor pellets are mostly published as *Rattus* spp.

Impacts

R. norvegicus produces damage to crops; preys upon poultry and other animals; consumes and contaminates stored food and animal feed (Timm 1994b; Brown *et al.*, 2020); causes damage to leather and packaging materials, among others; and causes structural damage to buildings, ships, and furniture (Timm 1994b).

Its accidental introduction on many islands around the world has had significantly negative impacts on native species (Hilton and Cuthbert, 2010). It preys on nests causing the extinction of endemic island bird species. On isolated environments like Staten Island, and

South Georgias and Malvinas Islands, several bird species are under its hunting pressure (Massoia and Chebez, 1993; Catry *et al.*, 2007; Hilton and Cuthbert, 2010).

Worldwide, *R. norvegicus* is involved in the transmission to human and livestock of the pathogen agents of teniasis, trichinosis, babesiosis, rodentolepiasis, schistosomiasis, capillariasis, brachylatmiasis, cryptosporidiosis, chagas, leptospirosis, salmonellosis, campylobacteriosis, rat-bite fever, hemolytic uremic syndrome, Q-fever, cholera, hepatitis, typhoid fever, toxoplasma, cowpox, hepatitis E, swine fever, and hemorrhagic fever with renal syndrome (Meerburg *et al.*, 2009; Himsworth *et al.*, 2013; Gürtler and Cardinal, 2015; Cavia *et al.*, 2019b). It is also involved in the transmission of bubonic plague, murine tifus, Lyme disease, scrub typhus and vesicular rickettsiosis, transmitted by their ectoparasites (mites, fleas and lice; Meerburg *et al.*, 2009; Bitam *et al.*, 2010; Eisen and Gager, 2012; Lareschi *et al.*, 2016). Particularly in Argentina, it was found infected by the pathogen agents of the taeniasis, trichinosis, rodentolepiasis, capillariasis, toxoplasma, cryptosporidiosis, leptospirosis and haemorrhagic fever with renal syndrome (Arango *et al.*, 2001; Seijo *et al.*, 2003; Cueto *et al.*, 2008; Gómez Villafañe *et al.*, 2008b; Hancke *et al.*, 2011; Lovera *et al.*, 2017; Hancke and Suárez, 2018a, 2018b, 2020, 2022; Fitte *et al.*, 2021).

Management

See management programs in *M. musculus*.

***Rattus rattus*, Linnaeus, 1758**

Familia	Muridae Illiger, 1815
Subfamilia	Murinae Illiger, 1815
Género	*Rattus* Fischer, 1803

General description of the species

Smaller than the Norway rat, the black rat is slim and has a light body. It has big eyes, an extended head and pointed snout. Its conspicuous, big ears are almost hairless. Ears can be pulled to the eyes covering them completely. Its incisors have orange enamel. Its legs are agile and have slim thighs. The tail has conspicuous rings and is longer than the head and body length together (larger proportions compared to the Norway rat). The tail is almost hairless. Overall, it has rough and hard fur. Its dorsal fur is moderately spiny, while long, black guard hairs along the back are characteristics of this species (Fig. 5). Highly variable in color, the dorsal zone is usually grey-brown to greyish or black. The belly fur is more pale than the dorsal, but also variable in color. The species has a variable mammary formula with five or six pairs of teats (one pectoral, one or two postaxillary and three inguinal). The total adult length ranges 327 to 430 mm, the body-head is 166 to 205 mm, the body is 190 to 215 mm and the hind foot is 35.5 mm. The weight is 120 to 350 g. This rodent has a dental formula of 1/1 0/0 0/0 3/3. It is omnivorous, preferring vegetables, fruits, and cereals. It is more herbivorous than the Norway rat. It is resistant to the lack of water.

Reproductive activity depends on environmental conditions. In temperate climates, it may reproduce year-round, but with activity peaking in the spring and fall and declining in the winter. In rigorous climate conditions, reproduction is markedly seasonal with peaks in spring and fall, declining in summer and with a reproduction break in winter (Coto, 1997). Six to twelve young are born after 21 to 23 days of gestation. It can be sexually mature at the age of three to five months.

Figure 5. *Rattus rattus*. (Photo: Isabel Gómez Villafañe).

This species is nocturnal, but with high abundances it can present diurnal activity. It often makes nests in high and inaccessible places like in tree crowns and trunks, inside walls, attics, and ceilings, or on climber and creeper plants (Marsh, 1994). It builds its nests with different materials like plastic bags, paper, fabrics, threads, straws, and sawdust. It is less aggressive than the Norway rat. It is an agile climber. It is also good at jumping, swimming (but not as good as Norway rat) and it gains entry into buildings by gnawing. Its home range is about 30 to 45 m in diameter. If necessary, it can travel distances of 90 m for food (Marsh, 1994).

It inhabits mainly the residential or industrial areas of cites like the Ciudad Autónoma de Buenos Aires (Cavia *et al.*, 2009), and in a variety of environments of Río Cuarto, including in riverbanks and streams (Castillo *et al.*, 2003). In rural areas, black rats often occupied sugarcane fields and citrus groves and are less frequent in rice fields or livestock farms (Gómez Villafañe *et al.*, 2005; Lovera *et al.*, 2015; Montes de Oca *et al.*, 2020).

History of the invasion

The specific origin of the black rat is uncertain. This pest arrived to the Americas at the middle of the 18th century, but rats inhabited this continent before European colonization, dispersed by successive Asian migrant populations (Coto, 1997).

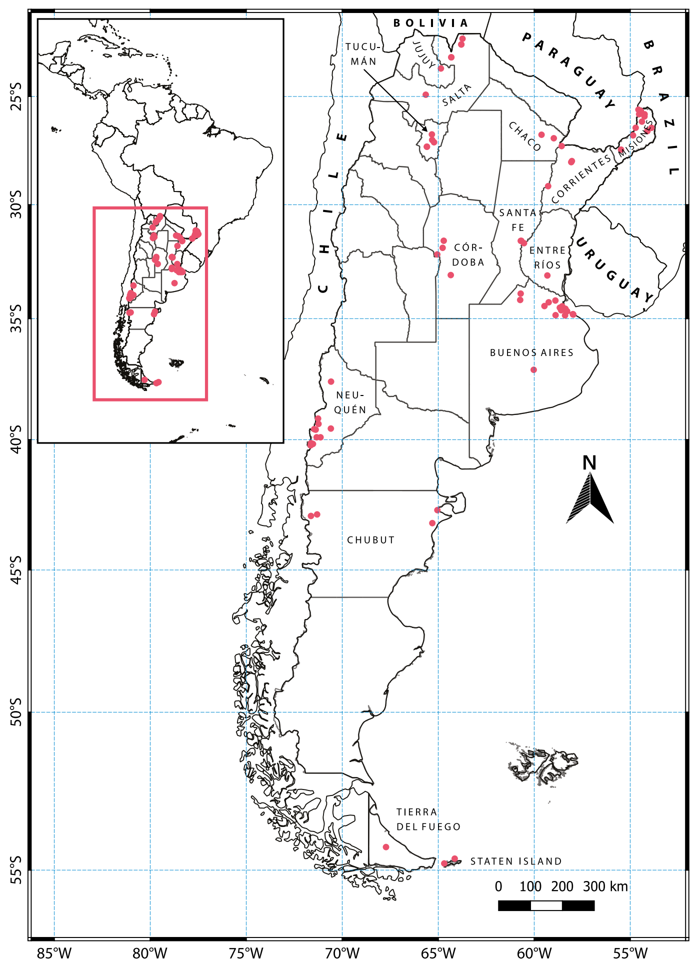

Figure 6. Distribution of *Rattus rattus* in Argentina. Modified from Cavia *et al.* (2019c). (Mapping: Ian Barbe and Alfredo Claverie).

Patterns of expansion and current distribution

This species has today a worldwide distribution, principally associated to human activities. It does not inhabit cold zones. This species apparently has not been spread on sylvan environments of the Fuegian Archipelago like Norway rats, being limited to human constructions (Coto, 2015), but it does also inhabit the Malvinas Islands (Catry *et al.*, 2007). Like *R. norvegicus*, there are many Argentine provinces without published data or collected specimens of this species (Fig. 6), probably due to the same reasons as *R. norvegicus*.

Impacts

Similar to *R. norvegicus*, the black rat can produce damage to crops; prey on poultry and other animals; consume and contaminate storage food and animal feed; cause damage to leathers and packaging materials among others; and cause structural damage to buildings, ships and furniture (Marsh, 1994; Brown et al., 2020).

Its introduction on islands also has negative impacts on native species and ecosystems, with greater negative impacts than *R. norvegicus* and *M. musculus* (Hall *et al.*, 2001; Harris, 2009; Mulder *et al.*, 2009).

Worldwide, *R. rattus* is involved in the transmission to humans of various pathogen agents (*e.g.*, taeniasis, trichinosis, babesiosis, rodentolepiasis, schistosomiasis, human fasciolosis, capillariasis, brachylatmiasis, cryptosporidiosis, chagas, leishmaniasis, leptospirosis, salmonellosis, rat-bite fever, Q-fever, cholera, typhoid fever, toxoplasma, hepatitis E, Kyasanur forest disease and haemorrhagic fever with renal syndrome) to both humans and livestock (Meerburg *et al.*, 2009; Himsworth *et al.*, 2013; Gürtler and Cardinal, 2015; Cavia *et al.*, 2019c). It is also involved in the transmission of bubonic plague, murine typhus, Lyme disease, scrub typhus and vesicular rickettsiosis, transmitted by their ectoparasites (mites, fleas and lice; Meerburg *et al.*, 2009; Bitam *et al.*, 2010; Eisen and Gager, 2012; Lareschi *et al.*, 2016). Specifically in Argentina, it was found to be infected by the following pathogenic agents: taeniasis, trichinosis, rodentolepiasis, capillariasis, toxoplasma, cryptosporidiosis, leptospirosis, and hemorrhagic fever with renal syndrome (Arango *et al.*, 2001; Cueto *et al.*, 2008; Hancke *et al.*, 2011; Lovera *et al.*, 2017; Hancke and Suárez, 2018a, 2018b, 2020, 2022; Fitte *et al.*, 2021).

Management

See management in *M. musculus*.

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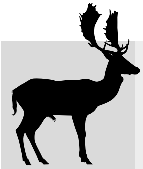

Dama dama

fallow deer, ciervo dama

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Resumen. El ciervo dama o gamo es un ciervo de tamaño mediano, cuya principal característica es la presencia de motas blancas en los flancos de ambos sexos, y astas aplanadas en forma de paleta en los machos. La especie es nativa de Europa occidental, pero fue introducida en Buenos Aires y Neuquén a principios del siglo XIX y luego transportada a diversas estancias y cotos de caza en las provincias de Córdoba, Corrientes, Entre Ríos, La Pampa, Río Negro, San Luis y Santa Fe. La población de la Isla Victoria y Península Huemul, Neuquén, parece ser la más abundante, mientras que en las otras localidades se mantiene restringida principalmente a las estancias o cotos de caza. Existe muy poca información sobre los impactos del ciervo dama, ya que fueron descriptos solo en Isla Victoria, Neuquén, donde ocurre junto al ciervo colorado. Los impactos incluyen reducción de la cobertura vegetal y regeneración de especies palatables, y cambios en la composición vegetal aumentado las especies resistentes a la herbivoría. Además, el ciervo dama raspa y descorteza los árboles, pero este comportamiento solo afecta muy pocos ejemplares (~3%). También se ha observado que los ciervos introducidos pueden facilitar la invasión de pinos introducidos, suprimiendo la vegetación nativa y dispersando hongos micorrízicos. En la Argentina, el único plan de control de ciervo dama se realiza en la Isla Victoria, Neuquén, y tiene como objetivo la erradicación por medio de caza. Además, en la mayoría de los cotos de caza está permitida la caza deportiva, pero se conoce que no es efectiva para controlar las poblaciones de la especie.

General description of the species

The fallow deer is a medium-sized deer, having about 130–160 cm in length and 75–95 cm in height at the shoulder, and weighing about 50–100 kg (Fig. 1). It has much variation in coat color, commonly being reddish brown with numerous white spots on the flanks, which are most pronounced in summer. Only males have antlers, which are up to 70 cm long, palmate, with short tines, that are shed about October. Mainly diurnal and crepuscular, males and females occur in separate single-sex groups, except during the rut, when individual males tend to gather harems (Long, 2003). The rut peaks in April, and one calf is usually born after 235–250 days of gestation. Their life span is about 16–20 years, with males rarely attaining more than 8–10 years (Long, 2003). This deer's home range varies by sex; males may occupy an area of 300–900 ha, while females only 130–200 ha (Ciuti *et al.*, 2006; Borkowski and Pudełko, 2007). Fallow deer graze and browse on a variety of items including grasses and shrubs' leaves, buds, shoots and berries.

History of the invasion

The fallow deer is native to western Eurasia, but it has been introduced in many places around the world. In Argentina, the first introduction appears to have been in Parque Pereyra Iraola, Buenos Aires, in early 19th century (Long, 2003). However, most of invasive populations seem to originate from individuals brought by Ernesto Tornquist from Spain and Poland and released around his home in 1905 near the Sierra de la Ventana hills in southern Buenos Aires province (Chapman and Chapman, 1980; Navas, 1987). Later, individuals were released in nearby ranches and/or spread to several locations across Buenos Aires, including Huetel Ranch, Maipú, Sierra de la Ventana, Tandil, etc. (Chapman and Chapman, 1980). In the 1930s, fallow deer were introduced by Aarón Anchorena in Victoria Island and Huemul Ranch (Daciuk, 1978; Navas, 1987); and by Carl Vogel in Parque Diana and Primavera Ranch, all in Neuquén province. Afterwards, the fallow deer was introduced in several hunting ranches in Córdoba, Corrientes, Entre Ríos, La Pampa, Río Negro, San Luis, and Santa Fe, but unfortunately there are no detailed records.

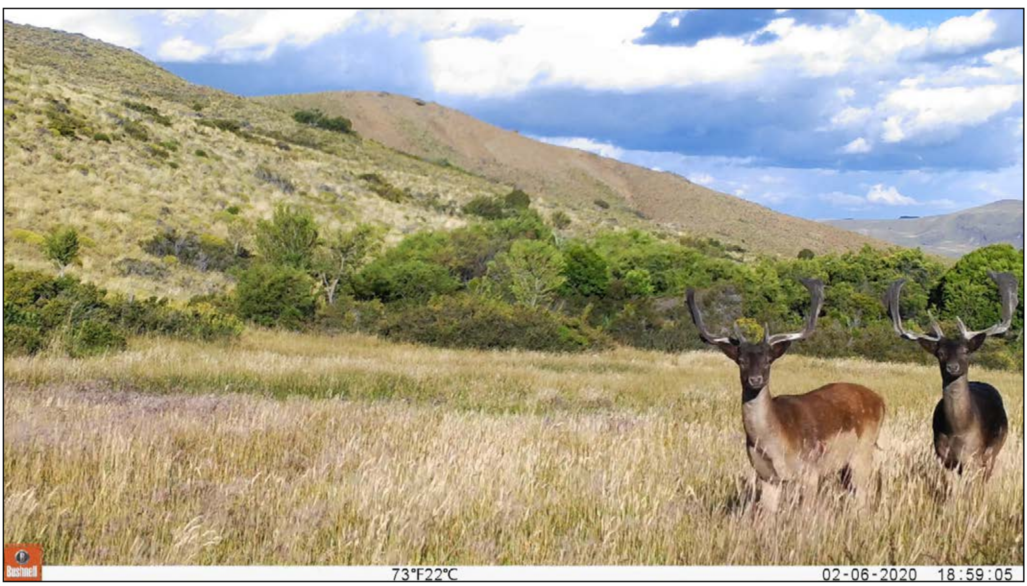

Figure 1. *Dama dama* in Parque Nacional Nahuel Huapi, Argentina. (Photo: Sebastián Ballari).

Patterns of expansion and current distribution

While the fallow deer was introduced in several locations, they are only very abundant on Victoria Island and the Huemul Peninsula in Neuquén province (Daciuk, 1978; Navas, 1987). Otherwise, fallow deer seem to be scarce or restricted to hunting ranches (de Vos *et al.*, 1956; Navas, 1987; Bonino, 1995; Long, 2003; Canevari and Vaccaro, 2007; Novillo and Ojeda, 2008; Fig. 2).

Impacts

Although the effects of fallow deer on native vegetation have been described as detrimental (Daciuk, 1978), there have not been any systematic evaluations of the impact (Bonino, 1995). The only two available studies describe the impact of both fallow and red deer on Victoria Island, Neuquén (Veblen *et al.*, 1989; Barrios-Garcia *et al.*, 2012). These studies indicate that browsing is species-specific, reducing plant cover and regeneration of palatable species, altering plant composition to browse-resistant species (Veblen *et al.*, 1989; Relva and Veblen, 1998; Relva *et al.*, 2009; Barrios-Garcia *et al.*, 2012). Tree fraying and bark stripping is also species-specific, but occur at a very low incidence (only ~3% of the individuals), suggesting that impact might be negligible (Barrios-Garcia *et al.*, 2012).

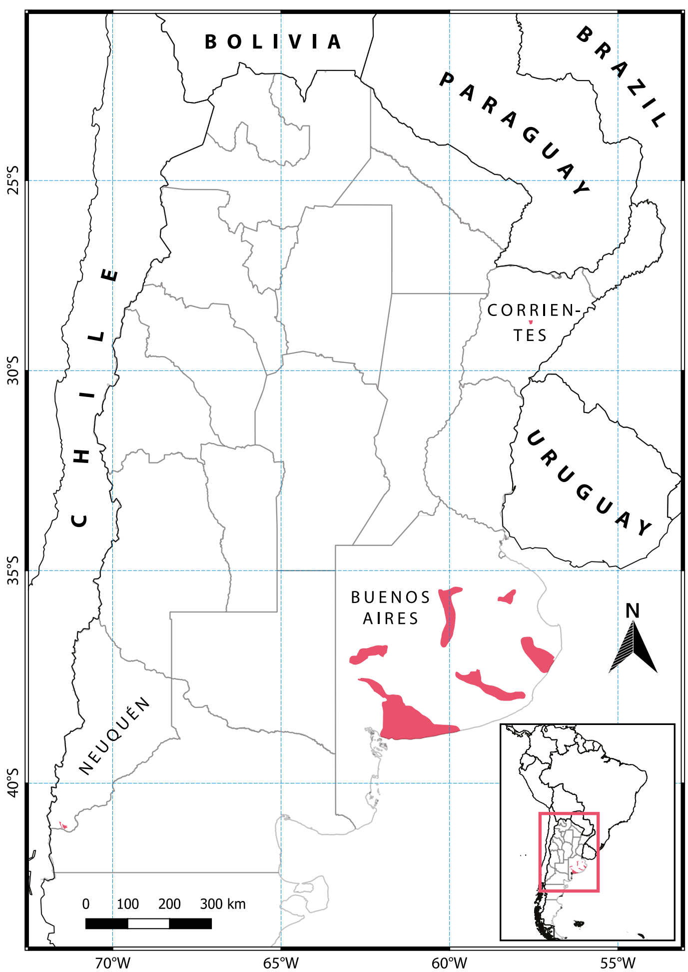

Figure 2. Distribution of *Dama dama* in Argentina. Modified from Barrios-García *et al.* (2019). (Mapping: Alfredo Claverie and Ian Barbe).

Similarly, one study reported no effects of deer on soil physical and chemical properties (Relva *et al.*, 2014). Lastly, another study showed that introduced deer on Victoria Island facilitate pine invasion by browsing on native species and dispersing ectomycorrhizal fungi (Relva *et al.*, 2010; Nuñez *et al.*, 2013).

Management

Like other deer species, hunting is the main control measure for fallow deer. In Argentina, the only approved management plan aims to eradicate fallow deer on Victoria Island, Neuquén, by means of hunting. Otherwise, sport hunting is allowed in most of the hunting ranches across the country, but it is known to be ineffective to control fallow deer populations.

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Felis sylvestris catus
domestic feral cat, gato doméstico asilvestrado

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Resumen. El gato doméstico semiasilvestrado, cuyo origen se encuentra en Medio Oriente, es un depredador ágil y eficiente de gran adaptabilidad a diversos entornos y condiciones climáticas. Es una especie solitaria y de actividad nocturna-crepuscular y presenta un número medio de entre 3 y 6 crías por camada. Si bien no existen estudios específicos para Argentina, analizando las tendencias poblacionales mundiales es muy probable que las poblaciones de este felino se encuentren en franca expansión en ambientes silvestres. Según la descripción global, fueron introducidos deliberadamente probablemente con los primeros colonizadores como mascotas, comensales o control de plagas. La especie ha colonizado con éxito buena parte del territorio argentino y se ha registrado su presencia en numerosas áreas protegidas del país. Su propagación se asocia principalmente a las personas, debido a su papel como mascotas, y a su capacidad de dispersión natural cuando son asilvestrados. Su principal impacto es la depredación sobre especies nativas y pueden desplazar a los carnívoros nativos debido a la competencia por los recursos. El gato doméstico asilvestrado puede ser portador de numerosas enfermedades que pueden transmitirse al ser humano o a otros animales salvajes. Hasta el momento no se ha realizado una gestión nacional y el único caso documentado es el control no letal de gatos domésticos asilvestrados en la Reserva Natural Isla Martín García, Buenos Aires, cuyos primeros resultados lograron reducir el número de felinos circulantes en la isla (alrededor del 20%) y, con ello, el impacto en algunas especies de la fauna nativa.

General description of the species

The domestic cat (*Felis sylvestris catus*) is one of the smallest members of the family Felidae. It is an agile and efficient predator, with morphological adaptations, such as a flexible body, great vision, retractable claws, sharp teeth, and a long and flexible tail that helps balance. Color variations include shades of brown, black and white in spotted, striped and smooth patterns. Feral populations present adaptations that would be associated with the habitat where they live, such as longer and denser coats in cold areas and shorter hair in warmer environments (Fig. 1). There are more than 100 domestic cat breeds, mostly of similar size, with an average length of 76.5 cm and weighing between 2–6 kg (Long, 2003).

Figure 1. *Felis sylvestris catus* in Reserva Natural Isla Martín García, Argentina. (Photo: Ian Barbe).

Habitat

Cats are highly adaptable animals to various environments and climatic conditions. There are resident feral populations of domestic cats on every continent except Antarctica, including several oceanic islands. They can survive in almost all environments, from the sub-Saharan desert to sub-Antarctic islands, even in the absence of humans. It is estimated that at least 500 million domestic cats are kept as pets in the world and several million more are estimated to live with little human contact or completely feral. Terrestrial with crepuscular to nocturnal activity patterns, the cat is a solitary generalist carnivore (Palacios *et al.*, 2019).

Reproduction

Female cats reach sexual maturity on average at six months of age, while males become reproductive at around 10 months. Females are seasonal polyesters, varying the number of estrus periods based on environmental conditions, but generally with two per year. Complete estrus lasts approximately 15 days and the gestation period from 62–64 days. The average number of kits per litter is between three to six (Palacios *et al.*, 2019).

Native range distribution

Archaeological records, supported by genetic and morphological evidence, suggest that cat domestication arose from its relative the African wild cat (*Felis silvestris lybica*), which must have occurred about 9,000–10,000 years ago in the Fertile Crescent region of the Near East (Driscoll *et al.*, 2007; Macdonald *et al.*, 2010). This fact could have been related to the increase in agriculture and the consequent need to protect crops from rodents. Wild cats probably approached grain accumulation areas, and humans took advantage of their hunting skills to protect the production, taking kittens to breed in captivity (Wilson and Mittermeier, 2009). Although there are no specific studies for Argentina, analyzing world population trends it is highly probable that the populations of this feline are expanding in wild environments.

History of the invasion

There are no records of the date of introduction, but according to the global description (Nogales *et al.*, 2004), they were deliberately introduced, probably with the first European colonizers, as pets, commensals or pest control agents (Nogales *et al.*, 2004; Valenzuela *et al.*, 2014; Ballari *et al.*, 2016). Subsequently, cats must have become feral as a result of escapes or abandonment. It is probably also the case that the species has successfully colonized most of Argentina, with stable populations of feral/semi-feral/semi-domestical individuals associated to the peripheries of urban centers, rural establishments, and even isolated houses; but also, the species is surely found in natural environments (Palacios *et al.*, 2019).

Patterns of expansion and current distribution

The spread of the domestic cat is mainly associated with humans and their infrastructure (including routes, etc.) or vehicles (ships, etc.). Although there are few records of the presence of this species in Argentina, its reproductive and ecological characteristics suggest that feral cats could be occupying different habitats in natural areas, but urban areas as well, making it likely that its distribution is almost continuous in the country (Fig. 2). However, there are only a few published records of feral cat populations: 1) Tierra del Fuego Island (Lizarralde and Escobar, 2000) and Observatorio Island (A. Raya Rey, pers. comm.), both in Tierra del Fuego province; 2) several national parks (Merino *et al.*, 2009); 3) Tova and Tovita Islands in Chubut province (Udrizar Sauthier *et al.*, 2017); 4) Reserva Natural Isla Martín García in the La Plata River (Barbe, 2020); and recently, 5) the species was detected for first time in the Parque Nacional Tierra del Fuego (Rodríguez Planes *et al.*, 2019).

Regarding Tierra del Fuego province, in 2008 there were at least 15 feral cats in the Reserva Provincial Corazón de la Isla in Tierra del Fuego Island and the previously mentioned first record in the Parque Nacional Tierra del Fuego, while on Observatorio Island there is only one individual, probably abandoned by Navy personnel associated with the lighthouse, like on other islands in the archipelago (Anderson *et al.*, 2006).

The cat was introduced to Martín García Island (Buenos Aires province) by Europeans in the 16th century, when the first individuals of this species arrived, used on ships to control rodents. In 2018, the cat population in the Reserva Natural Isla Martín García reached 224 individuals of domestic and semi-feral cats (Barbe, 2020). On the other hand, there are

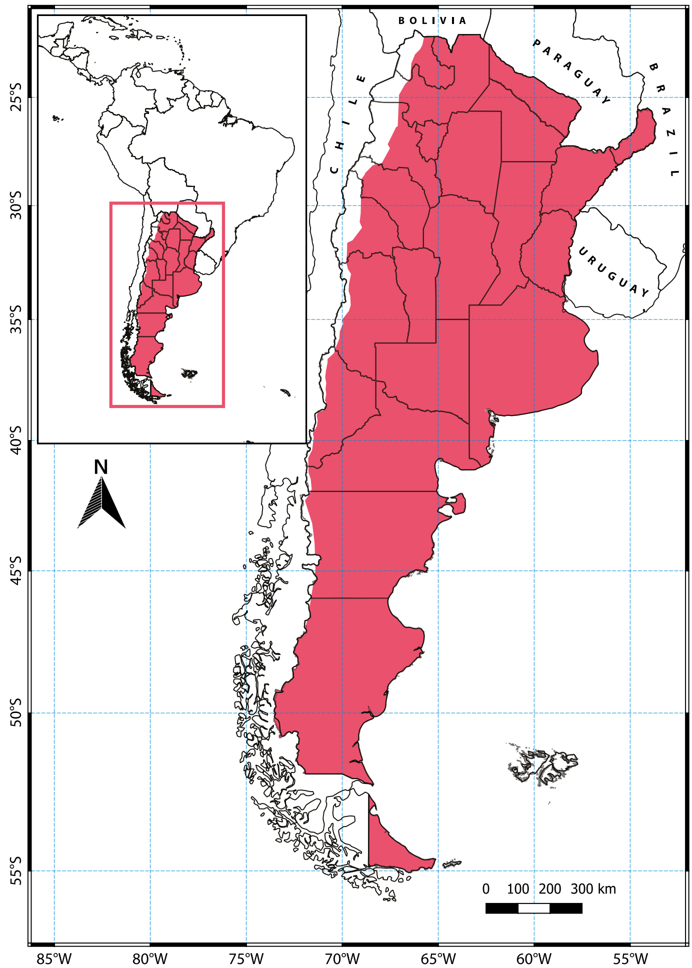

Figure 2. Distribution of *Felis sylvestris catus* in Argentina. Modified from Palacios *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

records of feral, semi-domestic or domestic cats in at least 10 different national and provincial protected areas (Merino *et al.*, 2009).

In the case of Tova and Tovita Islands, at least three different adult specimens have been observed, identified by their different fur, and two dead kittens (indicating reproduction; Udrizar Sauthier *et al.*, 2017). It is likely that cats arrived to these islands with seaweed collectors around the 1970s (Udrizar Sauthier *et al.*, 2017).

Impacts

Ecological impact

Felis sylvestris catus is one of the world's 100 most harmful introduced invasive species (Lowe *et al.*, 2004). The main impact of cats is by predation on native species—generally underestimated—, reaching billions of birds, rodents and reptiles annually just in the USA (Loss *et al.*, 2013; Mcruer *et al.*, 2016). Additionally, they depredate marine bird nests on islands located in the south-east portion of Chubut province and in the Fuegian Archipielago, Argentina (Palacios *et al.*, 2019). Also they can displace native meso-carnivores due to competition for resources. Incursions of free-range domestic cats into natural environments favors the transmission of diseases, which can be potentially devastating for native species (Funk *et al.*, 2001). Additionally, hybridization with small wild cats is possible (Wayne and Brown, 2001; Sunquist and Sunquist, 2002) and can lead to local extirpation of native species (MacDonald *et al.*, 2010).

Economic impact

The population control exercised by domestic cats over rat populations in food production areas produces a positive effect on yield (Palacios *et al.*, 2019). Additionally, economic cost of management should be accounted as economic impact, since programs to reduce free-range domestic or feral cat populations through capture-castration-release or removing individuals are expensive (Andersen *et al.*, 2004; Robertson, 2008).

Health impact

Domestic and feral cats carry numerous diseases that can be transmitted to humans or other wild animals (Palacios *et al.*, 2019), including rabies and *Toxoplasma gondii* (Perez *et al.*, 2011). Parasites of epidemiological importance were detected in feral cats from the Reserva Natural Isla Martín García, such as hemotrophic mycoplasma (Perez *et al.*, 2019).

Management

To date, there is no national management plan for cats (Palacios *et al.*, 2019). Due to its status as a pet, the social perception of the species and its impacts by large sectors of society do not necessarily correspond to the ecological reality, generating a potential conflict regarding the management of feral or semi-feral populations. The management of an introduced invasive charismatic species needs the support of the society (Guichón *et al.*, this volume), not only through responsible ownership, but also by supporting feral populations reduction actions. A cat management plan was carried out in the Reserva Natural Isla Martín García, Buenos Aires province, through non-lethal control of domestic and feral cats, reducing the number of cats on the island by about 20%, leading to decreases in the impact on some native species (Barbe, 2020). Since 2011, a National Program for Responsible Ownership and Health of Dogs and Cats has been in effect, with the dual goal of preserving native biodiversity and avoiding cruelty to these species (National Decree #1088/2011).

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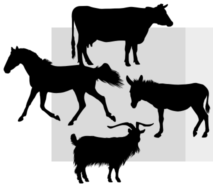

Feral livestock
Ganado cimarrón

Equus ferus caballus
feral horse, caballo cimarrón

Equus africanus asinus
feral donkey, burro orejano

Bos primigenius taurus
feral cattle, vaca

Capra aegagrus hircus
feral goat, cabra

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Resumen. El ganado doméstico fue introducido en la Argentina en el siglo XVI por los colonizadores españoles. Caballos, burros, vacas y cabras se trajeron con el propósito de criarlos de manera extensiva, para usar sus cueros, grasa, carne, o para usarlos como animales de trabajo. Se dispersaron ampliamente y originaron numerosas poblaciones cimarronas. A fines del siglo XIX la mayoría de las poblaciones de ganado cimarrón habían desaparecido. El ganado criado en forma extensiva es una importante fuente de animales escapados que pueden formar poblaciones cimarronas. Actualmente existen poblaciones de caballos, burros y vacas cimarronas en varias áreas protegidas del país. Su impacto sobre la biodiversidad ha sido muy poco estudiado, excepto el caballo en Parque Provincial Tornquist y el burro en varias áreas protegidas de Cuyo. Recientemente se manejó ganado cimarrón en algunas áreas naturales protegidas: caballos en el Parque Provincial Tornquist, vacas en el Parque Nacional El Rey y burros en Parque Nacional Los Cardones. El manejo ha sido esporádico y sin planes de manejo organizados. Para un manejo adecuado del ganado cimarrón en Argentina sería importante conocer mejor la distribución de las especies y su abundancia. Integrar su manejo a la Estrategia Nacional de Especies Exóticas Invasoras (ENEEI) resulta un imperioso desafío.

General description of the species

Feral horse

Horses (*Equus ferus caballus*) are large mammals, members of the family Equidae and the order Perisssodactyla (Fig. 1). They are herbivorous and cecal digestors (Long, 2003). Adults of the Argentine Criollo breed are on average 1.45 m in height and weigh about 450 kg. They have numerous coat colors. Horses' ears are short, and their mane is long and lies flat along their neck. Their gestation period is 315–387 days. Mares usually have one

Figure 1. Feral horse population in Parque Provincial Tornquist, Argentina. (Photo: Alberto Scorolli).

foal during each reproductive season. Horses are gregarious, and their social organization type is female-defense polygyny, forming stable harem-bands with overlapping home ranges (Long, 2003). Annual population growth rate averages 1.18, and longevity is up to 25 years (NRC, 2013).

Feral donkey

As with horses, donkeys or burros (*Equus africanus asinus*) are Equids and cecal digestors (Long, 2003). Their height at the shoulder is lower, ranging between 1.10–1.50 m. The predominant coat color is grey, but it can also be black, brown and dun. Their ears are longer than those of horses; their mane is thin; their hooves are narrow; and their tail is tufted (Long, 2003). They are more adapted to arid environments than other equids, because they are highly tolerant to dehydration and thirst. Burros are grazers and browsers and can shift their diet seasonally. Gestation last about 365 days. Females usually have one foal. Longevity in the wild is 10–15 years. Their social organization type is territorial with resource defense polygyny (Long, 2003). Donkey population growth rate is high under good environmental conditions and averages 1.19 (NRC, 2013).

Feral cattle

Cattle (*Bos primigenius taurus*) are large ruminants, members of the family Bovidae and the order Artyodactila. Adults of the Argentine Criollo breed weigh about 400 kg and the height at shoulder averages around 1.30 m (Martínez *et al.*, 1998). Coat color varies from whitish to black, with also red and brown. Their habits are diurnal. They graze and browse and have a broad diet. Cattle are gregarious and form large unstable herds and also bachelor groups. They breed all year round, with a 9.5-month gestation period, usually producing one calf, rarely two. Cow longevity in feral populations can be 20 years (Long, 2003).

Feral goat

Goats (*Capra aegagrus hircus*) are medium-sized ruminants, and as are cattle, they are Bovids (Fig. 2). Adults of the Criollo breed weigh an average of 45 kg, and the height at the shoulder is about 0.65–0.75 m. Coat colors of the Argentine Criollo breed are very variable, but usually black or brown with white patches (Capote and Fresno, 2016). Goats are diurnal with a main crepuscular activity peak. They feed on many plant species, grasses, forbs and browse. They are sedentary and loyal to a home range. This species breeds all year, with 150 days of gestation; usually two kids are born. Their longevity in feral populations is around 12–13 years (Long, 2003).

Figure 2. Feral goats in Reserva Provincial Isla de los Estados, Argentina. (Photo: Ulises Balza).

History of the invasion

Eurasian livestock were introduced by the Spanish colonizers during the 16th century with the purpose of breeding them for meat, hide, fat, milk and wool. Horses, donkeys, cattle and goats from Spanish breeds were introduced, and in the following centuries gave rise to the Argentine Criollo breeds of these species, which then dispersed widely and also formed feral populations (Brailovsky and Foguelman, 1991; Martínez *et al.*, 1998; Capote and Fresno, 2016).

Patterns of expansion and current distribution

In the 19th century, when land use changed and fields became parceled, feral horse and cattle were almost eradicated in the country (Brailovsky and Foguelman, 1991; Martínez *et al.*, 1998). Only small populations of feral horses persisted in the Andean portion of southern Patagonia, until the present time. Feral horse populations of more recent origin inhabit some natural protected areas, such as Parque Nacional Bosques Petrificados de Jaramillo, Parque Nacional Los Glaciares and Parque Provincial E. Tornquist (Fig. 3; Scorolli, 2016, this volume). Some populations also exist in the Patagonian steppe and Cuyo region, but their geographic location and size are not well described (Scorolli *et al.*, 2019).

Donkeys were introduced mainly in the Cuyo region and parts of the Northwest as pack animals, and also with the purpose of mule breeding. They probably became feral in earlier

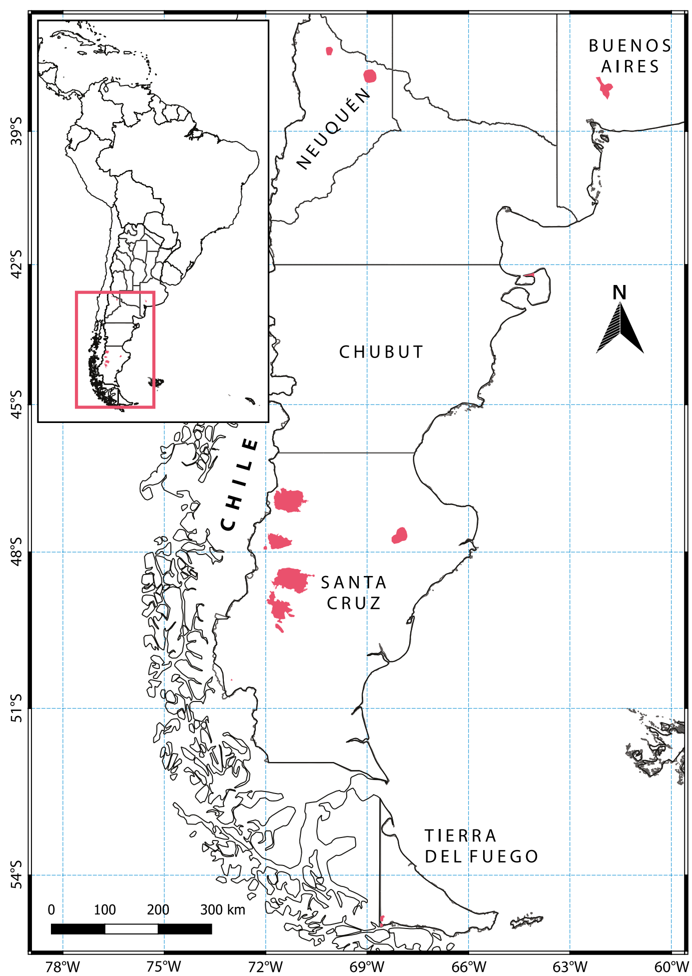

Figure 3. Distribution of *Equus ferus caballus* in Argentina. Modified from Scorolli *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

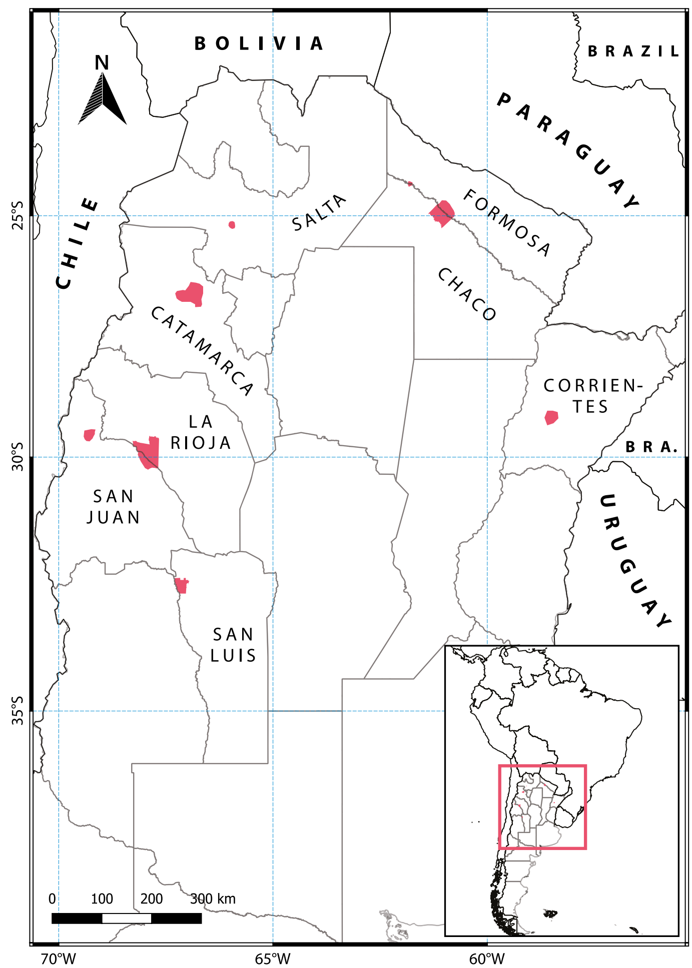

Figure 4. Distribution of *Equus africanus asinus* in Argentina. Modified from Borghi *et al.* (2019a). (Mapping: Alfredo Claverie and Ian Barbe).

times, but there are no good historic records. Only recently, their populations have been surveyed and reported in many areas like Parques Nacionales Los Cardones, Ischigualasto, and Talampaya in the northwestern region, and Parques Nacionales El Impenetrable and Iberá in the northeastern region (Fig. 4; Novillo and Ojeda, 2008; Merino *et al.*, 2009; Borghi *et al.*, 2019a).

At present, feral cattle are reported for many locations and national parks in the Yungas, Arid and Humid Chaco, and Patagonian Forest and Steppe ecoregions of Argentina (Aprile *et al.*, 2019). The better known locations of these invasive populations include Parque Nacional El Rey in northwest Argentina and Parque Nacional Los Glaciares in southwest Patagonia (Fig. 5).

Given that goats were bred extensively in many regions of Argentina, it is highly likely that some feral population exist, but there is no information about this. Only one population of feral goats has been described as invasive at Reserva Provincial Isla de los Estados in Tierra del Fuego province (Novillo and Ojeda, 2008; Borghi *et al.*, 2019b), where goats were introduced in 1886 in an area that in the 1990s was declared provincial reserve.

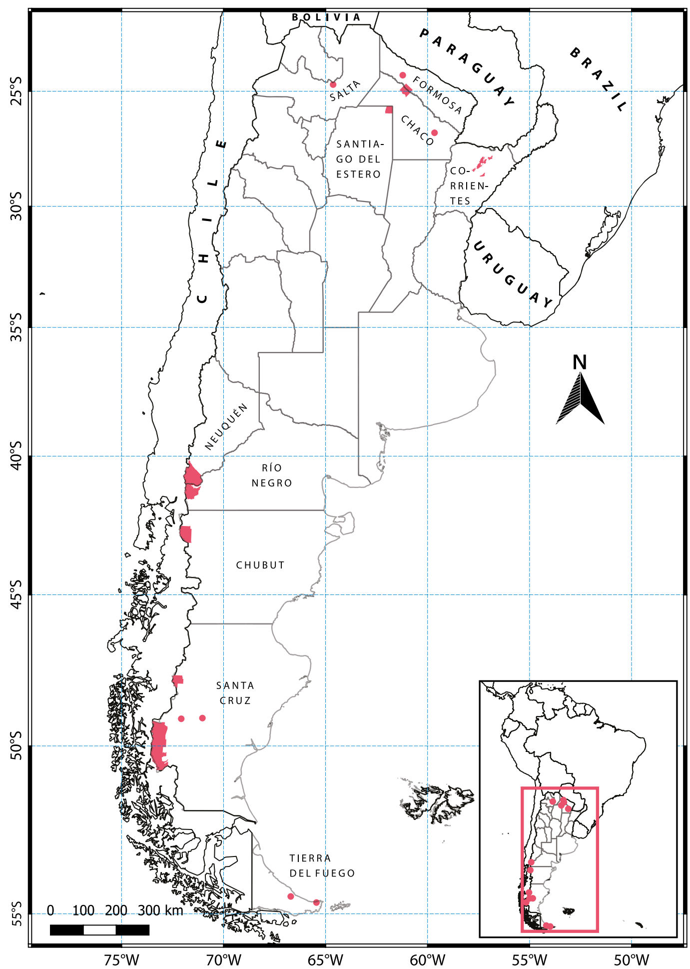

Figure 5. Distribution of *Bos primigenius taurus* in Argentina. Modified from Aprile *et al.* (2019). (Mapping: Alfredo Claverie and Ian Barbe).

Impacts

In Argentina, the impacts of feral livestock are still not well quantified. There are only some recent local scale projects and much remains to be studied. To date, the feral horse's impact on biodiversity has only been studied in Parque Provincial Tornquist in Buenos Aires province. The results suggest significant changes in vegetation structure and composition, facilitation of invasive plants and alteration of the bird community (Scorolli, 2016, this volume). Feral donkey impacts have been described for some populations in national parks, mostly affecting columnar cacti (Malo *et al.*, 2011), and competing for food with native camelids (Borgnia *et al.*, 2008; Reus *et al.*, 2014). In other countries, a significant impact on vegetation and accelerated soil erosion have been reported as well (Abella, 2008). For their part, the feral cattle in Parque Nacional El Rey modified the woody habitats and affected ecosystem structure (Giménez *et al.*, 2010). In many areas where feral cattle populations exist, a significant impact on vegetation structure and composition was reported (Long, 2003). Finally, feral goats are known worldwide to have severe environmental impacts (Long, 2003). On Reserva Provincial Isla de los Estados, they probably have affected the grasslands and the animals living there, but the impact on biodiversity is only recently being studied.

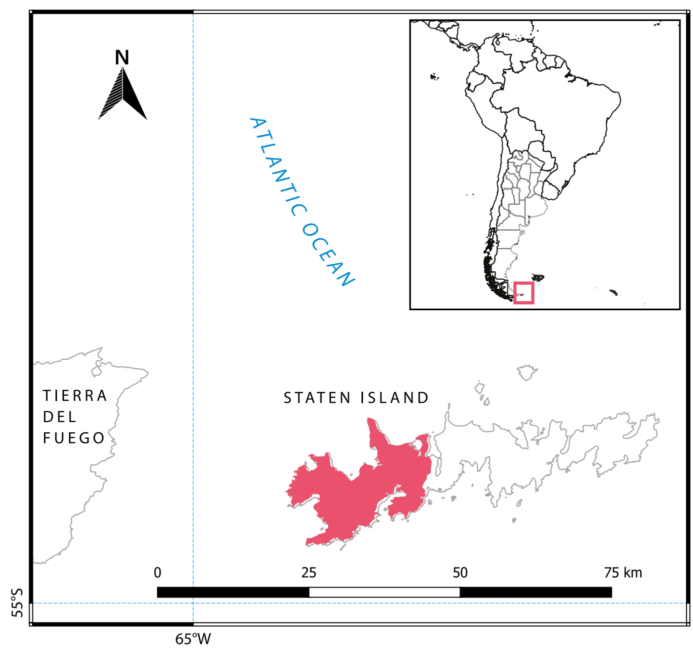

Figure 6. Distribution of *Capra aegagrus hircus* in Argentina. Modified from Borghi *et al.* (2019b). (Mapping: Alfredo Claverie and Ian Barbe).

Management

Management of feral livestock in Argentina has been discontinuous and unorganized. Only some populations have been controlled in natural protected areas. For example, feral horses were managed in Parque Provincial Tornquist, where the population was reduced by 50% in 2006–2007 and 220 horses were live-trapped with mobile-corrals. Since 2008, however, the management was suspended, and the population recovered and reached a size similar to that before the control (Scorolli, 2016, this volume).

For their part, feral donkeys were controlled in Parque Nacional Los Cardones, where they were captured in corrals by horse driving. A total of 571 individuals were removed.

After the management, recovery of the vegetation and native ungulates populations was observed (Moschione *et al.*, 2010). Feral cattle also have been managed recently in Parque Nacional El Rey. In 2001–2010 a reduction in population size was implemented. Cattle were hunted using trained dogs and later euthanized; a total of 727 animals were eliminated, 70% of the estimated population (Giménez *et al.*, 2010). Management was not continued and the population slowly recovered (Giménez *et al.*, 2010). In Parque Nacional Los Glaciares an eradication plan of feral cattle has been implemented since 2015 (Aprile *et al.*, 2019). Finally, to date, there has been no attempt to manage feral goats on Reserva Provincial Isla de los Estados.

In contrast, studies and experiences regarding the management of feral livestock have been intense in other countries like USA, Australia, New Zealand, Ecuador and France. In these countries management plans with goals of eradication or control have been implemented (Tab. 1).

Table 1. Examples of feral livestock management plans in different countries.

Species	Country	References
Horse	USA	NRC, 2013
	Australia	Dawson *et al.*, 2006; OEH NSW, 2017
	New Zealand	DOC NZ, 2012
Donkey	USA	NRC, 2013
	Ecuador	Carrion *et al.*, 2007
Cattle	France	Micol and Jouventin, 1995
Goat	New Zealand	Forsyth *et al.*, 2003
	Ecuador	Campbell and Donlan, 2005

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Lagomorpha

European hare and rabbit, liebre y conejo europeos

Lepus europaeus

European hare, liebre europea

Oryctolagus cuniculus

European rabbit, conejo europeo o de Castilla

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Resumen. La liebre europea (*Lepus europaeus*) y el conejo de Castilla (*Oryctolagus cuniculus*) son especies de lagomorfos nativas de Eurasia y la Península Ibérica respectivamente. Son pequeños herbívoros con una gran capacidad reproductiva. Ambas especies fueron introducidas en la Argentina hace más de un siglo, lo cual implica que en algunos casos ambas especies pueden ser consideradas por las personas como nativas, a lo cual se suma que son especies carismáticas. En ambos casos el objetivo de las introducciones fue primariamente para su utilización como alimento y también por sus pieles. La liebre ha colonizado toda la Argentina, excepto Tierra del Fuego, mientras que el conejo tiene presencia en todas las provincias patagónicas, Mendoza y San Juan. Los lagomorfos introducidos invasores pueden alterar la estructura y función de los ecosistemas, y representan una amenaza potencial a la agricultura, la horticultura, la ganadería, las plantaciones forestales y los ambientes naturales, principalmente por herbivoría. También, ambas especies pueden ser vectores de diferentes enfermedades y parásitos. Cabe destacar que tanto la liebre como el conejo sirven de alimento para depredadores nativos y exóticos, lo que implica que cualquier decisión de manejo debe tener en cuenta el potencial impacto sobre los primeros. De todos modos, no existen actualmente planes formales de manejo de estas especies.

General description of the species

The European hare (*Lepus europaeus*) is a Eurasian medium to small herbivore with a fur from yellow-gray to brown and white, that ranges in size from about 48 to 70 cm and in weight from 3 to 6 kg, with long hind limbs adapted to jump (Fig. 1). The species presents sexual dimorphism, with females bigger and heavier than males (Monteverde *et al.*, 2019). It reaches sexual maturity at approximately six to eight months of age and gives birth to a litte of two young (called leverets) on average, with two or three gestations periods per year, with two or three calvings per year (Monteverde *et al.*, 2019).

Figure 1. *Lepus europaeus* in Argentina. (Photo: Gabriel Rojo).

The European rabbit (*Oryctolagus cuniculus*) is a species native from the Iberian Peninsula. This small herbivore presents a brown-gray coloration with a size between 45 to 65 cm and a weight between 1 to 3 kg (Fig. 2; Bonino and Donadío, 2010). The species reaches sexual maturity at approximately three to six months of age, with five to seven litters per year with three to nine young (called kits) each (Cuevas *et al.*, 2019).

History of the invasion

European hares were brought from different parts of Europe (Germany and France) between 1888 and 1930 for sport hunting (Bonino *et al.*, 2010).

Rabbits were brought to southern South America in multiple introductions from Spain and France, beginning in the 1760s, to several islands of the Tierra del Fuego Archipelago (Jaksic and Yáñez, 1983; Jaksic *et al.*, 2002). The objective of these releases was for food and pelts (Camus *et al.*, 2008). Subsequent to the first introduction in Tierra del Fuego, the species was also brought and released on the mainland on several occasions, mostly in Chile (Cuevas *et al.*, 2019).

Patterns of expansion and current distribution

After the first introduction, the European hare expanded between 18–20 km/year until it occupied almost all of Argentina (Fig. 3) and different areas of Chile, Uruguay, Paraguay, Peru, Brazil and Bolivia, including urban areas (Bonino *et al.*, 2010; Jaksic and Castro, 2014). Because the European hare shows great ecological plasticity, Bonino *et al.* (2010) predicted that this species would continue to disperse towards the northern part of South America, particularly in the west where the Andean Mountains serve as a corridor (Ballari *et al.*, 2016).

European rabbits have expanded from their original introduction points and invaded other areas, and even crossed the Andes Mountains between Chile and Argentina (Jaksic *et al.*, 2002; Novillo and Ojeda, 2008). Currently, derived from different introductions events or expansions, the species is present in all Argentine Patagonian provinces and in Mendoza and San Juan (Fig. 4). Rabbits in Neuquén province were shown to have a dispersal rate that varied between two and 15 km/year, thus indicating their potential for expanding into new ranges (Bonino and Soriguer, 2009; Cuevas *et al.*, 2019). Human intervention could favor the invasion of the European rabbit, since translocations and releases are still common (Cuevas *et al.*, 2019).

Figure 2. *Oryctolagus cuniculus* in Tierra del Fuego, Argentina. (Photo: Nicolás Easdale).

Impacts

Introduced invasive lagomorphs could alter the structure and function of native ecosystems, representing a potentially significant threat to agriculture, horticulture, livestock, forestry and natural habitats (Novillo and Ojeda, 2008; Bonino and Soriguer, 2009). The herbivory done by these species changes the structural complexity of herbaceous vegetation, prevents tree and shrub regeneration and could compete with native herbivores and livestock for food resources (Bonino, 1995; Vázquez, 2002; Novillo and Ojeda, 2008; Ballari *et al.*, 2016). Additionally, both species can be vectors for several diseases and parasites (Kleiman *et al.*, 2004; González-Acuña *et al.*, 2005). Furthermore, predation on both species was reported, either by native raptors and carnivores (Jaksic, 1998; Castro *et al.*, 2008; Pavez *et al.*, 2010), or by introduced invasive carnivores, such as the American mink (*Neogale vison*), which would be favored by invasional meltdown (Valenzuela *et al.*, 2013, 2014). So far there is no overall estimation regarding the economic and environmental costs of the introduced invasive lagomorphs in this region (Bonino *et al.*, 2010).

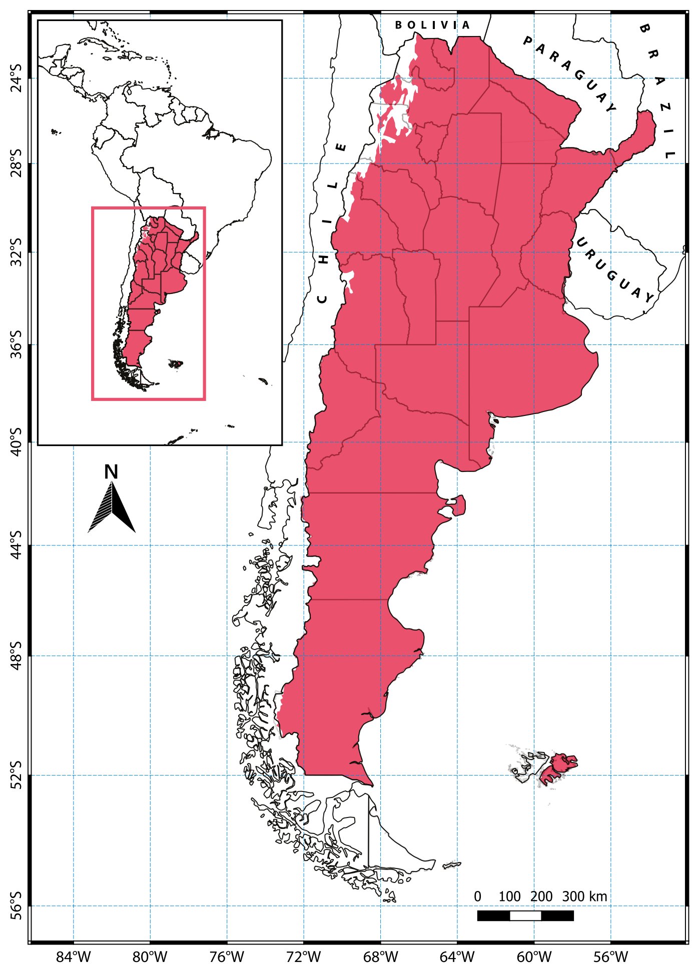

Figure 3. Distribution of *Lepus europaeus* in Argentina. Modified from Monteverde *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

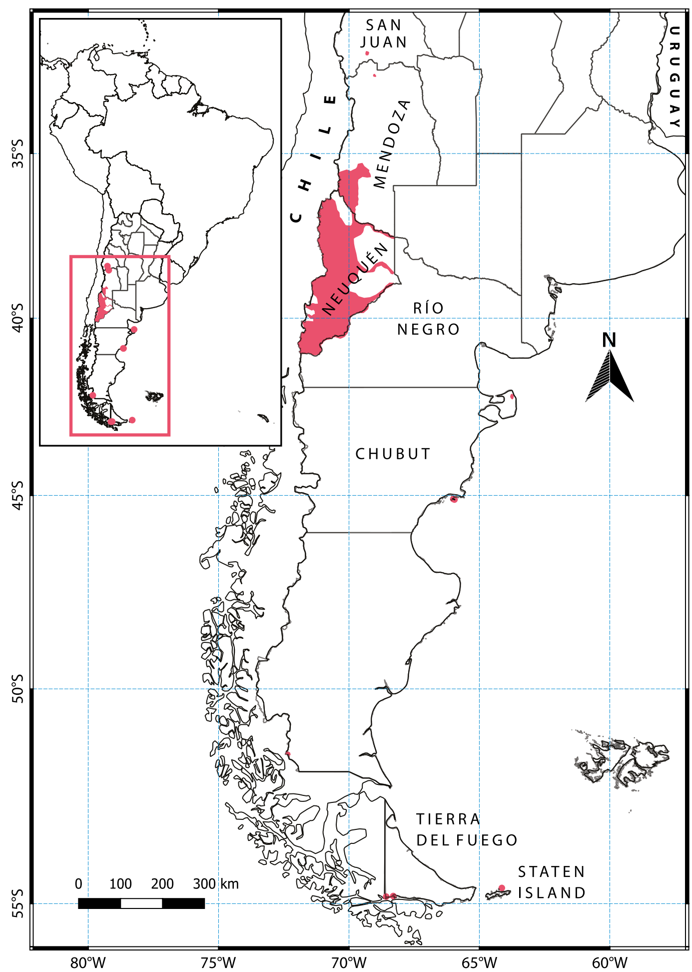

Figure 4. Distribution of *Oryctolagus cuniculus* in Argentina. Modified from Cuevas *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

Management

There are currently no formal management plans or actions to reduce hare and rabbit populations in Argentina (Ballari *et al.*, 2016; Cuevas *et al.*, 2019; Monteverde *et al.*, 2019), even when, for example, millions of hares are harvested per year for export (Bonino *et al.*, 2010). Some native predators (carnivores and raptors) have included these species in their diets (Ballari *et al.*, 2016) and may contribute to the regulation of their populations. However, for this reason, management actions should consider this interaction to safeguard the welfare of native predators. Additionally, as charismatic species, both are often perceived as "native" and "familiar," which makes further management and control actions difficult to perform (Ballari *et al.*, 2016; Guichón *et al.*, this volume).

In particular for rabbits, Pampa foxes (*Lycalopex gymnocercus*) were introduced into Tierra del Fuego Island as a biological control agent; however, no effects on the rabbits' populations were found (Valenzuela *et al.*, 2014; Ballari *et al.*, 2016). Therefore, inoculation with the myxomatosis virus was implemented and resulted in a significant decrease of rabbit populations (Jaksic and Yáñez, 1983, Jaksic and Castro, 2014), but several isolated populations survived. Myxomatosis virus was/is also used on several ranches in mainland Patagonia, but currently this approach is prohibited by law in Argentina (Ballari *et al.*, 2016; Cuevas *et al.*, 2019).

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Lycalopex gymnocercus
Pampa fox, zorro gris

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Resumen. El zorro gris (*Lycalopex gymnocercus*) es una especie de cánido pequeño, oportunista y de hábitos plásticos. Nativo al sector continental de Argentina, fue introducido en la Isla Grande de Tierra del Fuego en 1951 con el objetivo de controlar la población de otro mámifero introducido invasor, el conejo de Castilla (*Oryctolagus cuniculus*). Luego de su introducción en el sector norte, el zorro gris colonizó casi la totalidad de la isla, incluso cruzando a algunas islas en el Canal Beagle. Actualmente, es común verlo hasta en la ciudad de Ushuaia y en algunos sectores del Parque Nacional Tierra del Fuego. El zorro gris es omnívoro y como tal puede afectar a un gran número de especies por depredación o por competencia. También se mencionó la posibilidad de hibridación con el zorro colorado fueguino (*Lycalopex culpaeus lycoides*). Adicionalmente, esta especie puede transmitir diversas enfermedades y parásitos a la fauna nativa local. Si bien la caza está permitida, no existen planes de manejo de la especie en Tierra del Fuego.

General description of the species

The Pampa fox (*Lycalopex gymnocercus*) is a small canid that ranges in size from about 2.5 to 4.5 kg (Fig. 1). It reaches sexual maturity at approximately one year of age and gives birth to a litter of between four and six pups during spring. *L. gymnocercus* is a very plastic species that adapts to inhabit a broad diversity of habitats, from grasslands to urban areas. Its diet is opportunistic and generalist, consuming small mammals, birds and reptiles, insects, fruits and even carrion (Luengos Vidal *et al.*, 2019).

History of the invasion

Native to mainland Argentina, 24 Pampa foxes were intentionally released near Onaisín, in the Chilean side of Tierra del Fuego Island in 1951 (Pine *et al.*, 1979). Lizarralde and Escobar (2000) also indicate that 32 individuals were released near Cullen ranch on the Argentine side of the island in 1980. The objective of these introductions was the biological control of invasive European rabbits (*Oryctolagus cuniculus*; Fabbro, 1989), but there is no evidence this goal was achieved (Quintana *et al.*, 2000).

Patterns of expansion and current distribution

The Pampa fox is now common throughout most of Tierra del Fuego Island (Fig. 2) with the exception of the southwest portion, and additionally, it has been reported to have crossed to Gable Island in the Beagle Channel (Valenzuela *et al.*, 2014). Its southward dispersal to the shores of the Beagle Channel was confirmed in 1997, and currently is present in the city of Ushuaia, even reaching the Parque Nacional Tierra del Fuego (Luengos Vidal *et al.*, 2019). The species became very abundant in the areas where it was first released, but despite being heavily exploited for their pelts, the Pampa fox seems to have not declined in numbers (González Del Solar and Rau, 2004).

Figure 1. *Lycalopex gymnocercus* in Tierra del Fuego province, Argentina. (Photo: Nicolás Easdale).

Impacts

As an omnivore, the Pampa fox could affect multiple native species and trophic levels (Ballari *et al.*, 2016). It has been shown, for example, to have niche overlap with the endemic and endangered Fuegian red fox (*Lycalopex culpaeus lycoides*; Valenzuela *et al.*, 2014). Its ecological impacts can include both competition and food web effects, and also probable

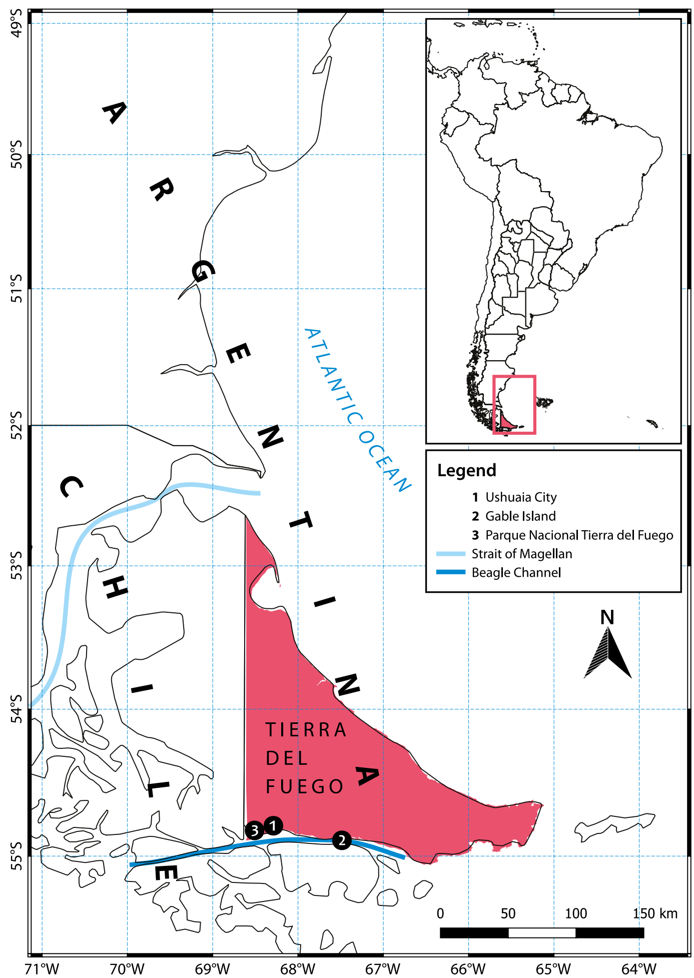

Figure 2. Introduced invasive distribution of *Lycalopex gymnocercus* in Argentina. Modified from Anderson *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

hybridization with the native fox, but there is no research focused on these issues (Valenzuela *et al.*, 2014). Studies also have shown that these foxes can carry viral diseases such as distemper (González-Acuña *et al.*, 2003) and host several parasites (*e.g.*, *Toxascaris leonina*, *Uncinaria stenocephala*, *Taenia* sp. and *Echinococcus granulosus*) that can be transmitted to native fauna (Aguilera, 2001).

Management

There are no formal systematic efforts to control Pampa fox in Tierra del Fuego, but hunting is permitted; however, their population appears to be increasing on the island (Ballari *et al.*, 2016).

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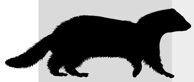

Neogale vison
American mink, visón americano

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Resumen. El visón americano (*Neogale vison*) es un mustélido originario de Norteamérica con cuerpo alargado y pelaje marrón oscuro-negro. Carnívoro estricto, pero generalista, suele habitar riberas de agua dulce y costas marítimas con alta cobertura vegetal. La plasticidad en su dieta y sus adaptaciones reproductivas le han permitido colonizar fácilmente diversos hábitats alrededor del mundo. Han sido introducidos en Europa, Asia y Sudamérica para la explotación en la industria peletera. Liberaciones intencionales han dado lugar al establecimiento de poblaciones exóticas silvestres. En Argentina fue introducido durante la década de 1930 en Patagonia y la provincia de Buenos Aires. Actualmente se distribuye en gran parte de la región Patagónica, y existen avistamientos recientes de potenciales poblaciones en la provincia de Buenos Aires. Sus impactos tienen alcances variados, siendo una amenaza para la avifauna nativa por depredación y para los carnívoros nativos principalmente por una potencial transmisión de enfermedades. Estos impactos afectan distintas actividades económicas como el ecoturismo, las pisciculturas y la cría de aves de corral. Los visones americanos pueden actuar de vectores de enfermedades para la salud humana, como toxoplasmosis y leptospirosis; también son portadores de SARS-CoV-2, aunque se necesitan más estudios para demostrar su potencial contagio a humanos. Se recomiendan planes de manejo basados en el control de las poblaciones, con métodos de captura o muerte selectiva. En Patagonia se llevan a cabo planes de control de visón destinados a la conservación de la fauna nativa en Santa Cruz, Tierra del Fuego, Neuquén y Río Negro.

General description of the species

The American mink (*Neogale vison*) is a crepuscular semi-aquatic generalist carnivore with an elongated tubular body (total length: 50–70 cm) with short limbs and a hairy tail that constitutes approximately 33% of the total length of the body (Fig. 1; Dunstone, 1993; Laviere, 1999). The mink has a wedge-shaped head, narrowing towards the snout, with small ears that are barely visible and a long neck; all of these characteristics help these animals avoid hydrodynamic resistance while swimming (Long, 2003). Additionally, a thick coat provides thermal insulation, with dark brown-black hair with white spots on the chin and chest, but also other pigmentations derived from fur farming can be found in nature (Laviere, 1999). Adult weights vary between 400–1800 g, and the species presents a marked sexual dimorphism, where males can double the size of females (Dunstone, 1993). Minks live an average of 5 years in the wild (Long, 2003).

Habitat

Mink are solitary territorial animals that usually inhabit highly vegetated habitats associated with freshwater shores (rivers, streams, lakes, lagoons, swamps, peat bogs, etc.) and marine coasts (Valenzuela *et al.*, 2013). Mink use natural holes between rocks and trunks as dens (Dunstone, 1993). Their territories are lineal, following the coastlines and riverbanks, and vary between 0.5–3.4 km in length, depending on individual (age and sex) and habitat characteristics, but also prey availability (Dunstone, 1993).

Figure 1. *Neogale vison* in Tierra del Fuego Island, Argentina. **a.** Regular color. **b.** Farm color. (Photos: Sergio Anselmino).

Reproduction

The mink's mating season is during winter; only the female takes care of the cubs, that are born around the end of spring and leave the mother's territory as juveniles at the end of summer (Macdonald and Strachan, 1999). Females are able to reproduce in their first year of life and can have litters of more than four individuals per year with different males, and present delayed implantation of fertilized eggs (Macdonald and Harrington, 2003).

Native range distribution

Neogale vison is native to North America, including Alaska, Canada and most of the continental USA, with the exception of the driest areas in Arizona, California, Nevada, New Mexico and Texas (Long, 2003).

History of the invasion

Due to the high quality of its pelt and its easy domestication, the American mink was intensely bred and farmed for the fur industry at a global level (Laviere, 1999). For this reason, mink farms where established all around the world, and subsequent accidental escapes or deliberate releases caused the American mink to be present as an introduced invasive species in 33 countries of Europe, Asia and South America (Anderson and Valenzuela, 2011).

In Argentina, fur farms were established beginning in the 1930s in all Argentine Patagonian provinces and in Buenos Aires province (Godoy, 1963; Valenzuela *et al.*, 2019). After an initial period of success, the mink fur industry was no longer sustainable, and the farms were mostly abandoned. This led to many animals being released or escaping to ultimately found free-range populations (Valenzuela *et al.*, 2016). The first recorded release event occurred on Tierra del Fuego Island in 1948 (Fabbro, 1989), and further releases were recorded in continental Patagonia. By the 1960s there were already small populations established in the wild (Previtali *et al.*, 1998).

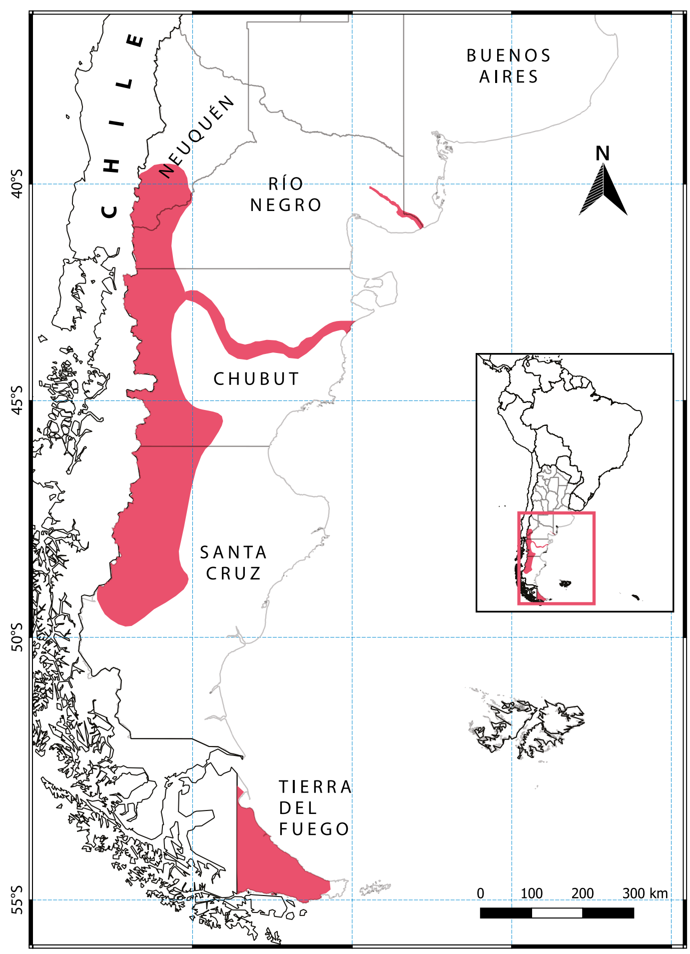

Figure 2. Distribution of *Neogale vison* in Argentina. Modified from Valenzuela *et al.* (2019). (Mapping: Alfredo Claverie and Ian Barbe).

American mink characteristics, including reproductive strategy, diet and habitat use flexibility, confer this species a great advantage to adapt and therefore to invade new habitats and environments (Anderson and Valenzuela, 2011).

Patterns of expansion and current distribution

American mink distribution is associated with water bodies, using banks and coasts to disperse, reaching distances of up to 20 km per day, and also being able to cross maritime barriers, such as channels (Valenzuela *et al.*, 2019). Currently, the mink is the most widely distributed introduced invasive carnivore in Patagonia (Valenzuela *et al.*, 2016), with feral populations in Tierra del Fuego, Santa Cruz, Chubut, Río Negro, Neuquén and Buenos Aires provinces (Fig. 2). American mink are still invading new parts of the region, even crossing the Andes range between Chile and Argentina (Jaksic *et al.*, 2002), and with a recently reported new population in Uruguay (Laufer *et al.*, 2022).

Impacts

Ecological impact

Negative impacts are observed on local fauna mostly due to predation, but also due to resources competition or disease transmission. In particular, the mink has a strong impact on aquatic birds (Peris *et al.*, 2009). Furthermore, the species can host and eventually transmit pathogens (*e.g.*, canine distemper virus) between domestic dogs and native carnivores (Sepúlveda *et al.*, 2014).

Economic impact

Economic impacts for nature-based tourism and ecotourism, such as rafting, sport fishing, and especially birdwatching, are inferred, but not quantified (Cerón and Trejo, 2012). Also, mink could affect productive activities, such as fish and poultry farming (Valenzuela *et al.*, 2019).

Health impact

Sepúlveda *et al.* (2011) found *Toxoplasma gondii* and Barros *et al.* (2014) detected *Leptospira* in wild mink. Additionally, recent studies have shown that the species could host SARS-CoV-2 (Aguiló-Gisbert *et al.*, 2021), influenza A virus (Gholipour *et al.*, 2017), and *Pseudomonas aeruginosa* (Salomonsen *et al.*, 2013).

Management

There is no national or regional management strategy or plan for American mink, and rather there are only local efforts (Fasola and Valenzuela, 2014; Valenzuela *et al.*, 2019). Different actions related to the conservation of the native torrent duck (*Merganetta armata*) have been implemented in the north of Neuquén province, and in Parque Nacional Nahuel Huapi in Río Negro province (Valenzuela *et al.*, 2019). In the southern region of Parque Nacional Lanín, a mink control plan has been carried out since 2010 to promote bird community recovery (Sanguinetti, 2015; Girini, 2018). In Santa Cruz province, a mink control plan has been carried out since 2014 to specifically protect the critically-endangered hooded grebe (*Podiceps gallardoi*; Fasola and Roesler, 2016). Finally, a comprehensive approach to control the species is carried out in Parque Nacional Tierra del Fuego (Valenzuela *et al.*, 2019).

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Ondatra zibethicus
muskrat, rata almizclera

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Resumen. *Ondatra zibethicus*, comúnmente conocida como «rata almizclera» o *muskrat* en su región de origen, es un roedor semiacuático que fue introducido desde Canadá a la Isla Grande de Tierra del Fuego en la década de 1940 para el aprovechamiento de su piel, considerada valiosa en el mercado comercial de pilíferos. En líneas generales, las especies introducidas son en su mayoría especies generalistas y oportunistas que se adaptan más fácilmente y llegan a incrementar rápidamente su población y uso de hábitats. En ese sentido, la ausencia de predadores y de un régimen de caza permitió a la especie colonizar tanto ambientes lóticos como lénticos en la isla, ocupando actualmente la totalidad de los cursos de agua, y tolerando una amplia diversidad de ambientes. La colonización de rata almizclera está asociada a la sucesión de ambientes inundados, incluyendo a aquellos generados por castor (*Castor canadensis*), en donde son importantes los cambios en la profundidad del agua y la heterogeneidad de la vegetación emergente, ya que influyen particularmente en la supervivencia de invierno, cuando el acceso al alimento y la presencia de predadores son críticas. El análisis de su historia de vida demostró que la rata almizclera es 100% herbívora, consumiendo preferentemente plantas acuáticas y terrestres, con las cuales también construye sus casas y madrigueras. La especie no es explotada ni se han presentado planes de manejo históricamente. Su impacto no ha sido mayormente evaluado, aunque es considerado bajo.

General description of the species

Ondatra zibethicus, known as muskrat or *rata almizclera*, is a semi-aquatic rodent of the Arbicolinae subfamily that was introduced into Tierra del Fuego Island (TDF) in the 1940s for its fur. It is the largest species of the Cricetidae family (Fig. 1), reaching a total length of approximately 55 cm and an adult weight between 700 and 1800 g (Willner, 1980).

One of muskrats' main adaptations to semi-aquatic habits are lips that close behind the incisor teeth, allowing them to gnaw while submerged. The small forelegs are used to handle food and burrow-building material, while the hind legs present an interdigital membrane to swim. Muskrats can stay underwater up to 20 minutes, and their coat retains air between hairs, favoring impermeability and increasing thermal insulation.

Muskrats live for 3 to 4 years. Both sexes possess functional musk glands in a perianal position. Females commonly have three pairs of breasts (1 pectoral and 2 inguinal) and sometimes 4 or 5 pairs. Muskrats are considered monogamous (Messier and Virgl, 1992), with a gestation period that varies between 25–30 days.

In general, the reproductive period on TDF extends practically from the end of winter to the beginning of autumn, with a peak of births during the summer. More than one successive calving can occur, with a litter size of 5–6 animals (Deferrari, 1996).

Figure 1. *Ondatra zibethicus* in Tierra del Fuego province, Argentina. (Photo: Guillermo Deferrari).

The environments invaded by the muskrat in TDF are characterized, as in the Northern Hemisphere, by two main types of construction, depending on the environment if the muskrats build houses or dig burrows in the substrate (Messier and Virgl, 1992). The houses have the shape of a dome or conical elevation built with remnants of aquatic vegetation, while the burrows are underground cavities connected by tunnels or channels in peatland or riverside areas. These constructions serve as a protective structure after spring and as a shelter during winter. Houses are built above the water level and connected by underwater tunnels, and in general, construction generally begins using local floating vegetation (Willner, 1980).

Vegetation density, water level and plant phenology influence the degree to which certain plans are used in diet, with the root and base of various hydrophytes being the most important portion of what is consumed in North America and Europe (Danell, 1978).

Despite bibliographic data indicating the consumption of a significant percentage of animal material in the species' native range (Danell, 1978; Convey *et al.*, 1989; Neves, 1989; Parmalee, 1989) its diet in TDF appears to only be vegetarian.

History of the invasion

Muskrat is native to North America, where it occupies almost the entire territory. This species was introduced for the economic value of its pelt. Current areas with introduced populations of *Ondatra* include western Europe, Scandinavia, Japan, Russia (Willner, 1980), and southern South America.

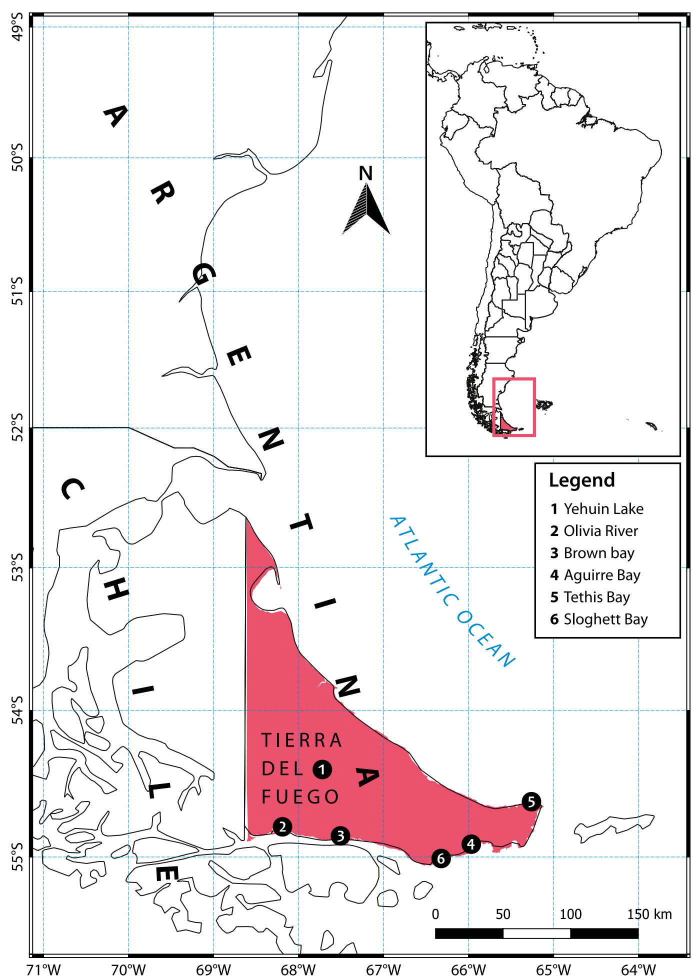

Figure 2. Distribution of *Ondatra zibethicus* in Argentina. Modified from Deferrari (2019). (Mapping: Ian Barbe and Alfredo Claverie).

Between 1940 and 1950, the Argentine Ministerio de Marina decided to introduce several fur-bearing species to TDF to enhance natural resources, and released North American beavers (*Castor canadensis*; Anderson and Roulier, this volume) and muskrats brought from Canada. Daciuk (1978) indicates that 225 individuals (75 males and 150 females) were released in different sites in the island: Yehuin Lake (14 males and 15 females), Olivia River (4 males and 5 females), Brown Bay (10 males and 37 females), Aguirre Bay (28 males and 36 females), Tethis Bay (12 males and 14 females), and the rest of the individuals in Sloghett Bay. These animals have colonized a wide range of habitats, evidencing the plasticity of the species to adapt to different environmental conditions.

Patterns of expansion and current distribution

The native distribution of muskrat is in North America, from Labrador in Canada to Arizona and Louisiana in USA. Due to its fur, muskrat farms were established in Europe, and later escapes resulted in the invasion of this continent and north Asia.

In Argentina, muskrats are present in all freshwater bodies of TDF province, including lentic (lakes, lagoons, wetlands, etc.) and lotic (rivers and streams) environments (Fig. 2). The species was recorded not only in the main island of TDF but also in almost all islands in the Beagle Channel. The Fagnano Lake area is the most beneficial environment for this species, with an estimated abundance of 15–125 individuals per hectare, before and after reproduction respectively (Deferrari, 2007).

Impacts

Muskrat impacts have been mainly studied in Europe and Asia, where the species high density generates problems of habitat degradation due to its tunneling activities in river banks, leading to control actions in different countries (Le Boulenge, 1972). The impacts on TDF, Argentina, are not quantified, but they may not be significant given their relatively low abundance. Additionally, the species seems to be controlled, at least to some degree, by the invasive American mink (*Neogale vison*; Valenzuela *et al.*, 2014). The species is not affected by human presence, since individuals have been recorded inside houses or even in urban areas, where dogs could limit their activities.

Management

Muskrat exploitation was regulated in 1981, more than 30 years after its introduction. However, this activity was not successful due to several issues, such as lack of biological information in TDF, adequate traps, management plans, etc.

Muskrat trapping is open through the year in TDF as a way to control its population; however, until now, annual harvesting is practiced in a very small scale by few seasonal hunters, mostly due to the low value and use of their fur. Even when muskrats' musk glands are used in the perfume industry, the exploitation of the species remains at low levels. In TDF, the use of Conibear® 110-2 traps was recommended (Lizarralde *et al.*, 1996).

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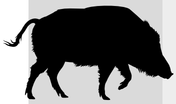

Sus scrofa

wild boar, jabalí

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Resumen. El jabalí es una especie exótica invasora que fue introducida en Argentina por primera vez en 1906 para la caza deportiva. Es una especie con una alta tasa reproductiva y que se adapta a diferentes condiciones climáticas, por lo que en Argentina actualmente se la encuentra en al menos 10 ecoregiones. Esta especie es omnívora y oportunista, con una dieta mayormente herbívora. El jabalí en Argentina genera una amplia variedad de impactos negativos relacionados con la composición, estructura y biomasa de la vegetación, y cambios en las propiedades del suelo; como también con la transmisión de enfermedades, principalmente a través del consumo de su carne. Por ejemplo, en el Desierto del Monte genera un aumento de la degradación del mismo, mientras que en los Bosques Patagónicos reduce la tasa de descomposición y favorece el establecimiento de especies de plantas exóticas. En cuanto al manejo, si bien el jabalí es considerado como prioritario, los esfuerzos para su control son ineficientes hasta el momento, por lo que es necesario desarrollar una estrategia a nivel nacional para mitigar sus impactos, reducir sus poblaciones y evitar su dispersión.

General description of the species

The boar is a medium-sized species, reaching in some places up to 100 kg. It has a large head with small ears, and the neck is short and thick (Fig. 1; Rosell *et al.*, 2001). Its coat color ranges from black to brownish-red, and it has sexual dimorphism, where males are bigger and with more developed canine teeth than females (Rosell *et al.*, 2001). Their dental formula is 3/3 1/1 4/4 3/3.

The wild boar is an omnivorous species with a diet dominated by plant material (87%–99%) and a smaller representation of animal matter (Schley and Roper, 2003). It has a high reproductive capacity due to characteristics, such as early sexual maturity (5–12 months), a relatively short gestation period (120 days), and a large litter size (5–7 piglets) (Gethöffer *et al.*, 2007; Herrero *et al.*, 2008). Its social organization consists of a matriarchal society, formed by one or more females with their piglets. Also there are groups of young males and solitary adult males.

The boar has a high tolerance to different climatic conditions, reflected in its wide geographic range (Oliver *et al.*, 1993). For that reason it occupies different Argentine ecoregions, such as the Paraná Flooded Savanna, Iberá Marshes, Patagonian Forests, Pampa,

Figure 1. *Sus scrofa* in Argentina. (Photo: Gabriel Rojo).

Patagonian Steppe, High Andean, Espinal, Arid Chaco, and Monte Desert (Ballari *et al.*, 2015a). This species is diurnal and crepuscular although its activities can vary according to type of environment and hunting pressure (Baber and Coblentz, 1986; Baubet *et al.*, 2004).

History of the invasion

The wild boar is native to Eurasia and northern Africa (Long, 2003), but now has one of the widest geographic distributions of any introduced mammal (Oliver *et al.*, 1993). It was first brought to Argentina in 1906, specifically to San Huberto Ranch in La Pampa province, for hunting purposes (Daciuk, 1978). After that, wild boar reintroductions occurred several times in different parts of the country, such as in Collun-có Ranch in Neuquén province in 1917, and in Huemul Ranch in Río Negro province in 1924 (Daciuk, 1978). Furthermore, the continuous installation of game reserves has led to the introduction of new populations of this species around the country (Cuevas *et al.*, 2016). On the other hand, feral populations of domestic pigs have been documented by Carpinetti *et al.* (2016) since their arrival to Argentina in 1536 with the Spanish conquistadors. By the end of the 16th century, the number of free-ranging animals increased, until they eventually became feral.

Patterns of expansion and current distribution

The creation of game reserves throughout the country from the boars' first introduction to the present, and the subsequent escape of animals, make it a very difficult task to determine the spread pattern. The wild boar is a very successful invader, using rivers and streams, roads, paths, and cattle trails as dispersal routes (Ballari *et al.*, 2019). This invasive species is present in almost the entire country (20 of the 23 provinces; Fig. 2) due to natural dispersion and human translocations from one place to another, and it occupies not only ecoregions similar to those found in its native range, but also new habitat types, such as the temperate Monte Desert (Cuevas *et al.*, 2010; Ballari *et al.*, 2019; Cuevas *et al.*, 2021). Today, most of the naturalized populations in Argentina are crossbreeding among the three morphotypes (domestic pigs, feral pigs and wild boar) (Figueroa *et al.*, 2022).

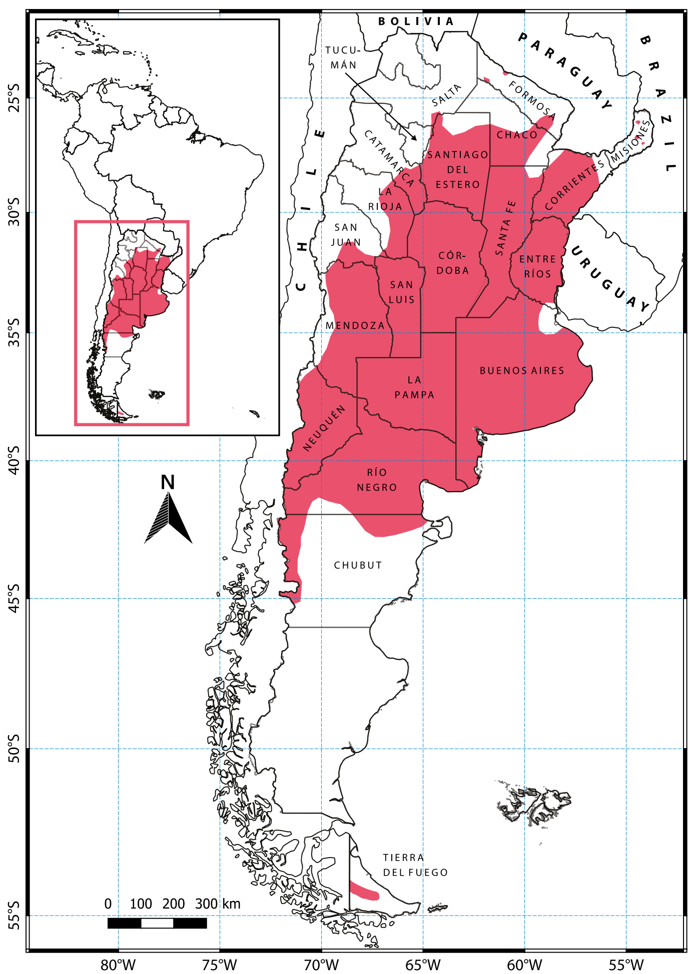

Figure 2. Distribution of *Sus scrofa* in Argentina. Modified from Ballari *et al.* (2019). (Mapping: Ian Barbe and Alfredo Claverie).

Impacts

Wild boar generate several impacts, affecting not only plant and animal communities, but also ecosystem processes (Ballari and Barrios-García, 2012). Studies have shown that boars reduce plant cover in the Monte Desert (Cuevas *et al.*, 2010; Cuevas *et al.*, 2012), but furthermore, over the long-term, disturbed soils show a relatively high (60%) extent of species turnover (rate of species replacement), mainly dominated by annual species. In this way, perennial plant species are negatively affected, and their recovery is very slow (Cuevas *et al.*, 2020). In Patagonian forests, wild boars affect vegetation composition and promote invasive plant establishment and growth (Barrios-García *et al.*, 2014). At the soil level, this species alters properties through its rooting behavior, where in Monte Desert biome this action modifies physical, chemical, and microbiological conditions, leading to wind erosion and subsequent contribution to the acceleration of desertification processes (Cuevas *et al.*, 2012); in Patagonian forests, it produces a substantial change in soil properties, decreasing decomposition rates and soil hardness (Barrios-García *et al.*, 2014). In Parque Nacional El Palmar, boars may serve dual roles as possible seed dispersers of the yatay palm (*Butia yatay*), as they defecate whole seeds upon eating its fruit, and also as predators upon yatay seedlings, where during non-masting periods boars dig around the plant, leaving their roots exposed and causing it to die (Ballari *et al.*, 2015b). This species also damages agricultural crops and preys upon small livestock (Navas, 1987), as well as dispersing introduced plant seeds and promoting its establishment (Ballari and Barrios-García, 2014; Ballari *et al.*, 2015b).

Regarding its social impact, the boar's presence is increasingly frequent in urban areas, which implies dangers of direct contact, rooting in landscaping and traffic accidents (Ballari *et al.*, 2019). In addition, *Sus scrofa* is a reservoir of many viral and bacterial diseases and parasites, which can be transmitted by direct contact with the species or their feces (Aujeszky's, foot-and-mouth disease, brucellosis, tuberculosis, paratuberculosis, toxoplasmosis, and leptospirosis), or by consuming contaminated food or uncooked meat (*Trichinella*) (Cohen *et al.*, 2010; Ballari *et al.*, 2019; Marcos *et al.*, 2021).

Management

The wild boar was categorized as high priority for management by Valenzuela *et al.* (2014). However, no national initiatives have been applied to control their populations, and localized efforts have been found to be mostly ineffective (Ballari *et al.*, 2015a). Nonetheless, various examples were found in the literature that provide seminal efforts to develop and execute control methods, such as in Parque Nacional El Palmar (Ballari *et al.*, 2015a) and Parque Nacional Nahuel Huapi (APN, 2011). Ballari *et al.* (2015a) found that 54% of surveyed protected areas apply some control method. Hunting was the most commonly used technique for wild boar control, a method that protected area managers (*e.g.*, Parque Nacional Islas de Santa Fe, Reserva Provincial Laguna de Llancanelo and Parque Nacional Campos del Tuyú) have reported to be effective for reducing boar populations. However, the methods used were in general ineffective and did not reduce the abundance of this invasive species. An example of effective wild board management occurs in Parque Nacional El Palmar, where since 2006 a control program for introduced mammals has been applied, whereby hunting has been maintained regularly, managing to remove around 2,000 animals from the area in 10 years. This effort caused a decrease in boar abundance and their negative impacts, such as predation of yatay palm (*Butia yatay*) saplings and rooting the park's soil (Gürtler *et al.*, 2017, 2018). The methods in Parque Nacional El Palmar use bait to attract wild boar with supplemental feeding (*e.g.*, corn), which could in fact have the unintended consequence that boars more frequently use the protected area, rather than the private agricultural lands that surround the park, due to the supplemental food being available the whole year (Cuevas *et al.*, 2016). For that reason the use of baiting to hunt the species remains controversial (Cellina, 2008; Cuevas *et al.*, 2016). In Parque Nacional Nahuel Huapi, the control plan for introduced species is made through the implementation of sport hunting, but to date few individuals have been hunted in the context of this plan (Ballari *et al.*, 2019). Another example is in Reserva Privada Rincón del Socorro, Corrientes province, where between 2006 and 2014 feral pig controls were implemented and 6,500 individuals were hunted. However, this effort was not enough to decrease the pig population (Ballari *et al.*, 2019). In the current scenario of population growth and dispersal, it is necessary to develop national and regional strategies for the control of wild boar populations along the edges of its distribution to reduce the probability of range expansion to new sensitive protected areas and agricultural and rangelands.

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