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Research Article

Feeding habits of the Asiatic red-bellied squirrel *Callosciurus erythraeus* introduced in Argentina

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Abstract

Knowledge of food habits of invasive species is necessary to predict invasion success and potential interactions in the invaded community. The Asiatic red-bellied squirrel *Callosciurus erythraeus* has been introduced in Asia, Europe and South America. We studied feeding habits of red-bellied squirrels in Argentina in two sites 600 km apart where wild populations have become established. We used both faecal microhistological analysis and behavioural records to describe diet composition and feeding habits. We also analysed diet selection and the potential role of the squirrels as seed disperser. Squirrels consumed items from 35 species of exotic trees and shrubs and one native tree species; fruits and seeds represented the bulk of the diet in all seasons (faeces analysis: >44%; behavioural observations: >38%). Squirrels also consumed epiphytic and climbing plants, ferns, invertebrates, fungi, lichens, mosses and bird eggs. Diet composition varied throughout the year according to food availability. We did not find evidence of endozoochoric dispersal but we observed squirrels carrying and dropping nuts and acorns during transport. The consumption of a wide range of food items and species, the ability to modify the diet according to food availability, and the capacity to hoard food indicate that feeding habits of red-bellied squirrels favour their invasive potential.

Introduction

Exotic species usually face several barriers at different stages of the invasion process (Blackburn et al., 2011). Characteristics of the species, of the recipient community and of the introduction event are all important aspects affecting establishment and invasion (Williamson, 1996). The probability of surviving and reproducing in a new habitat is strongly linked to resource availability and predator pressure (Blackburn et al., 2011). The complexity of multiple and new interactions established within the recipient community, and the variable conditions that can be found in the new habitat, challenge any attempt at generalisation. However, the capacity of animals to modify their behaviour in response to novel conditions is a key attribute for their success as invaders (Sol and Lefebvre, 2000; Wright et al., 2010). Plasticity in foraging behaviour can play an important role when individuals are released into unknown habitats. Examples of successful invaders include species that are generalist and opportunistic foragers (Holway and Suarez, 1999; Rehage et al., 2005). These could constitute strong traits for invasion success especially if they are combined with behavioural flexibility (Wright et al., 2010). Data on feeding habits of a species in its native and introduced ranges can help understand its invasive success and predict the risk of invasion of different habitats. Foraging behaviour also provides important information to design management or mitigation actions such as using toxic baits or scaring devices (Williamson, 1996; Holway and Suarez, 1999).

Squirrels are successful invaders; introduced populations of 18 squirrel species have already been reported in 23 countries over five continents (Bertolino, 2009; Jessen et al., 2010). These populations have originated from escapes or releases related to the pet market, to enrich wildlife or as game animals for their fur (Palmer et al., 2007; Bertolino, 2009). Exotic squirrels cause economic losses and environmental damages that include disease transmission (e.g., Eastern grey squirrel *Sciurus carolinensis*, Chantrey et al., 2014), damage to plantations (e.g., Eastern fox squirrel *Sciurus niger*, Bertolino, 2009), reduced survival of native seeds (e.g., Barbary ground squirrel *Atlantoxerus getulus*, Nogales et al., 2005), bark stripping (e.g., Finlayson's squirrel *Callosciurus finlaysonii*, Bertolino et al., 2004), predation on native birds (e.g., American red squirrel *Tamiasciurus hudsonicus*, Martin and Joron, 2003), and competition with native fauna (e.g., Asiatic red-bellied squirrel *Callosciurus erythraeus*, Mazzamuto et al., 2017).

The Asiatic red-bellied squirrel *C. erythraeus* (Pallas, 1779) has been successfully introduced in Italy, France, Belgium, The Netherlands, Hong Kong, Japan, and Argentina (Bertolino and Lurz, 2013; Lurz et al., 2013; Mazzamuto et al., 2016a). This is the first known introduction of a squirrel into South America and it has achieved the status of an established invasion of major proportions in Argentina (Guichón and Doncaster, 2008). The invaded range increases gradually from already colonized areas and abruptly from transportation and release of individuals into new areas (Guichón et al., 2015). The main invasion focus in the country has been originated by the intro-

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duction of 10 individuals in the Argentine Pampas in 1970 (Aprile and Chicco, 1999). This first population occupied 680 km^2 in 2004 (Guichón et al., 2005) and in the next five years it had doubled the invaded area (>1300 km^2 in 2009, Benitez et al., 2013). This squirrel causes economic damage in agricultural and urban areas by debarking, eating fruits and seeds, and chewing through cables and irrigation pipes (Guichón et al., 2005; Pedreira et al., 2017). Moreover, its spread could affect indigenous birds (Azuma, 1998; Messetta et al., 2015) and transmit diseases and parasites to humans or other animals (Dozières et al., 2010; Gozzi et al., 2013; Deng et al., 2016; Mazzamuto et al., 2016b). The formation of several invasion foci in Argentina favoured by the squirrel's charismatic appeal and ability to establish in new and different habitats (Benitez et al., 2013; Borgnia et al., 2013; Guichón et al., 2015) indicate a high probability of a marked increase in abundance and distribution in the coming years (Guichón and Doncaster, 2008).

In this study we analysed the feeding habits of red-bellied squirrels in two different biogeographical regions in Argentina. We used faecal analysis and behavioural observations to achieve a comprehensive description of their diet composition and foraging behaviour. Under the hypothesis that this species has a generalist and opportunistic diet, we predicted that: 1) squirrels will eat a wide range of plant species and items, and 2) squirrels will select food resources according to their site and seasonal availability. We also assessed the potential role of these squirrels as endozoochoric and/or epizoochoric disperser of exotic plants.

Methods

Study areas

This study was conducted in two sites 600 km apart where the red-bellied squirrel has been introduced in Argentina (Benitez et al., 2013): (1) La Cumbrecita (31°53′ S, 64°46′ W, 1360 m a.s.l., Córdoba province), a small mountain and tourist village, where squirrels were released in the year 2000, and (2) Jáuregui (34°36′ S, 59°9′ W, 25 m a.s.l., Buenos Aires province), a small rural town in the Pampas region, where squirrels were introduced in 1970 and which is the core of the main invasion focus in Argentina (Fig. 1). In both sites, arboreal vegetation is mainly composed of exotic species used in commercial plantations and to block wind, for shade or as ornamental species in gardens, parks and along roads, railways, or rivers (Benitez et al., 2013). The climate is temperate in La Cumbrecita, with a mean temperature of 7.3 °C in winter and 19.5 °C in summer, and a mean annual rainfall of 850 mm, falling mostly in the warm season (Cabido et al., 1987). In Jáuregui, the climate is also temperate but warmer (mean temperature of 9.1 °C in winter and 23.8 °C in summer) and more humid (mean annual rainfall of 944 mm) (Goldberg et al., 1995). No native squirrels are present in these regions.

In La Cumbrecita, the three sampling areas (16 ha in total) were dominated by *Rubus ulmifolius*, *Fraxinus excelsior*, *Cotoneaster franchetii*, *Robinia pseudoacacia* and *Ligustrum sinense*. In Jáuregui, the sampling area (3 ha) was located in the Nautical Club El Timón and dominant tree species were *Casuarina* sp., *Eucalyptus* sp., *Pinus* sp., *Populus* sp., *Quercus* sp., *Tilia* sp., *Gleditsia triacanthos*, *Juglans regia*, *Ligustrum lucidum*, *Melia azederach* and *Morus alba*.

Faeces analysis

We collected squirrel faeces to describe diet composition using microhistological analysis. Sampling in La Cumbrecita was between October 2006 and August 2007 and in Jáuregui, between August 2004 and July 2005. Faeces were collected during 3–6 days per month at 15 locations in each site. Each collection point was 1 m^2–2 m^2 and consisted of a permanent table (in Jáuregui) or a large rock (in La Cumbrecita) under high arboreal cover, where movement of squirrels was commonly observed in preliminary surveys. At the beginning of each sampling period, we carefully cleaned collection points as described in Bobadilla et al. (2016). Squirrel faeces were identified in the field based on their size, color and shape, and subsequently in the laboratory by microscopic inspection of their rugosity and the presence of hairs of red-bellied squirrel as described by Fasola et al. (2005). All faeces collected at one collection point in a given month were pooled into a sample. Each sample was submerged in distilled water for 30 min to facilitate pellet disintegration and then filtered to retain fragments >500 mm. The retained sample fraction was carefully inspected under a 10× binocular magnifying glass to isolate both whole and damaged seeds, which were later identified by comparison with a reference collection using an optical microscope. Each sample was processed according to the method used by Williams (1969) and modified by Latour and Pelliza-Sbriller (1981). For each sample, 20 microscopic fields were examined to identify all the epidermic fragments contained at 40× magnification. We compared fragments with a reference collection of epidermic tissues of bark, bracts, flowers, fruits, leaves, and seeds of trees, bushes, epiphytic and climbing plants present in both study sites, following Dacar and Giannoni (2001). Due to high similarity among tissues of some species, the material was identified at genus level. We recorded the presence of all plant species in each sample and identified which part of the plant had been consumed, as well as all other material belonging to animals or fungi. We calculated relative frequencies for each item (mean number of fields where each item was recorded per sample). We analysed differences in items consumed among seasons in each site using a chi-square test of homogeneity (Zar, 2010).

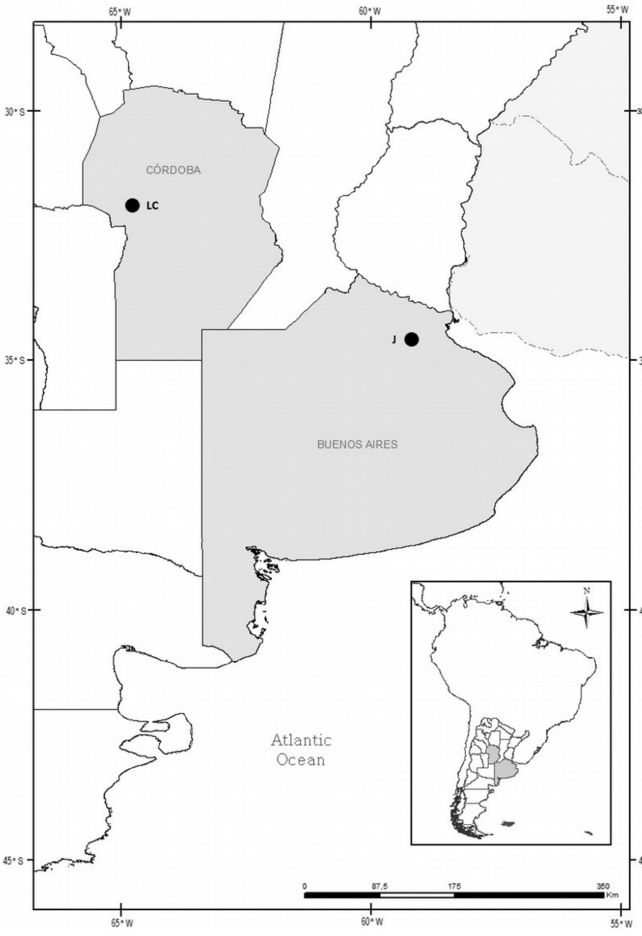

Figure 1 – Location of the two study sites (LC: La Cumbrecita, J: Jáuregui) in Argentina.

Behavioural observations

We conducted behavioural observations to describe foraging behaviour in both study sites. In La Cumbrecita, we conducted observations monthly between October 2006 and July 2007, throughout one complete day from dawn until sunset (61 h recording squirrel activity, 240 h total observation time). In Jáuregui, we conducted observations in April, May, August and September 2004, from 9:00 to 17:00 h (15 h recording squirrel activity, 29 h total observation time). We conducted focal sampling with continuous recording (Martin et al., 1993), using binoculars (8×32 mm, 12×50 mm and 20×60 mm) and telescope (15–60×60 mm) when necessary. Each observation period on a single animal lasted a maximum of 1 hour (Bertolino et al., 2004) and was ended when the focal animal was not observed for 5 minutes. At that time, the observer searched for a new squirrel >60 m away walking in the opposite direction to the direction the previous squirrel had moved, to reduce the chance of recording the same individual.

We recorded activities associated with food acquisition and consumption. When squirrels were feeding, we identified species (or taxonomic group) and items (e.g. bark, flower, fruit, leaf, seed) consumed. The female and male cones of coniferous species were included in the item "fruits and seeds" and "flowers and cones", respectively. We calculated the percentage of time devoted to feeding activities and to the consumption of each item seasonally. To evaluate differences among items consumed in each season, we performed a Test for Differences for More than Two Proportions (Tests DMTP, Zar, 2010) and a Test for Differences for Two Proportions (DTP, Zar, 2010), using the number of times that squirrels were observed consuming each item. We used post hoc Tukey comparisons when needed.

Diet selection

We sampled tree and shrub abundance in La Cumbrecita to estimate the availability of the various species used as food sources. In January 2007, we placed three transects (50×10 m) >30 m apart in each sampling area to record the number of shrubs (>1 m height) and trees (>2 m height) of each species. Saplings and herbaceous vegetation were not recorded due to the highly arboreal habits of these squirrels. Taxonomic identification of trees and shrubs followed Dimitri and Parodi (1987) and Instituto de Botánica Darwinion (2017). We evaluated diet selection using the Ivlev Electivity index (EI, Gras and Saint-Jean, 1982) using behavioural and faeces data. EI values range from -1 to 1, with positive selection of plant species for EI values >0.5, rejection for EI values <-0.5, and consumption in accordance to availability for EI values from -0.5 to 0.5.

Endo- and epizoochoric dispersal of exotic plants

We evaluated the germination potential of the seeds found in the faeces collected in La Cumbrecita. All unbroken seeds were placed in Petri dishes on filter paper moistened with distilled water and incubated in a germination chamber (22 °C, 12 h light / 12 h darkness) throughout one month (Baskin and Baskin, 2014). Protrusion of the radicle was the criterion used to indicate seed germination.

Also, given that squirrels can be epizoochoric dispersers (Xiao et al., 2009), we recorded caching and hoarding of fruits or seeds while we made behavioural observations.

Results

Faeces analysis

Squirrel faeces contained remains of trees and shrubs and also ferns, bryophytes, lichens, fungus, invertebrates, and traces of egg shells and feathers. Consumption of food items differed among seasons in both sites (La Cumbrecita: $\chi^2=369$, df=18, $p<0.0001$; Jáuregui: $\chi^2=42$, df=12, $p<0.0001$); fruits and seeds represented the bulk of the diet in all seasons (La Cumbrecita: 65–84%; Jáuregui: 44–66%) (Fig. 2). Squirrels consumed items of several species of trees and shrubs (La Cumbrecita: 16 species; Jáuregui: 13 species). All species were exotic except for one tree species in La Cumbrecita (*Polylepis australis*). Bark consumption was recorded in all seasons (La Cumbrecita: 2–5%; Jáuregui: 4–13%) and included the genus *Cedrus*, *Cupressus*, *Fraxinus*, *Polylepis*, *Prunus* and *Robinia* in the first site and *Eucaliptus*, *Ligustrum*, *Melia*, *Morus*, *Pinus* and *Platanus* in the second site. In both sites only a few species dominated the diet; in La Cumbrecita the most frequent species in the diet were *Cupressus* sp. (41.3%), *Cotoneaster* sp. (10.2%), and *Pyracantha* sp. (5.8%) while in Jáuregui the most frequent species were *L. lucidum* (15.0%) and *M. azederach* (13.8%).

Behavioural observations

We observed squirrel activity throughout the year in La Cumbrecita (445 bouts of 1–60 minutes each that yielded 61 hours of effective observation time) and in autumn and winter in Jáuregui (55 activity bouts of 2–61 minutes, 15 hours of effective observation time). Time devoted to feeding represented 31–55% of observation time in La Cumbrecita and 49–73% in Jáuregui. Squirrels mainly fed on tree branches; locomotion was mostly associated with searching for food and accounted for 33–41% of observation time in La Cumbrecita and 18–19% in Jáuregui.

We observed consumption of parts of trees and shrubs, epiphytes and climbing plants, invertebrates and lichens. The proportion of items consumed in each season differed; fruits and seeds represented the bulk of the diet in all seasons (La Cumbrecita: 55±16%, spring: $\chi^2=169.2$, df=3, $p<0.0001$, summer: $\chi^2=126.2$, df=3, $p<0.0001$, autumn: $\chi^2=97.0$, df=3, $p<0.0001$, winter: $\chi^2=152.5$, df=3, $p<0.0001$; Jáuregui: 72±17%, autumn: $\chi^2=18.7$, df=1, $p=0.0003$, winter: $\chi^2=25.0$, df=1, $p<0.0001$, Fig. 2). In La Cumbrecita we recorded an increase of time devoted to eating leaves in winter ($\chi^2=105.2$, df=3, $p<0.0001$), other items (principally invertebrates) in autumn ($\chi^2=81.3$, df=3, $p<0.0001$), flowers in spring ($\chi^2=111.0$, df=3, $p<0.0001$), and bark in summer ($\chi^2=97.0$, df=3, $p<0.0001$); however, we did not find differences in fruit and seed consumption among seasons ($\chi^2=6.2$, df=3, $p=0.1006$). In Jáuregui we did not observe bark consumption in winter, and we found no differences in consumption of fruits and seeds ($\chi^2=0.17$, df=1, $p=0.2498$), leaves ($\chi^2=0.12$, df=1, $p=0.2676$), or other items ($\chi^2=0.09$, df=1, $p=0.3745$). Squirrels were observed consuming items of several species of trees and shrubs (La Cumbrecita: 23 species; Jáuregui: 8 species), all species were exotic. Bark consumption was observed in all seasons in La Cumbrecita (4–7%) and included the genus *Betula*, *Cupressus*, *Eucaliptus*, *Platanus*, *Populus*, *Prunus*, *Robinia* and *Salix*; in Jáuregui bark consumption was observed only in autumn (6%) and included *Ligustrum* and *Melia*. Only a few species dominated the diet in both sites; in La Cumbrecita, feeding on *Cupressus* sp., *Quercus robur*, *Q. palustris* and *Cotoneaster glaucophillus* accounted for 39% of foraging time observed throughout the year while in Jáuregui *M. azederach* and *J. regia* were the most consumed species (73% of foraging time). Squirrels searched for food on

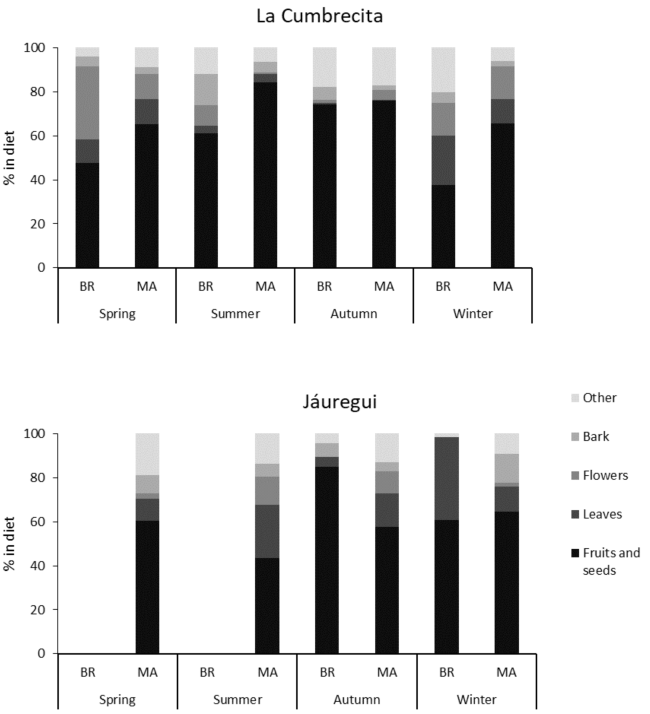

Figure 2 – Diet composition in La Cumbrecita and Jáuregui sites based on behavioural records (BR) and microhistological analysis of faeces (MA). Bars show the percentage of each item in the diet per season.

trees and shrubs but they also gathered food available on the ground (e.g., dropped acorns outside fruit season) that was usually carried to eat on tree/shrub branches.

Diet selection

The electivity index using faeces and behavioural data in La Cumbrecita indicated that selection of the species and items consumed varied according to their availability in terms of the relative abundance of each species and their phenology throughout the year (Tab. 1). Taking into account both data sources, 16 out of the 25 species of trees and shrubs consumed by squirrels (low shrubs, ferns, epiphytic and climbing plants were not analysed) were positively selected by squirrels in at least one season. Squirrels selected a maximum of 4–5 species of trees or shrubs per season, but no species was selected throughout the year. Squirrels mainly selected trees with fruits and seeds, such as conifers, cherry trees, linden trees, and oaks. Only two shrubs were positively selected (*C. glaucophylus* and *Pyracantha angustifolia*); in both cases selection occurred in winter when squirrels consumed their fruits.

Endo- and epizoochoric dispersal of exotic plants

We found entire seeds of three tree species in squirrel faeces in La Cumbrecita: *Cupressus* sp. (n=1 seed), *Pyracantha* sp. (n=3), and *Betula pendula* (n=76). All seeds were sown for 30 days in a germination chamber but no germination was recorded.

We observed food caching in La Cumbrecita but not in Jáuregui. Squirrels transported and hid acorns (*Quercus* sp.) in summer (n=6), autumn (n=6), and winter (n=1), and walnuts (*J. regia*) in summer (n=1) and autumn (n=2). Only one acorn and one walnut were presumably immature. Squirrels gathered the fruits from the mother plant and transported them for distances between 50 m and over 150 m. Fruits were hidden in tree holes and forks but also in abandoned nests (n=1), in vines (*Hedera helix*, n=1) or epiphytes (*Tillandsia capillaris*, n=2), always >1 m height. Also, we observed twice the loss of acorns that fell to the ground during transport, i.e. when squirrels were walking and/or running on branches with the fruit in their mouth.

Discussion

In accordance with our prediction, red-bellied squirrels fed on a variety of items and species although fruits and seeds were their main food items throughout the year. Feeding activity occurred mainly on trees and squirrels were rarely observed on the ground, as also described for this species in Taiwan (Chou et al., 2011) and Japan (Setoguchi, 1990), and for the congeneric Finlayson's squirrel introduced in Italy (Bertolino et al., 2004). Previous descriptions of the diet of red-bellied squirrels conducted both in native and non-native areas also indicated that their diet was primarily based on plant matter, mostly fruits and seeds, of a wide range of species (Tab. 2 and references therein). However, we recorded a larger number of food items and plant species consumed by this species than previous studies (Tab. 2). This could be explained by the combination of data obtained from behavioural observations and faecal analysis that allowed a more complete description of the diet given that limitations of each technique could be compensated by the other. Some items and species were only detected by one method. For example, in La Cumbrecita we observed bark consumption of *Eucaliptus cinerea* that had low density in the area and we identified fruits of *Rosa rubiginosa* in faeces collected in spring, though consumption of these fruits was not observed.

Table 1 – Diet selection of red-bellied squirrels based on Ivlev Electivity index (EI), calculated using data on the consumption of tree and shrub species obtained by behavioural and faeces analysis in La Cumbrecita. Positive selection (EI>0.5) is shown in bold and rejection (EI<-0.5) in italics. Items consumed of each species are indicated in parenthesis (Fr=fruits and seeds, L=leaves and/or buds, Fl=flowers, B=bark and/or sap). Shaded cells indicate plant phenology (white: no leaves, flowers and fruits; light grey: only leaves; darker shades of grey indicate leaves and fruits, leaves and flowers, and dark grey indicates leaves, flowers and fruits). Some items were collected by squirrels from the ground outside their production period. Due to high similarity among tissues in microhistological analysis, some species were identified at genus level.

	Behavioural analysis				**Faeces analysis**			
Species	**Spring**	**Summer**	**Autumn**	**Winter**	**Spring**	**Summer**	**Autumn**	**Winter**
Betula pendula	*-1*	-0.45 (Fr)	*-0.6 (B)*	-0.28 (B)	0.16 (Fr)	**0.86 (Fr)**	-0.15 (Fr)	0.17 (L)**
Cedrus deodara	*-1*	*-1*	-0.16 (Fr)	*-1*	*-1*	*-1*	**0.56 (Fr-B)**	0.42 (Fl)
Cotoneaster franchetii	*-1*	*-0.66 (Fr-Fl)*	*-0.55 (Fr)*	*-0.55 (Fr)*				
Cotoneaster glaucophyllus	*-1*	-0.13 (Fr-Fl)	-0.13 (Fr)	**0.7 (Fr)**				
Cotoneaster sp.					-0.03 (Fr)	-0.32 (Fr)	-0.02 (Fr)	0.12 (Fr)
Crataegus monogyna	*-1*	-0.34 (Fr)	*-1*	*-1*	*-1*	0.31 (Fr)	-0.47 (Fr)	*-1*
Cupressus sp.	-0.01 (Fr)	0.02 (Fr)	**0.69 (Fr-B)**	**0.69 (Fr-Fl)**	0.16 (Fr-Fl-L)	0.13 (Fr-L)	0.18 (Fr-Fl-B)	**0.77 (Fr-Fl-L)**
Eucalyptus cinerea*			**1 (B)**					
Fraxinus excelsior	*-1*	*-1*	*-1*	*-0.73 (L)***	*-1*	*-1*	*-0.74 (B)*	*-1*
Juglans regia	*-1*	**0.57 (Fr-L)**	0.23 (Fr)	*-1*	*-1*	-0.4 (Fr)	-0.39 (Fr)	*-1*
Ligustrum sinense	*-1*	*-0.63 (Fr)*	*-0.96 (Fr)*	*-0.96 (Fr)*	*-1*	*-1*	*-1*	0.16 (Fr-L)
Pinus sp.	*-1*	*-1*	*-1*	-0.34 (Fr)	*-1 (Fr)*	0.23 (Fr)	0.29 (Fr)	*-1*
Platanus orientalis	*-1*	0.19 (B)	*-1*	**0.97 (L)****				
Populus canadensis	**0.73 (B)**	**0.89 (B)**	*-1*	**0.95 (Fl)**				
Polylepis australis*								**1 (B)**
Prunus avium	-0.05 (Fr)	-0.27 (B)	*-0.88 (B)*	-0.46 (B)	**0.79 (Fr)**	**0.83 (Fr)**	*-1*	-0.4 (B)
Prunus cerasifera	**0.86 (Fr)**	*-1*	*-1*	*-1*				
Prunus domestica*				**1 (Fl)**				
Pyracantha angustifolia	*-1*	*-1*	*-1*	-0.44 (Fr)	-0.36 (Fr)	*-1*	-0.31 (Fr)	**0.94 (Fr)**
Quercus palustris	*-1*	0 (Fr)	**0.99 (Fr)**	**0.99 (Fr-L)**				
Quercus robur	*-1*	**0.97 (Fr)**	**0.97 (Fr)**	-0.05 (Fr-L)				
Quercus sp.					-0.05 (Fr)	**0.93 (Fr)**	**0.95 (Fr)**	**0.97 (Fr)**
Robinia pseudoacacia	**0.56 (Fl-L)**	-0.43 (Fr-L)	*-1 (B)*	*-1*	*-0.72 (Fl-B)*	*-1*	*-0.63 (B)*	*-1*
Rosa rubiginosa					-0.33 (Fr)	*-1*	*-1*	*-1*
Rubus ulmifolius	*-1*	*-0.9 (Fr)*	*-1*	*-1*	*-0.8 (Fr)*	*-0.86 (Fr)*	*-1*	*-1*
Salix alba	0 (B)	0.27 (B)	0.43 (B)	-0.11 (B)				
Tilia moltkei	*-1*	**0.98 (Fr)**	**0.99 (Fr)**	*-1*				

* species with low density and not found in the vegetation survey.
** consumption of winter buds.

Table 2 – Number of plant species and food items (indicating either presence or the number of different species identified in the diet for that item) described in the diet of red-bellied squirrels using different analytical methods in studies conducted both in native (N) and non-native (NN) habitats.

Study site	Species consumed	Fruits and/or seeds	Flowers	Bark and/or sap	Leaves	Buds	Fungi	Invertebrates	Lichens	Mosses	Hepaticophites	Egg shells and feathers	Method	Reference
La Cumbrecita, Argentina (NN)	28	18	9	11	9	7	yes	yes	yes	yes	yes	yes	Observations and faeces analysis	This study
Jáuregui, Argentina (NN)	13	13	5	7	8	5	yes	yes					Observations and faeces analysis	This study
Tomogashima Island, Japan (NN)	36	31	13	23	23	yes		yes					Observations	Setoguchi (1990)
Kamakura, Japan (NN)	31	28	13	11			yes	yes					Observations	Tamura et al. (1989)
Kien-ting, Taiwan (N)	30	27	9	2	1		yes	yes					Observations	Tamura et al. (1989)
Taiwan (N)	20	17	8		6		yes						Observations	Chou et al. (1985)
Sichuan, China (N)	23	19	2	3		1							Observations and stomach analysis	Sun et al. (2012)
Guangxi, China (N)	7	7	6	4	6	6		yes		yes			Observations	Yuan (2011)

In agreement with our findings, Setoguchi (1990) stated that although several species and items were consumed, only a few dominated the diet of red-bellied squirrels. Selection of food items and plant species varied between sites and among seasons, in support of our prediction that squirrels would select food resources according to their availability. Previous studies have also described diet variation related to seasonal food availability (see references in Tab. 2), all of which indicate opportunistic food choice and foraging plasticity. For example, although conifers had fruits throughout the year, these species were selected only in autumn and winter, when availability of other fruits decreased. Food resources were obtained principally from exotic trees and shrubs given that most plant species in our study sites were exotic. However, although native food items were found in low proportion (e.g. bark of native tree species, epiphytic plants, ferns, fungus, lichens, eggs and invertebrates), a potential negative impact to the recipient community or to particular species cannot be discarded (Aprile and Chicco, 1999; Guichón et al., 2005; Messetta et al., 2015). Given that their diet varies according to food availability in the invaded community, the squirrel's impact may change in novel areas with different species composition and species susceptibility. In La Cumbrecita, a village located near to Pampa de Achala that is a region of endemic flora and fauna, we found bark remains of *Polylepis australis*, a native vulnerable tree (Renison et al., 2013). Feeding plasticity in combination with their ability to consume novel foods (only three shrubs — *C. franchetii*, *C. glaucophyllus* and *L. sinense* — in La Cumbrecita, and two shrubs and two trees — *Pyracantha atalantioides*, *L. sinense*, *L. lucidum* and *M. azedarach* — in Jáuregui share the same native range with red-bellied squirrels), suggest a high capacity of this species to establish itself in natural and modified habitats.

Tree squirrels are distributed from tropical to subarctic forests and fruits compose the largest proportion of the diet of most species (Thorington et al., 2012). Extensive seed eating characterises the diet of red-bellied squirrels both in native and introduced ranges but also their role as seed dispersers has been reported through seed hoarding and epi– and endozoochory (Corlett, 1998; Xiao et al., 2009; Zhou et al., 2013; Bobadilla et al., 2016). However, it is still not clear how widespread these behaviours are, what species are involved and how new interactions may develop in novel, invaded communities. For example, hoarding by this tree squirrel has not been observed in areas where it was introduced in Japan (Setoguchi, 1990), although in its native range it is considered a key scatter-hoarder for the dispersal of large seeds (Xiao et al., 2009; Chou et al., 2011). Occasional observation of squirrels carrying and hiding nuts and acorns was recorded in La Cumbrecita but not in Jáuregui. This difference could be due to the shorter observation sampling period in Jáuregui (i.e. we missed detecting hoarding activity) or it could be related to differences in climate and food availability between sites (i.e. harder winters with snow accumulation in La Cumbrecita, where food storage could be vital). Hoarding behaviour may contribute to plant dispersal if seeds are lost during transport (this was observed in La Cumbrecita) or not retrieved from hidden sites. Viable seeds may also be deposited in suitable conditions far from the parental plant by endozoochoric dispersers. No germination was recorded in seeds extracted from faeces collected in La Cumbrecita in this study; however, the non-germination of *Cupressus* and *Betula* could be due to the physiological dormancy of these seeds (Baskin and Baskin, 2014). Nevertheless, we did observe germination of digested seeds corresponding to two exotic species (*Morus alba* and *Casuarina casuarina*) in a previous study conducted in the Pampas region (Bobadilla et al., 2016; the Jáuregui site was included in this study). Squirrel-plant interactions in invaded communities still need more study given that their role as predators or dispersers of seeds may not only vary according to seed size (Bobadilla et al., 2016) but also according to food availability and climate conditions in the recipient community.

Red-bellied squirrels are considered harmful to productive systems mainly for their feeding habits that affect fruit production, storage of cereals in silos, and for their gnawing of pipes and cables that damage irrigation and cooling systems in cultivation and poultry farms (Guichón et al., 2005). However, the most evident impact of this species results from debarking of trees and its negative effect on plantations and natural forests in both invaded and native ranges (Tsui et al., 1982; Tamura and Ohara, 2005; Hori et al., 2006; Pedreira et al., 2017). Control of red-bellied squirrels have been pursued in different regions in response to damage in conifer plantations and urban parks (Kuo, 1982; Bertolino and Lurz, 2013; Adriaens et al., 2015). Bark-stripping by this species has been related to nutrition in order to get sugar from sweet sap or insects adhered to the bark, and also to the use of peeled bark for nest construction (Setoguchi, 1990; Tamura and Ohara, 2005; Chou et al., 2011). In this study we found bark remains in faecal samples and observed bark consumption of 17 trees and shrubs species. The capacity of red-bellied squirrels to forage on hard seeds and to gnaw and chew tough tree bark has been related to structural features of their craniodental morphology (Koyabu et al., 2009). These squirrels possess a greater mechanical development of the masseter and temporalis muscles for chewing, and a more robust zygomatic arch, compare to the Asian red-cheeked squirrel *Dremomys rufigenis* (Koyabu et al., 2009). Koyabu et al. (2009) proposed that these features could be associated with differentiation of dietary resources to diminish competition and enable sympatry with other arboreal squirrels in their native range. These craniodental traits could also be beneficial in invaded habitats to incorporate new items to their diet and have the plasticity to consume a wide range of food resources.

Palmer et al. (2007) stated that diverse food habits is one of the biological characteristics of tree squirrels that enable their success as invasive species. Feeding plasticity of red-bellied squirrels facilitates the occupation of new areas. This ecological trait together with their high reproductive potential and probability of establishment from few founding individuals, their innate appeal to humans and their ability to inhabit natural, modified and urbanised habitats (Bertolino, 2009; Bertolino and Lurz, 2013; Borgnia et al., 2013) should altogether be considered to analyse their invasive potential.

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