

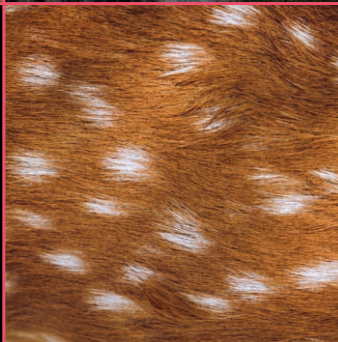


SAREM Series A  
Mammalogical Research  
Investigaciones Mastozoológicas

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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**SAREM Series A**  
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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  
Dr. Christopher B. Anderson  
Editors, Vol. III SAREM Series A

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## FOREWORD

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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.



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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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# 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 Environment), 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 lineages; 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 lineage. 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; Bebbler *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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# INTRODUCED INVASIVE MAMMALS OF ARGENTINA

Introduced Invasive Mammals (IIMs) are a major driver of global and local environmental change, including negative impacts on biodiversity, ecosystem processes, economies, health and other social values. However, as complex social-ecological systems, invasive species cannot be conceived solely as “negative,” nor merely as “biological” invasions. This book presents conceptual and practical perspectives from 49 authors with expertise in communication, ecology, education, genetics, history, philosophy, social sciences and veterinary medicine to better understand and manage IIMs in Argentina. It concludes by providing updated information on Argentina's IIM assemblage, which includes 23 species.

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



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