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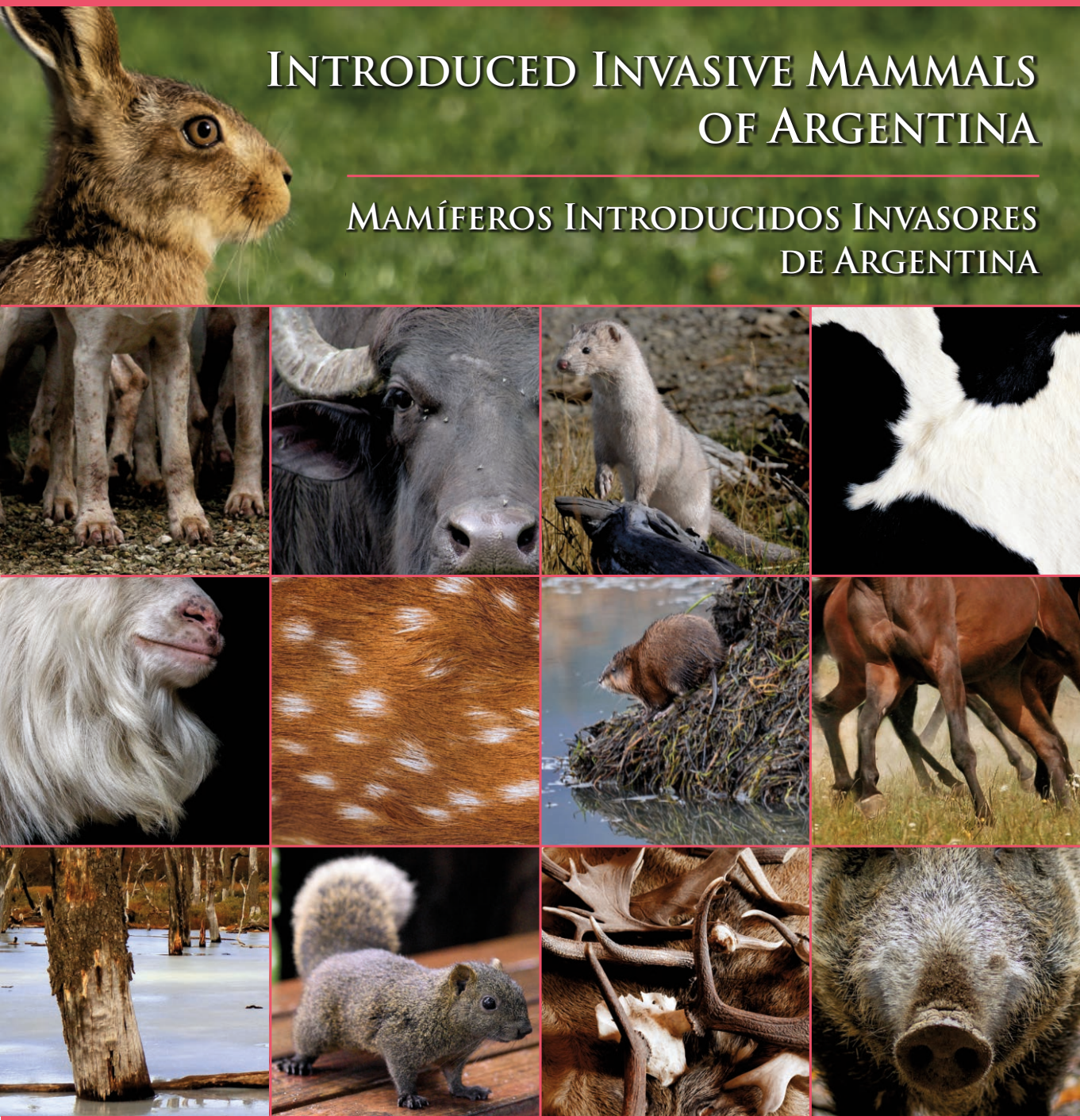
Introduced Invasive Mammals of Argentina

Mamíferos Introducidos Invasores de Argentina



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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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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.

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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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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

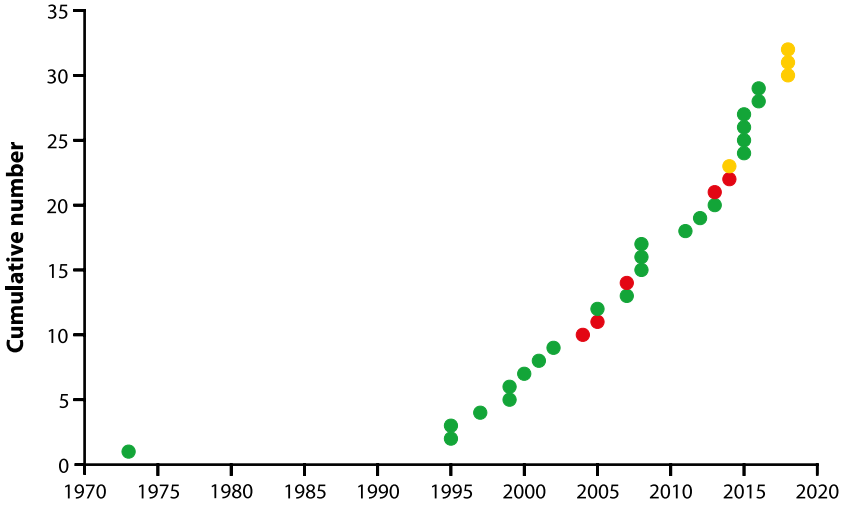

Figure 2. Cumulative number of *Callosciurus erythraeus* translocation events recorded in Argentina (data include records reported in Benitez *et al.*, 2013; Guichón *et al.*, 2015, 2020; Borgnia *et al.*, 2019). We indicate the translocations that resulted in successful (**green**) and failed (**red**) 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.

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