From a lag in vector activity to a constant increase of translocations: invasion of Callosciurus *squirrels in Argentina*

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ORIGINAL PAPER

From a lag in vector activity to a constant increase of translocations: invasion of *Callosciurus* squirrels in Argentina

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Abstract Arboreal squirrels of the Asiatic genus *Callosciurus* have shown high likelihood of establishment from few released animals, in particular, *C. erythraeus* has established wild populations in Argentina, Belgium, France, Hong Kong, Japan, and The Netherlands. We report the invasion process of *C. erythraeus* in Argentina in the last four decades and suggest management actions for each foci. Between February 2011 and November 2014 we conducted field surveys and interviews in nine sites in central Argentina to confirm the presence of *C. erythraeus*, describe their history of introduction, and estimate range expansion and squirrel relative abundance. We report a two decades lag-phase until the onset of translocations of *C. erythraeus* within national boundaries that resulted in a constant increase of the cumulative number of releases. We confirm nine new release events between 1995 and 2012 and six new invasion foci that yields a total of 13 deliberate releases and 10 invasion foci established in rural and urban areas of Argentina. Spread rate ranged from 0.12 to 0.66 km/year. An intermediate relative density of squirrels (2–7 ind/ha) was found close to release sites except in one case. All introduction events involved squirrels translocated from the first, 40 years old invasion focus, occasionally involving illegal trade. The rate of introduction events in the last decades and the translocation-lag phase described in this study should call the attention in all countries dealing with charismatic, introduced species. Translocation disruption requires urgent attention to slow down the invasion of this and other species.

Keywords Animal translocation · *Callosciurus erythraeus* · Introduced squirrels · Lag phase

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Introduction

New records of introduced species into novel areas are still being reported every year, even though the knowledge and awareness regarding their actual and potential impacts have largely increased in the last decades. Economic profit and cultural conceptions of wildlife play a key role in the ongoing trade and deliberate releases of individuals outside their native range (McNeely 2001). Several invasive species with known negative effects continue travelling across countries hand in hand with ornamental plant and pet trade. As a consequence, large investment and long-term management plans are then needed to mitigate their impacts and control or eradicate their populations (see case studies in Wittenberg and Cock 2001).

Squirrels are successful invaders as they combine their charismatic appeal with high reproductive potential and probability of establishment from 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. Consequently, introduced squirrel populations of 18 species have already been reported in 23 countries over five continents (Bertolino 2009; Jessen et al. 2010). The long-studied case of introduction of the grey squirrel *Sciurus carolinensis* in Europe illustrates their invasive potential, their impact on native fauna and plantations, and how social support may determine the failure or success of a control program (Bertolino and Genovesi 2003; Gurnell et al. 2004; Bertolino et al. 2014). Arboreal squirrels of the Asiatic genus *Callosciurus* have shown a particularly high likelihood of establishment from few released animals (Bertolino 2009). *C. finlaysonii* has been introduced in Italy, Singapore and Japan, while *C. erythraeus* has established wild populations in Argentina, France, Hong Kong, Japan, and The Netherlands, and also in Belgium where it has been successfully eradicated (Bertolino and Lurz 2013). Another *Callosciurus* sp. population has been reporded in Italy though taxonomic identification is still pending (Bertolino and Lurz 2013). In all countries of introduction, only one or two *Callosciurus* populations have been reported with the exception of Argentina and Japan where several invasion foci have been described (Benitez et al. 2013; Bertolino and Lurz 2013). Native habitat in Southeast Asia includes tropical and subtropical evergreen forests and also conifer forests, while various arboreal habitat types are inhabited by *C. erythraeus* in introduced ranges such as natural forests, fruit and timber plantations, and parks and gardens in rural and urbanised areas; its highly arboreal habits relates to nesting on trees and feeding on vegetable matter mainly obtained from trees and shrubs (Lurz et al. 2013).

Range occupancy of an introduced squirrel species within a country can be explained by a combination of one or multiple introduction events into a country, translocations from an already established population in the country, and short and long-distance individual dispersal (Palmer et al. 2007; Bertolino 2009). While long-distance dispersal of squirrels, i.e. extraordinary long dispersal distances covered by individual squirrels, may play a key role at the invasion front determining the spread rate of an established population, the number and location of all invasion foci will be determined by human mediated transport, either multiple introductions or translocation events. Continuous monitoring of the occurrence of new invasion foci provides necessary information to identify invasion pathways, understand the first steps of the invasion process, and evaluate the need and feasibility of an early warning-rapid response (Simberloff 2014). In this study we aimed to evaluate the rate and pathways of introduction events of red-bellied squirrels *C. erythraeus* within Argentina and confirm the existence of new invasion foci that have been recently reported by local residents. We estimated squirrel relative abundance and range expansion whenever a new foci was confirmed.

Methods

Between February 2011 and November 2014 we surveyed nine sites where squirrels have been observed by residents that were located in parks of the city of Buenos Aires and in rural and urban areas of the provinces of Buenos Aires and Santa Fé, Argentina (Fig. 1). The Pampas region has been largely modified by agricultural activities and urban-industrial development. Suitable arboreal habitat for red-bellied squirrels is highly fragmented and mainly composed of exotic tree species in small patches, wind curtains and tree lines along roads and railways, and in residential areas and urban parks and streets (Guichón and Doncaster 2008). Arboreal vegetation of the study sites was mainly composed of introduced species such as *Cupressus* spp., *Eucaliptus* spp., *Ligustrum* spp., *Morus* spp., *Pinus* spp., *Populus* spp., and *Quercus* spp. The climate is moist and temperate with a mean annual temperature of 15–19 °C and annual precipitation averaging 453–800 mm (SIGA 2014).

The nine study sites were located at 43–415 km from the first release site of squirrels within Argentina (Aprile and Chicco 1999), in the district of Luján in the province of Buenos Aires (Fig. 1). Two sites were located within the city of Buenos Aires: (1) an urban park named San Martín square (34°35′43″S,

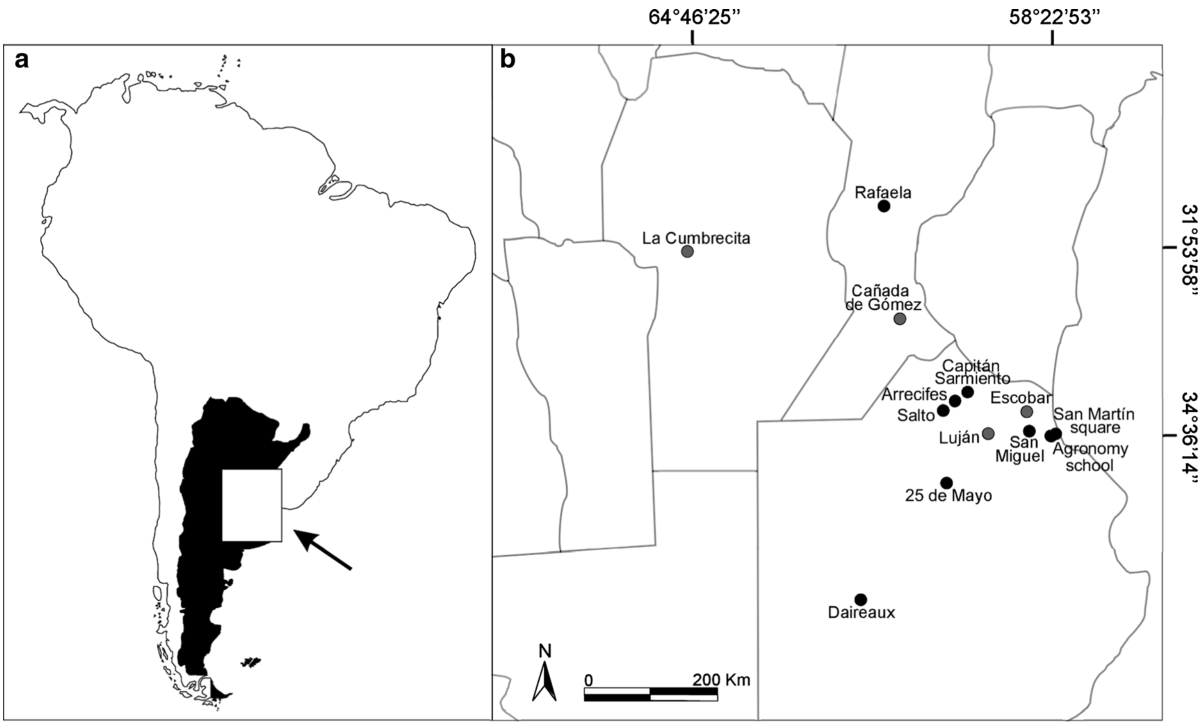

Fig. 1 **a** Location of the area of interest in Argentina (*white quare*) and **b** of the nine study sites (*black dots*) in the city of Buenos Aires (Agronomy School and San Martín square), in the province of Buenos Aires (25 de Mayo, Arrecifes, Capitán Sarmiento, Daireaux, Salto and San Miguel), and in the province of Santa Fé (Rafaela). Province borders (*grey lines*) and previously described invasion foci (*grey dots*, Benitez et al. 2013) are also shown

58°22′34″W) and (2) the university campus of the Agronomy School of the University of Buenos Aires (34°35′26″S, 58°28′55″W). Six other sites were located in rural and urban areas of the province of Buenos Aires: (3) an urbanised area that includes two contiguous localities named Bella Vista and Muñiz (34°10′16″S, 58°41′25″W), which are mainly residential neighbourhoods and suburban areas within the district of San Miguel, (4, 5) a rural area that included the towns of 25 de Mayo (35°25′57″S, 60°10′17″W) and Daireaux (36°35′57″S, 61°44′31″W) and surrounding ranches mainly used for agriculture and extensive farming within the district of 25 de Mayo and Daireaux, respectively, and (6, 7, 8) a rural area that included the cities of Capitán Sarmiento (34°10′16″S, 59°47′37″W) and Salto (34°17′30.43″S, 60°15′15.98″W) and surrounding ranches used for agriculture and bull and horses studs within the districts of Arrecifes, Capitán Sarmiento, and Salto. The last study site was located in the province of Santa Fé: (9) a rural area that included the city of Rafaela (31°15′10″S, 61°29′28″W) and surrounding ranches used for agriculture, extensive farming and dairy farms within the district of Rafaela.

In each site, we conducted field surveys and interviews with residents to confirm the presence of red-bellied squirrels, describe their history of introduction, and estimate their abundance and range expansion, as previously done in similar sites (Guichón et al. 2005; Benitez et al. 2013). Red-bellied squirrels are diurnal and no native squirrels inhabit the study region. No habituation to people has been observed by this species in Argentina, even in the >40 years old invasion focus. We made direct observations of squirrels using binoculars, analysed photographs, inspected dead animals found by residents, and recorded activity signs (e.g. nests and debarking on tree branches) to corroborate the presence of squirrels and whether they belonged to the same species established in the other invasion foci described in Argentina (Benitez et al. 2013). To estimate the invaded area at each site, we also interviewed local residents and people working or visiting the area on a daily basis (e.g. a park) asking whether they have observed squirrels, the place and date of observation, and data about the introduction history such as date and place, origin and number of squirrels released, and the person or entity responsible for the introduction. We initiated interviews and observations at the points where residents have reported their records, and then continued expanding outwards until we obtained consistent data on the absence of squirrels. We mapped each point in Google Earth to calculate the invaded area as the minimum convex polygon that contained all positive records (Earth Point, Clark 2014). Expansion rates were estimated as the square-root of the average square of the shortest and longest radial increases of the minimum convex polygon encompassing the invaded area over time (Andow et al. 1993).

We estimated relative abundance of squirrels using time-area counts based on previous squirrel studies (Bayne and Hobson 2000; Parker and Nilon 2008; Benitez et al. 2013). Our aim was not to estimate absolute population size but to compare relative abundances reached since squirrel release in each site. We used a stratified design based on habitat type (i.e. arboreal areas) close or within properties (i.e. ranches or private parks) where squirrels had been released to increase chance of observing squirrels. In each site, we placed 7–25 points in arboreal areas of 9–119 ha. We started from a randomly selected first point and placed the other points every 100–200 m. We recorded the maximum number of squirrels seen together within a radius of 20 m throughout 10 min of observation conducted between 7:00 and 11:00 h in clear days without rain or strong winds. We searched for squirrels heard but not seen during the 10 min period to confirm their presence and reduce bias in points where tree cover could reduce visibility. We calculated confidence intervals for estimates of relative abundance using a Poisson distribution (Zar 1996).

Results

Information obtained from interviewed residents (n = 539) and observations (n = 124) in all sites indicated the occurrence of nine translocation events of red-bellied squirrels between 1995 and 2012 (Table 1). Therefore, taking into account the four invasion foci previously described (Benitez et al. 2013), a total of 13 deliberate releases of squirrels have been recorded in Argentina (Fig. 1). After >20 years' lag period since the first introduction in the 1970s, we recorded a constant increase of the cumulative number of new releases, yielding a rate of 1.3 releases every 2 years between 1995 and 2014 (Fig. 2).

The two introduction events that occurred within the city of Buenos Aires failed to initiate permanent populations (Table 1). Solitary squirrels have been occasionally observed between 2004 and 2010 in these two sites, however, we found no squirrels or activity signs in our survey in agreement with interview reports. We did confirm six new invasion foci in the provinces of Buenos Aires and Santa Fé that were originated by deliberate releases in private properties, both in rural and urban areas (Fig. 1; Table 1). The two translocation events to Arrecifes and Capitán Sarmiento, 24 km apart from each other, have now overlapped ranges so we consider this site as one invasion focus originated by two independent releases. Spread rate ranged from 0.12 to 0.66 km/year in these six invasion foci (Table 1). An intermediate relative density of squirrels (2–7 ind/ha) was found close to release sites except for a high relative density at Arrecifes (Table 1). No squirrels were observed in abundance surveys in Daireaux, the most recent site.

Discussion

The first invasion focus that has established in Argentina subsequently functioned as a source of squirrels translocated to the other three invasion foci previously described (Benitez et al. 2013), as was corroborated by genetic studies (Gabrielli et al. 2014). The introduction events reported in this study also involved squirrels captured in the first invasion focus in Luján, occasionally involving illegal trade. The constant increase of the cumulative number of releases supports the reports indicating only one source of individuals that may well turn into an exponential increase of translocation events as soon as other invasion foci start acting as a source of squirrels. The two decades lag-phase until the onset of translocations within national boundaries indicates the occurrence of a lag in the rate of invader appearance (Crooks 2005).

Table 1 Year of introduction and number of red-bellied squirrels released at nine sites located in the city of Buenos Aires, and the provinces of Buenos Aires and Santa Fé, Argentina (see Fig. 1). For successful releases, we indicate the invaded area (year of estimation), spread rate since liberation, percentage of positive points (with squirrels) in time-area count surveys, relative abundance [95 % confidence interval] (year of estimation), and estimated relative density. At present we cannot distinguish the invaded area that initiated at Arrecifes release site from the invaded area initiated at Capitán Sarmiento, therefore, we treat them as a single invasion focus resultant from two independent releases

Year	Release site	Founding number	Invaded area (km^2)	Spread rate (km/year)	Positive points (%)[a]	Relative abundance (squirrel/point)	Relative density (squirrel/ha)[b]
1995	Arrecifes	30	317 (2014)	0.53[c]	71	1.9 [0.6–3.0] (2014)	14.8 [4.5–23.8]
1997	25 de Mayo	Unknown	122 (2012)	0.66	44	0.9 [0.5–1.2] (2012)	6.7 [3.9–9.4]
2001	Capitán Sarmiento	2	See Arrecifes	See Arrecifes	42	0.9 [0.5–1.5] (2014)	7.3 [3.9–12.2]
2004	San Martín square	Unknown	Not established				
2005	Agronomy School	Unknown	Not established				
2005	Salto	4	16 (2014)	0.41	14	0.3 [0.1–0.8] (2014)	2.3 [0.5–6.3]
2007	San Miguel	Unknown	7 (2012)	0.53	38	0.6 [0.2–1.3] (2012)	4.9 [1.9–10.2]
2008	Rafaela	20	3 (2014)	0.33	56	0.8 [0.5–1.5] (2014)	6.2 [3.6–11.6]
2012	Daireaux	Unknown	0.2 (2014)	0.12[c]			

[a] Percentage of points with squirrels records within a 20 m radius that were used to calculate relative abundance

[b] Calculated from relative abundance data obtained in a 20 m radius circular area

[c] Estimated as the average radial distance per year assuming symmetric spread (Andow et al. 1993)

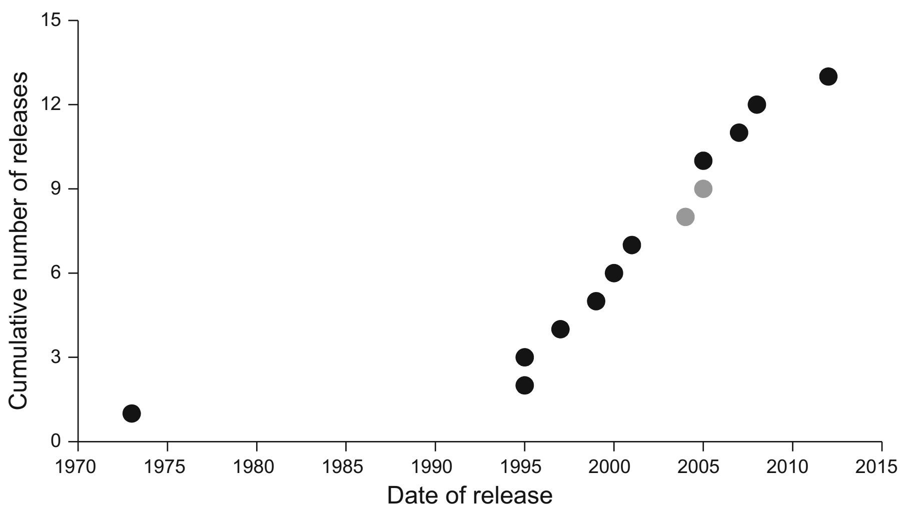

Fig. 2 Cumulative number of successful (*black dots*) and failed (*grey dots*) release events of red-bellied squirrels recorded in Argentina per year, taking into account the four invasion foci previously described (Benitez et al. 2013)

Apart from a lag in population growth or range expansion of each new invasion focus (Guichón and Doncaster 2008), we now describe a lag-phase in the foundation of new populations that could be explained by increased vector activity over time through translocations (Crooks 2005). Similarly, the introduction events listed by Bertolino and Lurz (2013) for red-bellied squirrels in Japan also indicate the occurrence of 17 new introductions after a lag period of approximately 20 years, though we cannot discriminate between multiple introductions and translocations within the country.

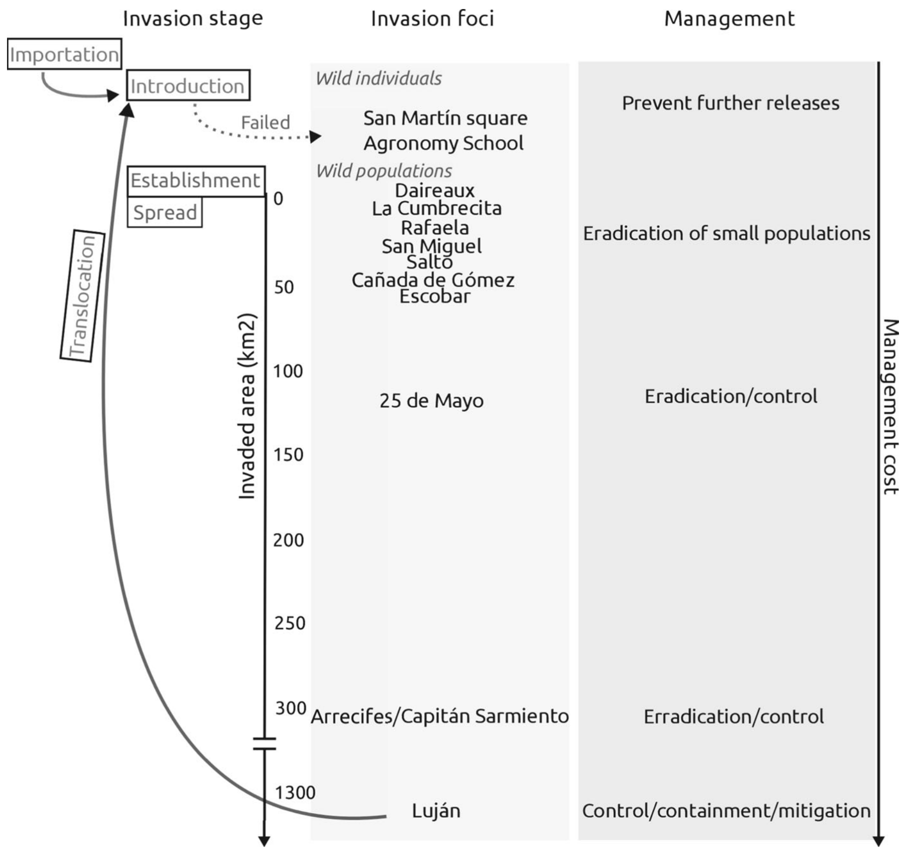

Fig. 3 Invasion stage of all invasion foci of red-bellied squirrels detected in Argentina indicating for each site the invaded area after establishment and recommended management actions, which increase in cost as the invasion process proceeds. The transport stage (Blackburn et al. 2011) results from the first importation into the country and successive translocations within national borders. At present we cannot distinguish the invaded area that initiated at Arrecifes release site from the invaded area initiated at Capitán Sarmiento, therefore, we treat them as a single focus resultant from two independent releases

The spread rate described in these new invasion foci is comparable to the expansion rate observed throughout the first 30 years in the main invasion focus in Luján (0.53 km/year) that increased to 1.66 km/year between 2004 and 2009 (Guichón et al. 2005; Benitez et al. 2013). The total invaded area in Argentina now exceeds 2100 km^2 though densities are quite variable. The high relative density of squirrels at Arrecifes release site, which was similar to densities reached in the main invasion focus in Luján (Benitez et al. 2013), could be explained by the large number of founding individuals, the time elapsed since release, and the highly fragmented habitat surrounding the ranch (M Borgnia and M Hertzriken, personal observation). Habitat fragmentation may not only affect squirrel abundance in a forested patch (Koprowski 2005) but may influence expansion rate (With 2002; Bridgman et al. 2012), which could also be modified by habitat carrying capacity (Guichón and Doncaster 2008). Processes involved in the successful squirrel establishment in each invasion focus still need more studies though at present the propagule pressure hypothesis that has broad consensus in invasion ecology (Lockwood et al. 2005; Jeschke 2014) does not seem to play an important role while the enemy release hypothesis (Heger and Jeschke 2014) cannot be discarded (Gozzi et al. 2013, 2014).

Lags associated with invaders, their impacts and vector activity can affect decision-making processes and the implementation of invasion control, which in turn can experience a lag in the form of delayed reactions (Crooks 2005). The absence of any coordinated plan in Argentina indicates difficulties in recognizing specific invasion threats and taking steps toward invasion management, mainly due to a lack of political commitment and social support (Borgnia et al. 2013). Invasion foci of red-bellied squirrels in Argentina can be placed at different stages of the invasion process (Blackburn et al. 2011), which should be taken into account to establish management priorities (Fig. 3). To this scenario, we must overlap the social context of each region given that resident's support and involvement could be obtained in rural areas, e.g. Rafaela or Cañada de Gómez (Fig. 3), but opposition to control actions is stronger in tourist and urban areas such as La Cumbrecita and Escobar (Fig. 3), even if the latter site has high conservation priority (Guichón and Doncaster 2008; Benitez et al. 2013; Borgnia et al. 2013). Prevention of new releases, which are illegal, should be a first national action that must prioritise areas of high conservation value and where native squirrels *Sciurus aestuans* and *S. ignitus* are present (Cassini and Guichón 2009; Borgnia et al. 2013). Red-bellied squirrels can establish in natural or implanted small and large forests. Within a framework for vector management (Ruiz and Carlton 2003), vector interruption consists of those actions designed to disrupt and reduce the flow of propagules to the recipient environment. Disrupting translocation would not only slow down the invasion of red-bellied squirrels but will also reduce deliberate movement of individuals of a large number of species, either for economic profit or recreational or aesthetic issues (McNeely 2001; Ruiz and Carlton 2003).

Social perception and attitude towards charismatic introduced species play a key role in determining vector activity. The role of people must be seriously taken into account to understand the process of invasion and decide management actions (Estévez et al. 2014; Jacobs et al. 2014). In the case of red-bellied squirrels, cuteness is their pathway and their shield. Their appeal to humans is the reason of repetitive transport and release into new sites, and also the reason of lack of support to control actions by various social groups (Borgnia et al. 2013). Their charismatic appeal adds to their ability to cope with modified environments showing high invasive potential, as observed in Argentina, Japan and several European countries (Bertolino and Lurz 2013). Far from being a picture of the past, we face a major and increasing problem due to the number of recent and potential future introductions.

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