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Research Article

Gastro-intestinal helminths in the red-bellied squirrel introduced in Argentina: accidental acquisitions and lack of specific parasites

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Abstract

Introduced species may lose their natural parasites when invading a new habitat, may acquire new, local parasites or may introduce parasites from their native range. We studied the gastro-intestinal helminth fauna associated with the red-bellied squirrel *Callosciurus erythraeus* (Pallas, 1778) introduced in Argentina to evaluate its role as a host of either specific or acquired parasites in two invasion foci. We analyzed entire digestive tracts of 72 red-bellied squirrels captured in the main invasion focus (Luján, province of Buenos Aires) between February and May 2011, and in a secondary focus (Cañada de Gómez, province of Santa Fe) in December 2008. We only found two nematode specimens: an adult male belonging to the genus *Pterygodermatites* (*Paucipectines*) Quentin, 1969 and another adult male belonging to the genus *Stilestrongylus* (Freitas, Lent and Almeida, 1973). None of these genera were previously listed for the red-bellied squirrel in introduced areas, but a species of the genus *Pterygodermatites* was previously reported for this squirrel in its native habitat. These results indicate that, to date, the red-bellied squirrel in Argentina is accidentally parasitised by nematodes acquired in its new environment and has no specific gastro-intestinal helminths. This could be related with a "founder effect" and/or the lack of sciurid rodents that prevent the red-bellied squirrel to be colonized by pre-adapted helminth taxa. Other factors that may play a role are the small number of mammals with arboreal habits and some "encounter barriers" in the new environment that prevent the acquisition of helminths with a wide host spectrum.

Introduction

Successful introduced species may show a pattern of low diversity and prevalence of parasites in the new environment (Torchin et al., 2003; Torchin and Mitchell, 2004). This pattern is usually linked with the loss of native specific parasites (Keane and Crawley, 2002; Torchin et al., 2003; Torchin and Mitchell, 2004), and with the low acquisition of new parasites from co-inhabiting hosts in the invaded area (Torchin and Mitchell, 2004; Pisanu et al., 2009). The acquisition of parasites in the new environment will depend in part, on the ability of native parasites to develop in a wide spectrum of hosts and/or if they are parasites of hosts phylogenetically related to the introduced host (Asakawa, 2005; Pisanu et al., 2009). The potential advantage of introduced species over native species due to the benefit caused by the loss of their natural enemies may enhance their success in the invasion process as stated by the Enemy Release Hypothesis (Torchin et al., 2003; Torchin and Mitchell, 2004). At the same time, introduced species can also introduce parasites from their native range and in some cases transfer them to native hosts (Smith and Carpenter, 2006; Taraschewski, 2006; Bordes et al., 2007).

The Asiatic red-bellied squirrel, *Callosciurus erythraeus* (Pallas, 1778), was intentionally introduced into Japan, Argentina, and three European countries (Belgium, France, and The Netherlands) (Lurz et al., 2013). Most squirrel introductions are intentional and related to pet trade (Palmer et al., 2007; Bertolino, 2009), which was the case of the 10 red-bellied squirrels introduced in Argentina in 1970 that had been acquired in a pet shop in The Netherlands and taken to a large ranch in the Pampas. This arboreal squirrel successfully established in rural and urban areas of the Pampas (Guichón et al., 2005; Guichón and Doncaster, 2008), and has already settled in other sites of three Argentinean provinces as a result of repeated translocations and illegal pet trade (Benitez et al., 2013).

Several parasitological studies on different introduced species belonging to different taxa have assessed their role as new hosts in the new environment, finding poorer parasites communities in the new environment in relation to the native range of the analysed species (Marr et al., 2008; Torchin et al., 2003; Ross et al., 2010). Introduced squirrels such as *Tamias sibiricus* Laxmann, 1769 in France were found to introduce helminth fauna in the invaded area, while they may also acquire other helminths from co-inhabiting hosts, especially if helminth parasites have a large spectrum of host species with similar behaviour, life-history and habitats (Pisanu et al., 2007, 2009). Recently, a common species of nematode, *Strongyloides robustus* Chandler, 1942, parasite of North American Eastern grey squirrels *Sciurus carolinensis* Gmelin, 1788, was found in two red squirrels *Sciurus vulgaris* Linnaeus, 1758 captured in Italy (Continental Region), suggesting that this nematode species may spillover from the introduced grey squirrel towards the native red squirrel (Romeo et al., 2013, 2014). Moreover, the grey squirrel acquired local parasites in Italy but the number of parasites acquired did not compensate the number of parasite species lost from their native range (Romeo et al., 2014).

Although there are no helminthological studies conducted on the red-bellied squirrel in Argentina, helminth fauna described for this spe-

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cies in other introduced areas comprises both native specific parasites introduced with the founders (Asakawa, 2005; Sato et al., 2007), and acquired parasites from co-inhabiting hosts (Dozières et al., 2010). The aim of this study was to describe the gastro-intestinal helminths fauna associated with the red-bellied squirrel in Argentina in order to evaluate its role as a host of specific or acquired parasites within the invaded community. We will consider specific parasite species those species that are characteristic of sciurid rodents and/or have been reported in the native range of the red-bellied squirrel.

Materials and methods

We analyzed the entire digestive tracts of 72 red-bellied squirrels captured during control campaigns conducted in two invasion foci in Argentina. Between February and May 2011, we collected 40 visceral samples of squirrels (mature:immature ♀: 9:13; mature:immature ♂: 8:10) captured in Luján, province of Buenos Aires (34°33′ S, 59°7′ W), which is the main invasion focus in the country, originated in 1970. In December 2008, we obtained 32 visceral samples of squirrels (mature:immature ♀: 13:3; mature:immature ♂: 14:2) in a secondary invasion focus in Cañada de Gómez, province of Santa Fe (32°49′ S, 61°20′ W), that originated in 1999 by the release of squirrels translocated from the main focus in Luján, located 285 km away. Estimated density of squirrels in Luján is at least three times higher than in Cañada de Gómez; 15.3 squirrel/ha and 4.86 squirrel/ha, respectively (Benitez et al., 2013). Arboreal vegetation dominated by exotic species is highly fragmented in both sites. Cañada de Gómez is surrounded mainly by a rural landscape with few woodland patches, and Luján is inserted in a rural/urban landscape with more woodland patches than Cañada de Gómez. In both study sites, woodland patches alternate with fields and crops (Benitez et al., 2013). Live-trapped squirrels were euthanized following animal handling procedures approved by international guidelines (AVMA, 2007) and the entire digestive tracts were removed and fixed in 10% formalin. For helminths prospection, complete gut walls and lumen from esophagus to rectum were dissected and analyzed using a stereomicroscope. The nematodes were preserved in 70% ethanol and cleared in temporary mounts of glycerine alcohol for identification. Drawings of worms and of the transverse section of the pattern of longitudinal ridges (synlophe) were done under a microscope Olympus BX 51 equipped with a *camera lucida*.

Results

Two nematodes belonging to two different families were found in two red-bellied squirrels captured in the main invasion focus in Luján (n=40), while no helminths were found in the squirrels captured in the secondary focus in Cañada de Gómez (n=32). One adult male belonging to the family Rictulariidae (Nematoda: Spirurida) was found in a male squirrel. The specimen studied had features that corresponded to the genus *Pterygodermatites* Wedl, 1861, given its denticulate, hexagonal oral opening, large buccal cavity with teeth, the presence of 38 pairs of combs and cuticular spines distributed in two rows on the ventral surface of the body and the presence of four fan-like cuticular processes anterior to the cloacal opening (Fig. 1; Tab. 1). In addition, the apical oral opening allows us to locate this specimen within the subgenus *Paucipectines* Quentin, 1969. The other intestinal parasite was an adult male belonging to the family Heligmonellidae (Nematoda: Strongylida: Trichostrongylina: Nippostrongylinae) found in a female squirrel. This specimen had a synlophe with 24 spines with greater number of ridges dorsally, asymmetrical copulatory bursa with externodorsal rays differing in size, and hypertrophied genital cone (Fig. 1), which are all features belonging to the genus *Stilestrongylus* (Freitas, Lent and Almeida, 1973) (Durette-Desset 1971 in Pérez-Ponce de Leon et al., 2000) (Tab. 2). The finding of a single specimen of each nematode did not allow us their identification to a species level.

Discussion

The results obtained in this study indicate that, to date, the red-bellied squirrel in Argentina is accidentally parasitised by nematodes acquired in the new environment and have no specific gastro-intestinal helminth parasites. The two parasite genera reported in this study, *Stilestrongylus* and *Pterygodermatites*, have not been previously listed for the red-

Table 1 – Characteristics of two species of *Pterygodermatites* subgenus *Paucipectines* found in co-inhabiting host mammals, native to the Pampean Region, and of the specimen found in the red-bellied squirrel in this study.

Characteristics	***Pterygodermatites (P.) azarai* (Sutton, 1984)**	***Pterygodermatites (P.) kozeki* (Navone, 1989)**	***Pterygodermatites* sp. (present study)**
Host	*Akodon azarae*	*Didelphis albiventris*	*Callosciurus erythraeus*
Total body length	2.44 mm (1.66–2.49)	2.14 mm to 2.86 mm	2.30 mm
Maximum width	265 µm (166–232)	221 µm to 260 µm	163 µm
Anterior end – nerv ring distance	156 µm	150 µm to 165 µm	150 µm
Total length of esophagus	730 µm (480–780)	765 µm to 855 µm	710 µm
Large spicule length	84 µm (70–104)	24 µm to 255 µm (subequals)	85 µm
Small spicule length	56 µm (48–60)		45 µm
Number of pairs of cuticular combs and spines	40 (39–43)	41	38
Number of precloacal unpaired fan-like cuticular processes	3 or 4	1	4

Table 2 – Characteristics of two species of *Stilestrongylus* found in co-inhabiting host mammals, native to the Pampean Region, and of the specimen found in the red-bellied squirrel in this study.

Characteristics	***Stilestrongylus azarai* (Durette-Desset and Sutton, 1985)**	***Stilestrongylus aureus* (Durette-Desset and Sutton, 1985)**	***Stilestrongylus* sp. (present study)**
Host	*Akodon azarae*	*Reithrodon auritus*	*Callosciurus erythraeus*
Copulatory bursa shape	Asymmetrical	Asymmetrical	Asymmetrical
Total body length	2.85 mm	3.9 mm	2.40 mm
Maximum width	70 µm	100 µm	50 µm
Total length of esophagus	340 µm	410 µm	175 µm
Distance anterior end – nerv ring	90 µm	200 µm	65 µm
Distance anterior end – deirids	180 µm	295 µm	93 µm
Spicules (subequals) length	410 µm	510 µm	220 µm
Gubernaculum	32 µm × 20 µm	20 µm × 20 µm	40 µm × 13 µm
Ridges of synlophe (middle line)	25	24	24

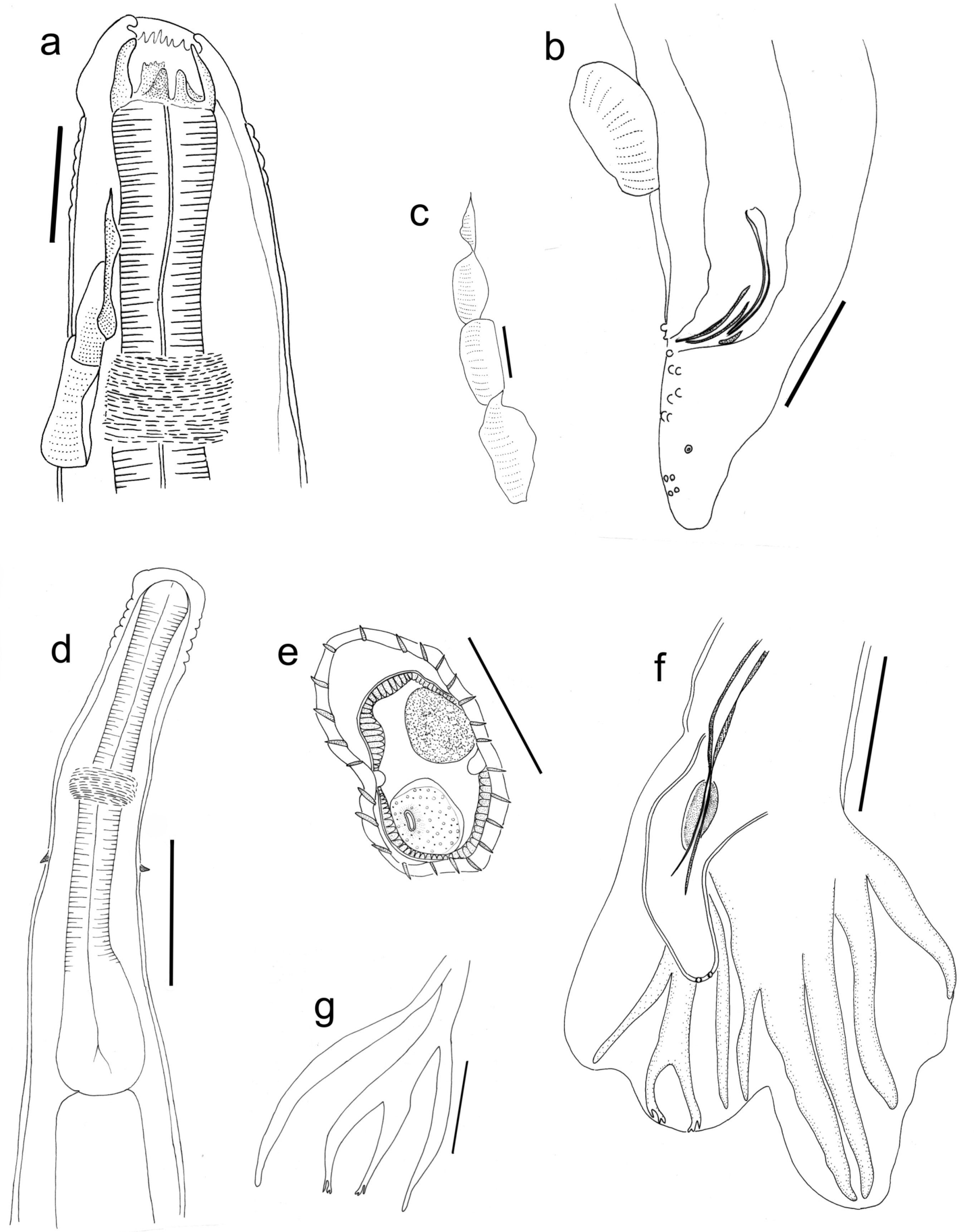

Figure 1 – a-c) *Pterygodermatites* sp. male: a) anterior portion showing the large buccal cavity, lateral view; b) posterior end lateral view, spicules, gubernaculum, papillae and fasmids, c) detail of the four fan-like cuticular processes anterior to the cloacal opening. d-g) *Stilestrongylus* sp. male: d) anterior portion, median view; e) synlophe, mid-body transversal cut; f) asymmetrical copulatory bursa lateral view, genital cone, spicules and gubernaculum. g) arrangement of the dorsal rays. Scale bars a,b,d,e,f,g = 50 µm; c = 60 µm.

Table 3 – Helminth parasites reported for *Callosciurus erythraeus* (*C. e.*) indicating the site of collection of the squirrel, its status regarding squirrel range distribution (native or introduced), and the relationship between the squirrel and the parasite species (specific or acquired parasite). We called specific parasites those species that are characteristic of sciurid rodents and/or have been reported in the native range of the red-bellied squirrel, while acquired parasites are species characteristic of other hosts and/or have not been reported in its native range.

Helminth species	Host species/subspecies	Collection site	Status	Parasite-host relationship	References
Nematode					
Strongylida					
Heligmosomidae					
Calypsostrongylus titasuthi Klis and Durette-Desset, 1976	*Callosciurus flavimanus*[1]	Thailand	Native	Specific	Kliks and Durette-Desset, 1976
Calypsostrongylus ogdeni Schmidt, Myers and Kuntz, 1967	*C. e. centralis*	Taiwan	Native	Specific	Schmidt et al., 1967
Brevistriata skrjabini (Schulz and Lubimov, 1932)	*C. e. centralis*	Taiwan	Native	Specific	Myers and Kuntz, 1964
	C. e. roberti	Taiwan	Native	Specific	Myers and Kuntz, 1964
	C. e. thaiwanensis	Taiwan	Native	Specific	Myers and Kuntz, 1964
Brevistriata sinensis Li, 1941	*C. e. castaneoventris*	China	Native	Specific	Li 1941 in Durette-Desset, 1970
	C. e. gordoni	China	Native	Specific	Yen 1973 in Lurz et al., 2013
Brevistriata callosciuri Supperer and Kutzer, 1963	*C. erythraeus*	Japan	Introduced	Specific	Matsudate et al., 2003; Asakawa, 2005
	C. e. ningpoensis	China	Native	Specific	Wang, 1981
Heligmonellidae					
Stilestrongylus sp.	*C. erythraeus*	Argentina	Introduced	Acquired	Present study
Trichostrongylidae					
Trichostrongylus columbriformis (Giles, 1852)	*C. e. michianus*	China	Native	Acquired[2]	Yen 1973 in Lurz et al., 2013
Spirurida					
Spiruridae					
Protospirura sp.	*C. e centralis*	Taiwan	Native	Acquired[3]	Myers and Kuntz, 1964
	C. e. roberti	Taiwan	Native	Acquired[3]	Myers and Kuntz, 1964
Spirocercidae					
Mastophorus sp.	*C. erythraeus*	Belgium	Introduced	Acquired[4]	Dozières et al., 2010
Rictulariidae					
Rictularia tani Hoeppli, 1929	*C. e. gordoni*	China	Native	Acquired[5]	Yen 1973 in Lurz et al., 2013
Pterygodermatites sp.	*C. erythraeus*	Argentina	Introduced	Acquired	Present study
Gongylonematidae					
Gongylonema neoplasticum Fibiger and Ditlevsen, 1914	*C. erythraeus*	Japan	Introduced	Acquired[6]	Asakawa, 2005
Rhabditida					
Oxyuridae					
Syphacia obvelata (Rudolphi, 1802)	*C. e. sub.*?	Taiwan	Native	Acquired[7]	Myers and Kuntz, 1964
Enterobius sp.	*C. e. roberti*	Taiwan	Native	Acquired[8]	Myers and Kuntz, 1964
Strongyloididae					
Strongyloides sp.	*C. erythraeus*	Japan	Introduced	Specific	Matsudate et al., 2003
Strongyloides callosciureus Sato, Torii, Une and Ooi, 2007	*C. erythraeus*	Japan	Introduced	Specific	Sato et al., 2007
Cestode					
Cyclophyllidae					
Hymenolepididae					
Hymenolepis sp.	*C. erythraeus*	France	Introduced	Acquired[4]	Dozières et al., 2010
Trematode					
Plagiorchiida					
Dicrocoellidae					
Zonorchis taiwanensis Fischthal and Kuntz, 1981	*C. e. centralis*	Taiwan	Native	Specific	Fischthal and Kuntz, 1981
Zonorchis callosciuri Nguyen Thi Le, 1968	*C. erythraeus*	Vietnam	Native	Specific	Fischthal and Kuntz, 1981

[1] Corresponds to *Callosciurus erythraeus taiwanensis* (Corbet and Hill, 1992).
[2] Cosmopolitan parasite of the small intestine of cattle and other ruminants (Anderson, 2000).
[3] Heteroxenous genus parasite, mostly found in rodents and carnivores (Anderson, 2000).
[4] Heteroxenous parasite. Accidentally acquired by consumption of an intermediate terrestrial insect host and by co-inhabiting with muroid rodents (Dozières et al., 2010).
[5] Corresponds to *Pterygodermatites* (*Mesopectines*) *tani* (Hoeppli, 1929), belongs to subgenus *Mesopectines*, parasites of rodents, carnivores and primates of Africa and Asia (Quentin, 1969).
[6] *Gongylonema* spp. are cosmopolitan spirurid nematodes that are common parasites of wild and domestic mammals and birds. Heteroxenous parasite. Accidentally acquired by consumption of an intermediary host insect (Sato et al., 2005; Dozières et al., 2010).
[7] Common parasitic nematode with a direct life cycle, inhabiting the cecum of feral domestic mice *Mus musculus domesticus* (Tattersall et al., 1994 in Pisanu et al., 2002) .
[8] Enterobiinae occurs in both Old World and New World Primates and rodents of the family Sciuridae (Hugot et al., 1995) but members of the genus *Enterobius* are found in catarrhine primates and Ethiopian Sciuridae (Anderson, 2000).

bellied squirrel in introduced areas, where squirrels are parasitised by four species of nematodes and one species of cestode (Tab. 3). Helminthological studies conducted in its native range reported two species of trematodes and 10 species of nematodes, one of which belongs to the genus *Pterygodermatites* (see *Rictularia tani* in Tab. 3). This species was found in *Callosciurus erythraeus gordini* from China. However while the male specimen *Pterygodermatides* found in this study has an apical oral opening, *Pterygodermatites tani* has a dorsal oral opening. This feature placed these specimens in different subgenera (*Paucipectines* and *Mesopectines* respectively) that differ in the range of host species and the geographical distribution (Quentin, 1969) (Tab. 3). The two genera of nematodes described in this study have been previously found in native mammals sympatric with the red-bellied squirrels in the invaded area (Navone and Suriano, 1992; Miño et al., 2012). None of the red-bellied squirrels examined in this study was found to host specific parasites. The lack of specific gastro-intestinal helminths parasitising this species in Argentina could be explained by its history of introduction (e.g. low number of founding hosts, animals bought in an European pet shop) which together with the aggregate distribution of parasites among hosts (Shaw et al., 1998), decreased the likelihood of introducing parasitised individuals. Our results did not allow us to assess whether these accidental acquisitions are linked with characteristics of the host population, but the fact that the nematodes were found only in squirrels captured in Luján (the main and older focus) could be related with the high population density achieve in this focus in relation to Cañada de Gómez and the time elapsed since their origin (Benitez et al., 2013).

At least five helminth species were found in *C. erythraeus* in introduced areas, two of which may have been acquired accidentally by the consumption of an intermediary insect host (e.g. cockroaches, fleas, mealworms, beetles) (Anderson, 2000), as occurred with *Gongylonema neoplasticum* Fibiger and Ditlevsen, 1914 and the also heteroxenous *Mastophorus* sp. (Dozières et al., 2010). Both parasites are usually associated with rodent hosts, mainly Murinae (Dozières et al., 2010). According to Asakawa (2005) and Sato et al. (2007), *Brevistriata callosciuri* Supperer and Kutzer, 1963 and *Strongyloides callosciureus* Sato et al., 2007 would have been introduced into Japan along with the founder squirrels (Tab. 3). The nematode genera associated to red-bellied squirrels in Argentina are usually found in native sigmodontine rodents and native marsupials (Navone and Suriano, 1992; Navone et al., 2010; Miño et al., 2012). In particular, the monoxenous genus *Stilestrongylus* parasitises cricetid rodents in Buenos Aires province (Durette-Desset and Sutton, 1985), being *Stilestrongylus* sp. the dominant nematode of the Pampean grassland mouse *Akodon azarae* Fischer, 1929 (Miño et al., 2012) (see Tab. 2). *A. azarae* is also parasitised, among others, by *Pterygodermatites* (*Paucipectines*) *azarai* (Sutton, 1984) and the cogeneric *P.* (*P.*) *kozeki* (Chabaud and Bain, 1981) is a parasite of the white-bellied opossum, *Didelphis albiventris* Lund, 1840 (Sutton, 1984; Navone, 1989; Navone and Suriano, 1992) (see Tab. 1). This nematode genus has also been found in several sciurid genera e.g. *Spermophilus*, *Eutamias*, *Sciurus* in North America (Lichtenfels, 1970; Ubelaker et al., 2010) and, as mentioned above, in *C. e. gordoni* in China (Lurz et al., 2013). *Pterygodermatites* is a heteroxenous genus, so the specimen could have been acquired by the consumption of an intermediate insect host (mainly dermapterans). The low acquisition of gastro-intestinal helminths parasites could be related to certain factors that may function as encounter barriers, which make the red-bellied squirrel not an easy target to be colonized, such as their highly arboreal habits and a mostly vegetarian diet mainly based on fruits and seeds (Aprile and Chicco, 1999; Lurz et al., 2013). Also, as there are no sympatric phylogenetically related mammals (sciurid rodents) in the invaded area, transmission of parasites and host switching are less probable because the likelihood of these processes increases whenever the new host is immunologically and physiologically similar to original hosts and have similar lifestyles (Poulin, 2004; Klimpel et al., 2007; Pisanu et al., 2009; Gozzi et al., 2013). In addition, the scarcity of mammalian species with arboreal habits in both sites may prevent the acquisition of more helminth species by red-bellied squirrels.

In conclusion, the red-bellied squirrel in Argentina is poorly parasitised with gastro-intestinal helminths in comparison with other sites of introduction (Sato et al., 2007; Dozières et al., 2010) and, also, compared with sympatric native mammals species (Navone and Suriano, 1992; Miño et al., 2012). These results are also in agreement with the low prevalence of arthropod parasites associated with this species in Argentina (Gozzi et al., 2013). Unfortunately, there is a lack of studies providing quantitative descriptors (e.g. prevalence, mean abundance) of populations of helminth parasites of the red-bellied squirrel in its native range. This fact together with the lack of reports of the parasitic load of this invasive species relative to its local competitors in other invaded areas, prevent further comparisons. Therefore, although we cannot confirm that the lack of specific parasites translates into an effective advantage for the red-bellied squirrel, these results suggest that an enemy release could be contributing to the success of the invasive squirrel in its new environment. As new introduced host-parasite associations are known to form progressively over time in the invaded range (Torchin and Mitchell, 2004; Poulin, 2007; Gendron et al., 2012), further long term studies should be done to provide new evidence about the accidental parasitism that today is taking place and its role on the invasion success of the red-bellied squirrel in Argentina.

References

Asakawa M., 2005. Perspectives of host–parasite relationships between rodents and nematodes in Japan. Mamm. Study. 30: S95–S99.

AVMA, 2007. American Veterinary Medical Association. Guidelines on Euthanasia. Available from http://www.avma.org/issues/animal_welfare/euthanasia.pdf [10 November 2011]

Anderson R.C., 2000. Nematodes Parasites of Vertebrates, their Development and Transmission. CAB International, Wallingford, UK.

Aprile G., Chicco D., 1999. Nueva especie exótica de mamífero en la Argentina: la ardilla de vientre rojo (*Callosciurus erythraeus*). Mastozool. Neotrop. 6(1): 7–14. [in Spanish]

Benitez V.V., Almada Chavez S., Gozzi A.C., Messetta M.L., Guichón M.L., 2013. Invasion status of Asiatic red-bellied squirrels in Argentina. Mamm. Biol. 78(2013): 164–170.

Bertolino S., 2009. Animal trade and non-indigenous species introduction: the world-wide spread of squirrels. Divers. Distrib. 15: 701–708.

Bordes F., Langand J., Feliu C., Morand S., 2007. Helminth communities of an introduced hare (*Lepus granatensis*) and a native hare (*Lepus europaeus*) in Southern France. J. Wildl. Dis. 43(4): 747–751.

Corbet G.B., Hill J.E., 1992. The Mammals of the Indomalayan Region: A Systematic Review. Oxford University Press, Oxford.

Dozières A., Pisanu B., Gerriet O., Lapeyre C., Stuyck J., Chapuis J.-L., 2010. Macroparasites of Pallas's squirrels (*Callosciurus erythraeus*) introduced into Europe. Vet. Parasitol. 172(2010): 172–176.

Durette-Desset M.C., 1970. *Brevistriata bergerardi*, noveau nématode heligmosome, parasite d'un écureuill de Corée. Bull. Mus. Natl. Hist. Nat. 42(2): 419–423. [in French]

Durette-Desset M.C., Sutton C.A., 1985. Contribución al conocimiento de la fauna parasitológica argentina X. Nematodes (Trichostrongyloidea) en *Akodon azarae* (Fischer) y *Reithrodon auritus* Fischer. Revista Mus. La Plata Sección Zoología. 14(151): 21–26.

Fischthal J.H., Kuntz R.E., 1981. Additional records of digenetic trematodes of mammals from Taiwan. Proc. Helm. Soc. Wash. 48(1): 71–79.

Gendron A.D., Marcogliese J.D., Thomas M., 2012. Invasive species are less parasitized than native competitors, but for how long? The case of the round goby in the Great Lakes-St. Lawrence Basin. Biol. Invasions 14: 367–384.

Gozzi A.C., Guichón M.L., Benitez V.V., Lareschi, M. 2013. Arthropod parasites of the red-bellied squirrel *Callosciurus erythraeus* introduced into Argentina. Med. Vet. Entomol. 27(2): 203–208.

Guichón M.L., Fasola L., Bello M., 2005. Expansión poblacional de una especie introducida en la Argentina: la ardilla de vientre rojo *Callosciurus erythraeus*. Mastozool. Neotrop. 12(2): 189–197. [in Spanish]

Guichón M.L., Doncaster C.P., 2008. Invasion dynamics of an introduced squirrel in Argentina. Ecography 31: 211–220.

Hugot J.-P., Gardner S.L., Morand S., 1995. The Enterobiinae subfam. nov. (Nematoda, Oxyurida) pinworm parasites of primates and rodents. Int. J. Parasitol. 26(2): 147–159.

Keane R.M., Crawley M.J., 2002. Exotic plant invasions and the enemy release hypothesis. TREE. 17(4): 164–170.

Kliks M., Durette-Desset M.C., 1976. Brevistriatinae (Nematoda: Heligmosomidae) II. Description de *Calypsostrongylus titasuthi* n. sp., parasite de *Callosciurus flavimanus* en Thailande. Bull. Mus. Natl. Hist. Nat. 270: 685–692. [in French]

Klimpel S., Förster M., Schmahl G., 2007. Parasites of two abundant sympatric rodent species in relation to host phylogeny and ecology. Parasitol. Res. 100: 867–875.

Lichtenfels J.R., 1970. Two New Species of *Pterygodermatites* (*Paucipectines*) Quentin, 1969 (Nematoda: Rictulariidae) with a Key to the Species from North American Rodents. Proc. Helm. Soc. Wash. 37(1): 94–101.

Lurz P.W.W., Hayssen V., Geissler K., Bertolino S., 2013. *Callosciurus erythraeus* (Rodentia: Sciuridae). Mamm. Species 45(902): 60–74.

Marr S.R., Mautz W.J., Hara A.H., 2008. Parasite loss and introduced species: a comparison of the parasites of the Puerto Rican tree frog, (*Eleutherodactylus coqui*), in its native and introduced ranges. Biol. Invasions 10: 1289–1298.

Matsudate H., Moyoshi Y., Tamura N., Murata K., Maruyama S., Kimura J., Nogami S., Maeda K., Fukumoto Y., Akasako R., Asakawa M., 2003. A survey of the parasitic

helminths of alien rodents (belly-banded squirrel *Callosciurus erythraeus* and nutria *Myocastor coypus*) in Japan. Jpn. J. Zoo. Wildl. Med. 8: 63–67.
Miño M.H., Rojas Herrera E.J., Notarnicola J., Robles M.R., Navone G.T., 2012. Diversity of the helminth community of the Pampean grassland mouse (*Akodon azarae*) on poultry farms in central Argentina. J. Helminth. 86(1): 46–53.
Myers J.B., Kuntz R.E., 1964. Nematode parasites form mammals taken on Taiwan (Formosa) and its Offshore Islands. Can. J. Zool. 42: 863–867.
Navone G.T., 1989. *Pterygodermatites* (*Paucipectines*) *kozeki* (Chabaud et Bain. 1981) n. comb., parásito de *Lestodelphys halli* Tate, 1934, *Didephis albiventris* L. y *Thylamis pusilla* (Desmarest) de la República Argentina. Anatomía y posición sistemática. Revista Ibérica de Parasitología 49(3): 219–226. [in Spanish]
Navone G.T., Suriano D.M., 1992. Species composition and seasonal dynamics of the helminth community parasitizing *Didelphis albiventris* (Marsupalia: Didelphidae) in savannas of central Argentina. Ecol. Austral. 2: 95–100.
Navone G., Lareschi M., Notarnicola J., 2010. Los roedores sigmodontinos y sus parásitos en la Región Pampeana. In: Polop J., Busch M., (Eds.). Biología y ecología de pequeños roedores en la Región Pampeana de Argentina. Enfoques y perspectivas, Universidad Nacional de Córdoba, Córdoba. 217–261. [in Spanish]
Palmer G.H., Koprowski J., Pernas T., 2007. Tree squirrels as invasive species: conservation and management implications. In: Witmer G.W., Pitt W.C., Fagerstone K.A., (Eds.). Managing Vertebrate Invasive Species: Proceedings of an International Symposium. USDA/APHIS/WS, National Wildlife Research Center, Fort Collins, CO. 273–282.
Pérez-Ponce de Leon G., Gardner S.L., Falcon-Ordaz J.J., 2000. Phylogenetic relationships among species of *Stylestrongylus* Freitas, Lent and Almeida, 1937 (Trichostrongyloidea: Helligmonellidae: Nippostrongylinae), parasites of Myomorph rodents (Rodentia: Muridae) in the Neotropics. J. Parasitol. 86(6): 1326–1335.
Pisanu B., Chapuis J.-L., Durette-Desset M.C., Morand S., 2002. Epizootiology of *Syphacia obvelata* from a Domestic Mouse Population on the Subantarctic Kerguelen Archipelago. J. Parasitol. 88(4): 645–649.
Pisanu B., Jerusalem C., Cindy Huchery C., Marmet J., Chapuis J.-L., 2007. Helminth fauna of the Siberian chipmunk, *Tamias sibiricus* Laxmann (Rodentia, Sciuridae) introduced in suburban French forests. Parasitol. Res. 100: 1375–1379.
Pisanu B., Lebailleux L., Chapuis J.-L., 2009. Why do Siberian chipmunks, *Tamias sibiricus* (Sciuridae) introduced in French forests acquired so few intestinal nematode species from native sympatric Murids? Parasitol. Res. 104: 709–714.
Poulin R., 2004. Macroecological patterns of species richness in parasite assemblages. Basic. App. Ecol. 5(2004): 423–434.
Poulin R., 2007. Host Specificity. In: Evolutionary Ecology of parasites, 2nd ed. Princeton University Press, New Jersey. 41–69.
Quentin J.C., 1969. Essai de classification des nematodes rictulaires. Mem. Mus. Natl. Hist. Nat. 54(2): 55–115. [in French]
Romeo C., Pisanu B., Ferrari N., Basset F., Tillon L., Wauters L.A., Martinoli A., Saino N., Chapuis J.-L., 2013. Macroparasite community of the Eurasian red squirrel (*Sciurus vulgaris*): poor species richness and diversity. Parasitol. Res. 112: 3527–3536.
Romeo C., Wauters L.A., Ferrari N., Lanfranchi P., Martinoli A., Pisanu B., Preatoni D.G., Saino N., 2014. Macroparasite fauna of alien grey squirrels (*Sciurus carolinensis*): composition, variability and implications for native species. PLoS ONE 9(2): e88002. doi:10.1371/journal.pone.0088002
Ross J.L., Ivanova E.S., Severns P.M., Wilson M.J., 2010. The role of parasite release in invasion of the USA by European slugs. Biol. Invasions. 12: 603–610.
Sato H., Une Y., Takada M., 2005. High incidence of the gullet worm, *Gongylonema pulchrum*, in a squirrel monkey colony in a zoological garden in Japan. Vet. Parasitol. 127(2): 131–137.
Sato H., Torii H., Une Ooi H.K., 2007. A new Rhabditoid nematode species in Asian Sciurids, distinct from *Strongyloides robustus* in north American Sciurids. J. Parasitol. 93: 1476–1486.
Schmidt B., Myers J., Kuntz R.E., 1967. Nematode Parasites of Oceanica. I. *Brevistriata sundasciuri* sp. n. and *Calypsostrongylus ogdeni* gen. et sp. n. (Heligmosomatidae: Longistriatinae) from Squirrels of Palawan and Taiwan. J. Parasitol. 53(3): 613–617.
Shaw D.J., Grenfell B.T., Dobson A.P., 1998. Patterns of macroparasite aggregation in wildlife host populations. Parasitology. 117: 597–610.
Smith K.F., Carpenter S.M., 2006. Potential spread of introduced black rat (*Rattus rattus*) parasites to endemic deer mice (*Peromyscus maniculatus*) on the California Channel Islands. Divers. Distrib. 12: 742–748.
Sutton C.A., 1984. Contribución al Conocimiento de la Fauna Parasitológica Argentina.XIII. Nuevos Nematodes de la Familia Rictulariidae. Neotropica. 30(84): 141–152. [in Spanish]
Taraschewski H., 2006. Hosts and parasites as aliens. J. Helminthol. 80(2): 99–128.
Torchin M.E., Lafferty K.D., Dobson A.P., McKenzie V.J., Kuris A.M., 2003. Introduced species and their missing parasites. Nature 421: 628–630.
Torchin M.E., Mitchell C.E., 2004. Parasites, pathogens, and invasions by plants and animals. Front. Ecol. Environ. 2(4): 183–190.
Ubelaker J.E., Shariq I., Chudhri S., Pamela P., Clifford P.P., Duszynski D.W., 2010. Helminth Parasites of the Spotted Ground Squirrel, *Xerospermophilus* (syn. *Spermophilus*) *spilosoma* (Bennett, 1833) Helgen, Cole, Helgen, and Wilson, 2009, from Central New Mexico, U.S.A. Comp Parasitol 77(2): 178–182.
Wang P.-Q., 1981. Six new species of nematodes from vertebrates in Fujian Province. Acta Zootax. Sin. 6(4):365-372.

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