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Original Investigation

Invasion status of Asiatic red-bellied squirrels in Argentina

Verónica V. Benitez, Sandra Almada Chavez, A. Cecilia Gozzi, M. Laura Messetta, M. Laura Guichón*

Ecología de Mamíferos Introducidos, Departamento de Ciencias Básicas, Universidad Nacional de Luján, Ruta 5 y 7, Luján (6700), Buenos Aires, Argentina

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ABSTRACT

The only known introduction of a squirrel species into South America is the case of the Asiatic red-bellied tree squirrel *Callosciurus erythraeus* that was introduced in the Pampas Region of Argentina in 1970. To inform management programmes, we analysed the current distribution, expansion rate, and abundance of the red-bellied squirrel in Argentina, and identified invasion pathways. Apart from the first and main focus of invasion, three other invasion foci have originated as a consequence of intentional releases between 1995 and 2000. The main invasion focus already extends over >1300 km^2, where estimated density averaged 15 ind ha^{-1} and numbers of squirrels may reach 100,000 individuals. The area invaded in the other three invasion foci varied between <1 and 34 km^2 and mean densities were around 3–5 ind ha^{-1}. Squirrel abundance and residents' attitude towards this introduced species in the main invasion focus make eradication unfeasible, though management actions such as control, containment and mitigation of damages should be undertaken. Eradication of the relatively small invasion foci must be immediately evaluated, with priority given to valuable conservation areas under high invasion risk.

Introduction

Numerous mammals have become successful invaders when introduced outside their native range (Clout and Russell 2007; Jeschke 2008). Introduced rodents have caused the extinction of native species, damages to agriculture and urban infrastructure, and increased risk of disease transmission (Courchamp et al. 2003; Frenot et al. 2005; Harris 2009; Pavlin et al. 2009). Negative impacts of introduced rodents have led to control or eradication programs, some of which were successful though mainly in isolated and/or small areas (Genovesi 2005; Howald et al. 2007). Once prevention and rapid response to new foci of invasion have failed, control of population numbers, containment and eradication require a comprehensive evaluation of feasibility and expected success (Davis 2009). Management of invasive rodents may pose a major challenge especially when dealing with charismatic species like squirrels (Sciuridae). For these species, public concern and involvement regarding animal rights issues may complicate control actions and proactive prevention of range expansion (Bertolino and Genovesi 2003), at least until major negative impacts can be demonstrated. And even then, control actions may not be supported by the general public, diminishing the chances of successful implementation of control/eradication programs. Squirrels have been introduced worldwide mostly by intentional release into the wild and, to a minor extent, escapes from zoos and private facilities (Bertolino 2009). Several introduced squirrel species represent a threat to biodiversity and produce economic losses in agricultural systems (Palmer et al. 2008). The emblematic case of the Eastern grey squirrel (*Sciurus carolinensis*), which has been introduced in Britain, Ireland and Italy, has shown detrimental impact on the native Eurasian red squirrel (*S. vulgaris*) by competition for resources (Gurnell et al. 2004; Wauters et al. 2005) and disease transmission (Rushton et al. 2006). Economic damages to agricultural systems, particularly forestry due to debarking, are a major reason for control of Eastern grey squirrel populations in the UK (Mayle et al. 2009).

Only two introduced squirrel species have been reported in South America; the first case was the introduction of the red-bellied squirrel *Callosciurus erythraeus* in Argentina and the second case was the translocation within Perú of the Guayaquil squirrel *S. stramineus* 500 km south of its original distribution (Aprile and Chicco 1999; Jessen et al. 2010). Asiatic tree squirrels of the genus *Callosciurus* have shown a high likelihood of establishment from only few introduced individuals (Bertolino 2009). The red-bellied squirrel has been successfully introduced in Argentina, Belgium, France, Italy, Japan, and The Netherlands (Aprile and Chicco 1999; Miyamoto et al. 2004; Dijkstra et al. 2009; Gerriet 2009; Stuyck et al. 2009; LIFE09 NAT/IT/095 EC-Square Project 2012). Trade in the pet market followed by intentional release in public or private parks, or occasional escapes, originated these wild populations. In Argentina, 10 red-bellied squirrels were imported in 1970 and kept in captivity, however, in the following three years some of these squirrels died while others (≤5 individuals) both escaped or were intentionally released initiating a successful invasion process in the Pampas (Guichón and Doncaster 2008). Impacts of the red-bellied

* Corresponding author. Tel.: +54 02323 423979/423171; fax: +54 02323 425795.
E-mail address: mlguichon@unlu.edu.ar (M.L. Guichón).

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squirrel on agricultural systems and urbanised areas include debarking, fruit consumption, and damage to irrigation systems and cables, whereas detrimental effects on shrubs and trees, which constitute the bulk of their diet, and on birds can also arise (Azuma 1998; Miyamoto et al. 2004; Guichón et al. 2005). The continued spread of red-bellied squirrels has already become a conservation concern in Japan as the species will likely encounter the native tree squirrel *S. lis* (Miyamoto et al. 2004). A similar threat could face the arboreal squirrels *S. aestuans* and *S. ignitus*, native to the subtropical forests of Argentina, if the red-bellied squirrel invasion proceeds.

The production of management strategies for introduced species requires the availability of data regarding invasion foci, spread and dimension of populations to be managed. For this reason, we have started a long-term monitoring programme of introduced squirrel populations in Argentina. In this study we have evaluated the current distribution, expansion rate, and abundance of the red-bellied squirrel in Argentina, and identified pathways of invasion. Our results will inform management plans for this species in Argentina and, hopefully, will increase the awareness of the problems raised by introduced squirrels worldwide.

Methods

Study area

We worked in all known invasion foci of the red-bellied squirrel in Argentina: the main invasion focus surrounding the original release site, and the other three areas subsequently invaded (Fig. 1a and b). The first invasion focus originated in the district of Luján (34°36′S, 59°11′W), North-eastern Buenos Aires Province, within a rural and urban landscape with highly fragmented woodland patches. Native grasslands of the Pampas region have been extensively modified by agriculture, livestock, and urbanisation and are suffering a woody invasion process (Ghersa et al. 2002). The arboreal vegetation is mainly composed of exotic species originally planted as windbreaks, for shade, or for ornamental purposes such as *Ailanthus* sp., *Araucaria* spp., *Casuarina* spp., *Cupressus* spp., *Gleditsia triacanthos*, *Ligustrum* spp., *Melia azedarach*, *Morus* spp., *Pinus* spp., *Quercus* spp., and *Tilia* spp. Timber plantations are also found, mainly of *Eucalyptus* spp. and *Populus* spp., while fruit production of *Actinidia* sp., *Citrus* spp., *Juglans* spp. and *Prunus* sp. occur to a lower extent. All of these exotic trees are used by red-bellied squirrels for food and nesting (Aprile and Chicco 1999; Guichón et al. 2005; Benitez and Guichón unpublished data). The climate is moist and temperate with a mean annual temperature of 16.6 °C and annual precipitation averaging 951 mm (Golberg et al. 1995).

The second focus of invasion was established in the district of Escobar (34°22′S, 54°48′W), Buenos Aires Province, that has an arboreal vegetation and climate similar to the Luján area, though it presents a more diverse array of urban, industrial, and agricultural land use resulting in an even greater woodland fragmentation. The third focus of invasion is located in Cañada de Gómez district (32°49′S, 61°24′W), Santa Fe Province, where land use is dominated by extensive crops and cattle production, and few original grasslands remain. Arboreal vegetation is highly fragmented and dominated by exotic species like *Eucalyptus* spp., *Ligustrum* spp., *Melia azedarach*, *Platanus* sp., *Populus* spp. Average annual temperature is 17.5 °C and annual rainfall is 1019 mm (EEAO-INTA 2008). The fourth focus of invasion is located in La Cumbrecita (31°53′S; 64°46′W; 1450 m.a.s.l.), which is a small tourist town in the hills of Valle Calamuchita, Córdoba Province. Native vegetation is composed of high-elevation grasslands with few native trees such as *Polylepis australis* and *Maytenus boaria* (Luti et al. 1979). However, dominant vegetation in the town and surroundings is composed of exotic trees like *Betula* sp., *Cupressus* sp., *Fraxinus* sp., *Robinia seudoacacia*, and shrubs like *Rubus ulmifolius*. Average annual temperature is 16 °C, though in winter it may well decline below −10 °C, and average annual rainfall is 1200 mm, which occurs mainly in summer (Capitanelli 1979).

Expansion rate

We estimated the range expansion of the main invasion focus between June 2008 and February 2009 by conducting interviews of local residents and direct observations. Interviews were first conducted at the border of the known 2004 distribution of the red-bellied squirrels (Guichón et al. 2005), and continued expanding outwards until we obtained consistent data on the absence of squirrels, totalling 470 interviews. Local residents answered a non-structured face-to-face interview (Dietrich 1995) that was used to assess whether residents had seen squirrels and, if they did, the place and date of observation. Interviews have proved to be useful in previous studies of invasive species (*e.g.* Guichón et al. 2005) and are particularly suitable for diurnal tree squirrels in regions lacking native squirrels. Direct observations were made in relatively small areas (<1 ha) with no residents or where interview responses were doubtful. Observations were made by slowly walking through small woodlands while recording the presence of squirrels, nests and signs of tree debarking. This species builds its nests in high, secondary branches using leaves and twigs on the outside, and have an ellipsoidal shape and a lateral entrance (Setoguchi 1990, personal observation).

We also conducted interviews of local residents in the other three foci of invasion, where we asked additional questions about the history of introduction such as date, place, origin, number of individuals, and the person or entity responsible for releasing the squirrels. Additionally, we made direct observations of squirrels in each study site. In Escobar, we interviewed 168 residents in a survey first conducted in April–August 2005. In January 2008, we conducted a second survey interviewing 211 residents in the range periphery of the previous distribution. In Cañada de Gómez, we interviewed 79 residents, and conducted direct observations at 44 points systematically distributed in the surroundings of the release site between December 2008 and June 2009. In La Cumbrecita, we interviewed 38 residents and conducted direct observations at 136 points systematically distributed over the town and surroundings in a first survey conducted in February 2006, and we conducted direct observations at 125 points in a second survey in February 2010.

The geographic location of all interviews and observation points were entered in a GIS database to calculate the minimum convex polygon that contained all positive records (Jenness 2004). A conservative criterion was used to assign positive values only to points where we obtained confident interview responses or direct observations of squirrels or activity signs. Therefore, we obtained a minimum estimate of range expansion, acknowledging that the presence of squirrels in the low density invasion front was difficult to detect. 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 (Andow et al. 1993).

Abundance

We estimated squirrel abundance in the main invasion focus of Luján based on distance sampling using point-transects, instead of line-transects, as recommended when dealing with high-density populations (Buckland et al. 2001), such as found at Luján. Between November 2006 and February 2007 we randomly selected 11 woodland patches (8–50 ha) within a radius of 15 km from the original

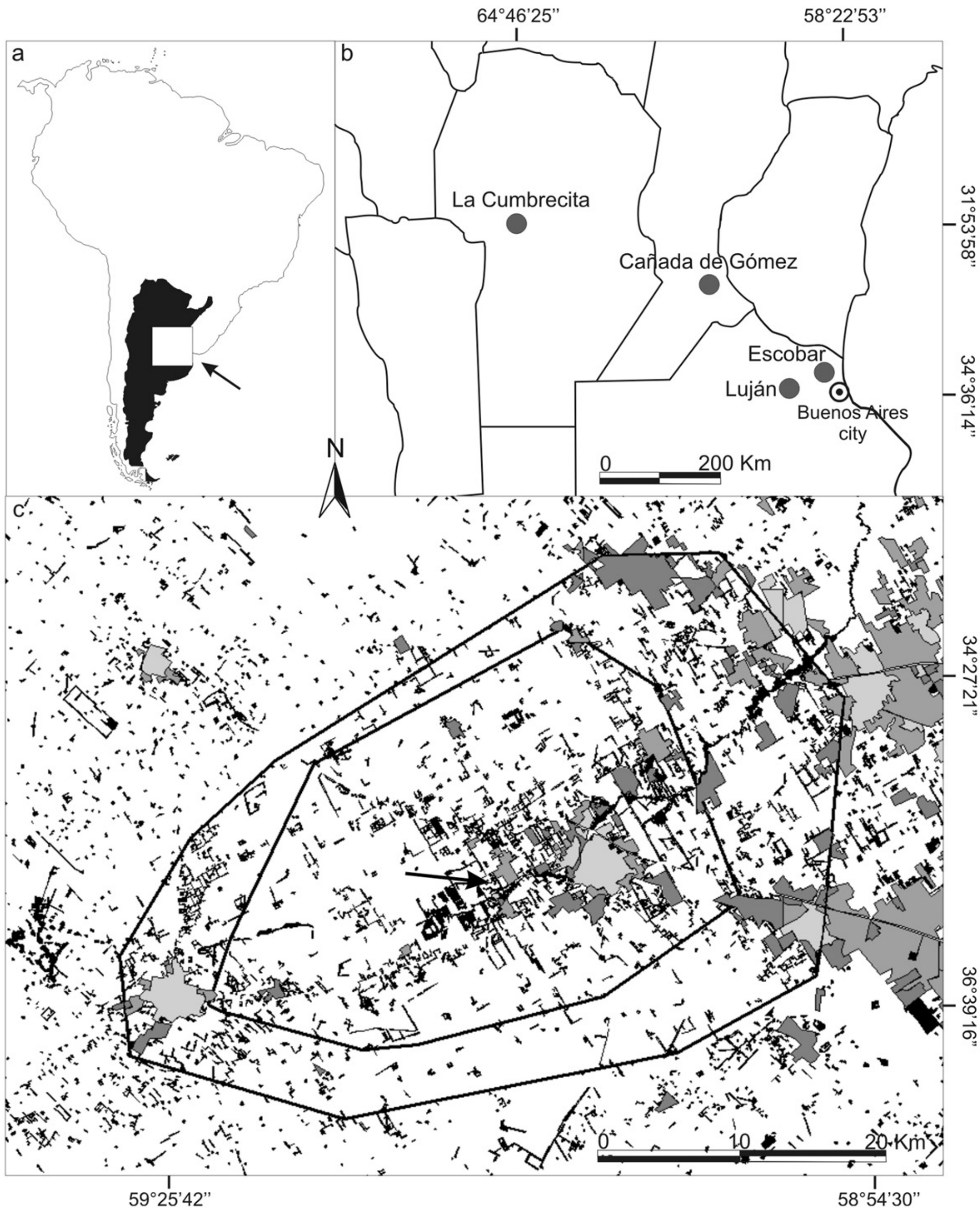

Fig. 1. (a) Location of the area of interest in Argentina (white square), (b) study areas next to the cities (black dots) of Luján and Escobar in Buenos Aires province, Cañada de Gómez in Santa Fé province, and La Cumbrecita in Córdoba province (lines divide provinces), (c) map of the main invasion focus in Luján showing suitable habitat for squirrels (woodland habitat in black and residential, suburban and urban habitats in shades of grey of decreasing intensity) and the matrix of unsuitable habitat (unforested areas in white), indicating the range expansion observed by 2004 (small polygon) and 2009 (large polygon). The original release point of red-bellied squirrels in 1970 is indicated with an arrow. Small habitat patches (<2 ha in size and distant >50 m from other patch) were eliminated only within the 2009 polygon to estimate number of squirrels.

release site. In each patch, 5–8 points were systematically located >100 m away from each other after randomly selecting the first point. At each point we waited quietly for 10 min and we recorded the number of squirrels and individual distances to the observer by instantaneous counts (snapshots), as recommended for sampling moving animals (Buckland et al. 2001). Observations were conducted between 7:00 and 11:00 h in clear days without rain or strong winds. We analysed point data using Distance 6.0 (Thomas et al. 2010) after truncation of records >35 m away from the observer to improve model fitting (Buckland et al. 2001). The detection function was estimated using ungrouped data to fit five models using the uniform, hazard rate and half normal adjustment key functions and the cosine, simple and hermitage polynomial adjustment terms. We estimated a global detection function assuming it was similar in all woodland patches, and we averaged the density obtained in each patch to calculate squirrel density in the main focus. Model performances were evaluated based on the lowest corrected Akaike's information criterion (AIC_c) and the weight of evidence in favour of model *i* being the best approximating model in the set (Buckland et al. 2001; Burnham and Anderson 2002).

We used estimated squirrel density in combination with the amount of available habitat within the invaded area by 2009 to calculate the number of squirrels in the main invasion focus of Luján. We updated the habitat map used by Guichón and Doncaster (2008) that contained four habitat categories for the red-bellied squirrel: woodland, residential, suburban, and urban; while open areas with no trees were considered the matrix of non-suitable habitat. Woodland habitat included all forested areas, woodland patches, and wooded corridors; in the absence of more specific information, all woodlands were considered of equal quality. Residential, suburban, and urban areas differed in their increasing degree of urbanisation and decreasing degree of arboreal cover. Woodland was considered to have the highest habitat suitability, followed sequentially by residential, suburban, and urban. We defined habitat patches by merging suitable habitat distant <50 m (based on estimated perceptual range between 20 and 100 m for this species, Bridgman et al. 2012), and then eliminated <2 ha isolated patches, which we assumed to have low probability of stable occupation (Fig. 1c). Density surveys were conducted in woodland habitat and relatively close to the original release site. Therefore, to avoid overestimation of the total number of squirrels in the Luján invasion focus we used lower squirrel densities for the other habitats types and in the area colonised between 2004 and 2009. To calculate squirrel density in residential, suburban and urban habitats, we considered a progressive 50% decrease of the density estimated in woodland habitat (*i.e.* density in residential habitat halved density in woodland, density in suburban habitat halved density in residential habitat, and so on) (Guichón and Doncaster 2008; Benitez and Guichón, personal observation). To calculate squirrel density in the area invaded between 2004 and 2009, we considered that density in woodland habitat decreased by 80% with respect to the same habitat type close to the original release site, and we maintained the same decrease for the other habitat categories as explained above. Though this is crude approximation, we are using all available information to provide the first estimation of the number of squirrels in the main invasion foci of Argentina.

To compare relative abundance amongst invasion foci we used time-area counts (Parker and Nilon 2008) because the number of sightings in the other three invasion foci was below the recommended value for reliable estimations using distance sampling (Buckland et al. 2001). Point counts were conducted in: (1) Luján, 66 observation points between November 2006 and February 2007, (2) Escobar, 32 points in January 2008, (3) Cañada de Gómez, 18 points in December 2009, and (4) La Cumbrecita, 19 points in February 2010. We placed each point every 100–200 m from a randomly selected first point and we recorded the maximum number of squirrels seen together within a radius of 20 m throughout 10 min of observation. We calculated confidence intervals for estimates of relative abundance using a Poisson distribution (Zar 1996). Restricted expansion in La Cumbrecita allowed us to conduct an intensive survey in February 2006 by identifying all nests within the occupied area, and recording the number of squirrels in the surroundings of each nest (Sutherland 2006). This preliminary estimate of abundance in 2006 was used to design the point counts survey in 2010 to obtain data comparable with other invasion foci.

Results

Expansion rate

The main invasion focus of the red-bellied squirrel in Argentina almost doubled by 2009 compared to the 680 km^2 area occupied in 2004 (Table 1 and Fig. 1c). The expansion rate since 1973 exceeded the expansion rate of 0.53 km year^{-1} previously estimated until 2004 (Table 1). The invasion front has been expanding more rapidly in recent years, showing an expansion rate of 1.66 km year^{-1} between 2004 and 2009.

Squirrels translocations from the main invasion focus in Luján originated other invasion foci within Argentina in the last 15–20 years. Around 1995 an unknown number of squirrels were released at a private property in Escobar, 42 km away from the original release site in Luján. The descendants of these released squirrels have since invaded 25 km^2 by 2005, showing an expansion rate of 0.36 km year^{-1}. In 2008 we recorded a 40% increase in the occupied area and a slight increase in expansion rate (Table 1), which increased to 0.82 km year^{-1} in the period 2005–2008 (Table 1). Trade and release of 8 squirrels in a private ranch in Cañada de Gómez originated a new invasion focus 285 km away from the release site in Luján (Table 1). The fourth focus of invasion was initiated by an intentional release of squirrels in the backyard of a hotel in the tourist town La Cumbrecita, 600 km away from Luján (Table 1). By 2006 squirrels have spread over the town covering 0.32 km^2 at a relatively slow rate of 0.09 km year^{-1} that continued at a low rate until 2010 (Table 1), probably limited by the absence of arboreal vegetation outside the urbanised area (Table 1).

Abundance

Red-bellied squirrels were present in the 11 woodland patches surveyed in Luján in 2006–2007, and we observed 132 squirrels in 83% of the 66 points within a 34 m radius of the observer. The best model to estimate squirrel density was a uniform key function with a 3-term simple polynomial adjustment, which greatly outperformed competing models (ΔAICc > 14 and w_i > 0.9), and also had the lower coefficient of variation for the estimated density (Table 2). The mean density was estimated as 15.3 squirrels ha^{-1} (Table 2). The 1336 km^2 polygon containing all positive records of squirrels in 2009 contained only 220 km^2 of suitable habitat and after discarding isolated patches <2 ha, we obtained a total of 210 km^2 of suitable habitat (woodland: 79 km^2, residential: 68 km^2, suburban: 31 km^2, urban: 32 km^2) (Fig. 1c). Minimum and maximum density of squirrels in suitable habitat within the area invaded by 2004 (woodland: 12.0–19.5 ind ha^{-1}, residential: 6.0–9.8 ind ha^{-1}, suburban: 3.0–4.9 ind ha^{-1}, urban: 1.5–2.4 ind ha^{-1}) and in the area colonised between 2004 and 2009 (woodland: 2.4–3.9 ind ha^{-1}, residential: 1.2–2.0 ind ha^{-1}, suburban: 0.6–1.0 ind ha^{-1}, urban: 0.3–0.5 ind ha^{-1}) yielded a rough estimate of 96,958–157,557 squirrels in the Luján invasion focus.

Relative abundance obtained by time-area counts was highest in Luján invasion focus, followed by Cañada de Gomez, La Cumbrecita, and Escobar (Table 1). In Luján, number of squirrels per point was close to 2, while in all other invasion foci it was much lower ($\leq$0.6) (Table 1). In the preliminary, intensive survey in 2006 in La Cumbrecita, we recorded a total of 7 nests used by 22 squirrels, with a mean of 3.14 $\pm$ 0.26 SE squirrels per nest. Based on range expansion by 2006, density was around <1 squirrel ha^{-1}, which tripled in 2010 (Table 1).

Discussion

Expansion rate

There are currently four invasion foci of the red-bellied squirrel in Argentina: the main focus where the original release took place 40 years ago and three new invasion foci that originated in the last 15–20 years by individuals translocated from the main focus into areas 40–600 km away. Interviewed residents also reported short distance relocation of squirrels that might have favoured

Table 1
Current status of the red-bellied squirrel at four invasion foci in Argentina indicating the invaded area (year of estimation), expansion rate since liberation, percentage of positive points (with squirrels) in time-area counts surveys, relative abundance [95% confidence interval] (year of estimation), and estimated density.

Invasion foci	Year of introduction	Founding number	Invaded area (km^2)	Expansion rate ($km\ year^{-1}$)	Positive points (%)[a]	Relative abundance (squirrel/point)	Density ($squirrel\ ha^{-1}$)
Luján	1970	2–5	1336 (2009)	0.61	73	1.89 [1.58–2.24] (2007)	15.3[b] [12.0–19.5]
Escobar	ca. 1995	Unknown	34 (2008)	0.39	16	0.41 [0.22–0.69] (2008)	3.23[c] [1.72–5.53]
Cañada de Gomez	ca. 1999	8	33 (2009)	0.44	50	0.61 [0.31–1.09] (2009)	4.86[c] [2.43–8.70]
La Cumbrecita	2000	30	0.42 (2010)	0.05	27	0.42 [0.18–0.83] (2010)	3.35[c] [1.45–6.60]

[a] Percentage of points with squirrels records within a 20 m radius that were used to calculate relative abundance.
[b] Estimated using distance sampling (see Table 2).
[c] Calculated using relative abundance data.

establishment and spread within each invasion focus. Colonisation of new areas resulted from individual dispersal at the invasion front into new woodland, long distance dispersal events using aerial cables and tree lines, and intentional short and long-distance translocations of individuals. Being a charismatic species, easy to capture and transport, and available in the illegal pet market, immediate action should be taken to prevent new invasion foci. Once a species is introduced into a country, there is a high risk that it will be translocated to other parts, increasing the spread and making control or eradication more difficult, as has happened with the red-bellied squirrel in Argentina as well as in Japan (Miyamoto et al. 2004) and with the Eastern grey squirrel in the UK (Middleton 1931) and Italy (Martinoli et al. 2010). In the context of the worldwide scenario of deliberate importation of exotic squirrels (Bertolino 2009), strong regulations regarding explicit prohibition of further introductions, translocations and trade of exotic squirrels, accompanied by broad public communication, are needed to prevent releases into new areas.

The expansion of the red-bellied squirrel in the main invasion focus in Argentina (1336 km^2 in 40 years) was higher than reported in Japan (304 km^2 in 52 years; Tamura 2004) and France (18 km^2 in ca. 40 years; Anne Dozières, personal communication). Comparison of expansion rates among invasive squirrels must be done cautiously given the use of different methods and insufficient data in some cases. The expansion rate reported for the Eastern grey squirrel introduced in Europe was 7.7 $km\ year^{-1}$ in England (Okubo et al. 1989) and 1.9 $km\ year^{-1}$ in Ireland (Teangana et al. 2000). The Eastern fox squirrel *Sciurus niger* introduced in California in 1904 has expanded at 0.44–3.44 $km\ year^{-1}$ (King et al. 2010). The expansion rate of the red-bellied squirrel in the main invasion focus of Argentina averaged 0.61 $km\ year^{-1}$ since released but almost tripled in the period 2004–2009. The expansion rates in the secondary invasion foci, although lower than in the main focus, are comparable with the initial invasion stage of the Eastern grey squirrel in Italy (Bertolino and Genovesi 2003).

Several factors can influence the expansion of invasive species and for arboreal squirrels highly fragmented woodlands explained the relatively slow spread of the Eastern grey squirrel in Ireland (Teangana et al. 2000) and during the first 20 years in Northern Italy (Bertolino and Genovesi 2003). Habitat fragmentation may only slow down their expansion given that the successful invasion of squirrels partly relates to their ability to persist in heavily fragmented landscapes, as suggested for Eastern grey squirrels that are found in smaller fragments and reach higher densities than Eurasian red squirrels (Wauters et al. 1997; Koprowski 2005). However, a relatively fast expansion was observed in the red-bellied squirrel in Argentina over highly fragmented woodland patches within agricultural and urbanised landscapes, where squirrels settle in arboreal habitats in rural and urban areas and use trees, cables and roofs to move around. The use of above-ground utility cables as relatively safe means of travelling within their home range and for dispersing into new areas was also reported for the Eastern fox squirrel (King et al. 2010). Red-bellied squirrels' spread can be accelerated by a decrease in habitat quality (Guichón and Doncaster 2008) and could also increase if squirrels move further searching for suitable habitat while avoiding open habitat, in the highly fragmented rural–urban landscape. The ability of this species to cope with novel environments, and establish and disperse in human-modified habitats was also reported in France and Japan (Miyamoto et al. 2004; Gerriet 2009), and for *C. finlaysoni* and the Eastern grey squirrel in Italy (Lurz et al. 2001). The predisposition of introduced mammals to human-modified habitats has long been considered a key of their success, *e.g.* the black rat *Rattus rattus* and the house mouse *Mus musculus* (Lever 1985).

Abundance

Red-bellied squirrel abundance in the four invasion foci in Argentina varied from high densities attained after 36 years in the main invasion focus to moderate densities after 10–13 years since releases in the other foci. Density range showed no clear relationship with the number of founding individuals. Estimated density in the main invasion focus was higher than previously reported both in native and introduced ranges. Densities in conifer plantations in their native Taiwan were of 0.5–1.0 $ind\ ha^{-1}$ using time-area counts and 2.5 $ind\ ha^{-1}$ by mark-recapture data (Lin and Yo 1981). Intermediate densities were obtained both in native forests of Taiwan (7 $ind\ ha^{-1}$) and introduced forests of Japan (6–7 $ind\ ha^{-1}$) using census routes (Tamura et al. 1989). A wide range of density variation was also reported for the Eastern grey squirrel that can reach very high densities in urban parks both in native (Koprowski 1994: >21 $ind\ ha^{-1}$; Parker and Nilon 2008: 38–49 $ind\ ha^{-1}$) and introduced (Bertolino 2008: 18 $ind\ ha^{-1}$) areas. Density values in small woodlots (<10 ha) can be as high as 16–21 $ind\ ha^{-1}$ in

Table 2
Model (key function + series expansion) selection for the detection function using distance sampling to estimate red-bellied squirrels density in the Luján invasion focus in 2007, indicating mean density of squirrels (95% confidence interval) and its coefficient of variation (CV).

Model (key + expansion)	AICc	ΔAICc	Number of parameters	Weight of evidence (w_i)	Mean density [CI] ($squirrel\ ha^{-1}$)	Density CV
Uniform + simple polynomial	853.4	0	3	0.999	15.3 [12.0–19.5]	0.12
Uniform + cosine	867.7	14.2	5	0.001	35.8 [21.6–54.4]	0.26
Half-normal + cosine	869.1	15.7	5	<0.001	25.1 [13.0–48.6]	0.34
Hazart-rate + cosine	871.3	17.9	3	<0.001	32.9 [19.7–54.7]	0.26
Half-normal + hermite polynomial	871.5	18.1	1	<0.001	19.7 [14.9–26.0]	0.14

native and introduced ranges (Koprowski 1994; Gurnell 1996). As reported for the Eastern grey squirrel (Koprowski 1994), habitat composition may affect density of red-bellied squirrels, however, insufficient data is still available and only a relationship between the presence of this species and the area of habitat patches and the proportion of broadleaved evergreen trees has been described in Japan (Miyamoto et al. 2004).

Density and range expansion reported in this study suggest that the four invasion foci of the red-bellied squirrel in Argentina are at different stages of the invasion process. While the newly established invasion foci are just overcoming establishment or initiating spread, the main invasion focus has attained high densities and has expanded over a large area. High squirrel numbers that are mainly found in private lands in combination with their charismatic appearance make eradication unfeasible though coordinated control actions should be undertaken to diminish damages and contain further expansion. The fact that new invasion foci were originated by trade and translocation highlights the need to involve the whole community to prevent further spread. Moreover, after several years working with residents, non-governmental organisations, governmental offices, producers, and school teachers on the problem posed by this introduced squirrel, the challenge to gain general support, long-term commitment and clear responsibilities for control actions still seems a huge task. Eradication could be feasible in the small invasion foci, however, both the biological and social context of each focus should be evaluated to decide appropriate actions. From a conservation viewpoint, priority should be given to the Escobar invasion focus, which is the closest to a natural reserve and a region of high biodiversity with suitable habitat for these arboreal squirrels.

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