

Poor parasite community of an invasive alien species: macroparasites of Pallas's squirrel in Italy

Maria Vittoria Mazzamuto^{1,*}, Benoît Pisanu², Claudia Romeo³, Nicola Ferrari³, Damiano Preatoni¹, Lucas A. Wauters¹, Jean-Louis Chapuis² & Adriano Martinoli¹

¹ Environment Analysis and Management Unit, Guido Tosi Research Group, Department of Theoretical and Applied Sciences, Università degli Studi dell'Insubria, Via J. H. Dunant 3, I-21100 Varese, Italy (*corresponding author's e-mail: maria.mazzamuto@uninsubria.it)

² Centre d'Ecologie et des Sciences de la Conservation (CESCO), UMR 7204, Sorbonne Universités, MNHN, CNRS, UPMC – CP53, 61 rue Buffon, F-75005 Paris, France

³ Department of Veterinary Sciences and Public Health, Università degli Studi di Milano, via Celoria 10, I-20133 Milan, Italy

Received 17 Apr. 2015, final version received 9 Sep. 2015, accepted 19 Oct. 2015

Mazzamuto, M. V., Pisanu, B., Romeo, C., Ferrari, N., Preatoni, D., Wauters, L. A., Chapuis, J.-L. & Martinoli, A. 2016: Poor parasite community of an invasive alien species: macroparasites of Pallas's squirrel in Italy. — *Ann. Zool. Fennici* 53: 103–112.

The aim of the present study was to investigate the macroparasite fauna of Pallas's squirrel, *Callosciurus erythraeus*, native to SE Asia, recently introduced to Italy and co-occurring with the native Eurasian red squirrel *Sciurus vulgaris*. A total of 161 Pallas's squirrels harboured a poor macroparasite fauna, characterized by two main ectoparasite species, the flea *Ceratophyllus (M.) sciurorum sciurorum* (prevalence 50%, mean intensity 1.0 ± 0.1) and the tick *Ixodes ricinus* (prevalence 47%, mean intensity 3.0 ± 0.7), and a few helminths (*Rodentoxyuris sciuri*, *Trichuris muris*, *Strongyloides callosciureus*) all with prevalence below 10%. All parasites, except *S. callosciureus*, are native to Europe and were acquired in the invaded range. The loss of native parasites might have contributed to their successful invasion. The acquisition of local parasites *C. sciurorum* and *Trichuris sciuri*, and the introduction of the Asiatic nematode *S. callosciureus* may lead to spill-back and spill-over processes towards red squirrels.

Introduction

Studies on biological invasions have long been carried out (Elton 2000), but interest in alien species has increased over the last decades. Biological invasions can affect native species through several ecological processes such as competition, predation and hybridization (Kats & Ferrer 2003, Cox 2004, Largiadèr 2007, Ehrenfeld 2010).

The outcome of the invasion may also be affected by parasites, as has been reported for several introduced species, and infection transmission can become a threat to native species and humans (Torchin & Mitchell 2004, Dunn *et al.* 2012, Marsot *et al.* 2013, Mazza *et al.* 2013). An invader can import parasites from its native range, transferring infectious agents to native species that may be more susceptible to

them (spill-over) (Asakawa 2005, Taraschewski 2006). Moreover, exotic species may acquire local parasites from native species (Tompkins & Poulin 2006, Pisanu *et al.* 2009, Romeo *et al.* 2014), thus altering their local dynamics and inducing higher transmission rates to native species because of the increased number of available hosts (spill-back; Kelly *et al.* 2009). Finally, introduced species may also lose part of their parasites during the introduction process as a consequence of founder effect, absence of intermediate hosts or unsuitable environmental conditions (MacLeod *et al.* 2010). This loss may translate into higher individual fitness, increasing invasion success (parasite release; Torchin *et al.* 2003).

Many introduced rodents have become invasive and cause harm to native wildlife and/or damage to urban infrastructure, agricultural crops, natural woods and tree plantations (Wauters *et al.* 2005, Tamura & Ohara 2005, Bertolino 2008, 2009, Bertolino & Lurz 2013). Among rodents, tree squirrels have been introduced to several countries, mainly through the international pet trade or to increase hunting opportunities (Davis & Brown 1988, Aprile & Chicco 1999, Long 2003), and their capability to establish viable populations from only few founders has made them excellent invaders (Wood *et al.* 2007, Bertolino 2009, Martinoli *et al.* 2010, Bertolino *et al.* 2014).

Pallas's squirrel, *Callosciurus erythraeus*, is a tree squirrel native to SE Asia that has been introduced to Japan, Argentina, Belgium, France, the Netherlands and Italy (Bertolino & Lurz 2013). This species causes damage by gnawing tree bark, parts of buildings, cables and irrigation systems (Hori *et al.* 2006, Guichón & Doncaster 2008, Stuyck *et al.* 2009). The first Italian sighting was recorded in 2007 but the date of introduction and the origin of the Italian population, located in the province of Varese (northern Italy: 45°58'09.2''N, 08°43'57.6''E), where it co-occurs with the native Eurasian red squirrel *Sciurus vulgaris*, is uncertain. No previous parasitological studies have been conducted on this exotic species in Italy. In countries where the species has been introduced, populations showed low parasite-species richness of imported macroparasite taxa, with most of the ecto- and endoparasite species detected

only locally and accidentally acquired (Durden & Musser 1994, Shinozaki *et al.* 2004a, Asakawa 2005, Sato *et al.* 2007, Dozières *et al.* 2010, Gozzi *et al.* 2013, 2014).

Therefore, the main aim of the present study was to investigate the macroparasite fauna of Pallas's squirrel established in Italy. In particular, we expected that introduced *C. erythraeus* harbours a macroparasite community poor in species, consisting of a few parasites imported by the founding hosts, but composed mostly of (i) local specialized parasites acquired from closely-related hosts (i.e. Eurasian red squirrels that co-exist with Pallas's squirrel) or (ii) local generalist taxa able to develop in a wide range of hosts.

Material and methods

Pallas's squirrels (females = 79, males = 82) were captured between May 2011 and June 2014 from the only known Italian population located in the north of Varese Province (45°58'09.2''N, 08°43'57.6''E, 5 km from the Swiss border). Trapping was carried out within a European Community LIFE Project (LIFE09 NAT/IT/00095 EC-SQUARE) aimed at eradicating the alien species from Italy. Traps (live-traps model 202, Tomahawk Live Trap Co., Wisconsin, USA) were set in the morning, baited with apple and hazelnuts and checked twice a day to minimise stress during trapping. For each trapped squirrel, sex and reproductive condition were recorded (Wauters & Dhondt 1989) and lactating females (nipples large, milk excretion if stimulated) were immediately released in order to ensure welfare of newborn animals. All males and non-reproductive females were euthanized by CO₂ inhalation, following the EC and AVMA guidelines (Close *et al.* 1996, 1997, Leary *et al.* 2013). Each individual was weighed to the nearest 5 g using a Pesola spring-balance. Each carcass was immediately placed in a sealed plastic bag and stored at -20 °C for further examination.

Among all trapped squirrels, only adult specimens were examined. The whole gastrointestinal tract was examined for endoparasites following standard parasitological procedures as described in Romeo *et al.* (2013). Helminths were counted

and stored in lactophenol for morphological identification using a microscope equipped with *camera lucida* (Romeo *et al.* 2013). In the laboratory, carcasses were also examined for ectoparasites by combing the whole body with a flea comb above a white surface. Recovered specimens were counted and stored in 70% ethanol for later identification. Identifications followed species descriptions and nomenclature provided by Quentin (1971), Moravec (1982), Hugot (1984), Feliu *et al.* (2000), Sato *et al.* (2007) for nematodes, Beaucournu and Launay (1990) for fleas, and Pérez-Eid (2007) for hard ticks (*see also* Pisanu *et al.* 2007, 2008, 2009, Dozières *et al.* 2010, Romeo *et al.* 2013, 2014).

The probability of squirrels being infested by ectoparasites was analysed using logistic regression to investigate the effects of hosts' characteristics (sex and body mass) and season on the presence/absence of fleas and ticks. In each model, the effect of the presence of the other species was also tested. We used Generalised Linear Mixed Models (GLMMs, Bolker *et al.* 2009) adding year of sampling as a random factor. Seasons were classified following the same criteria as those described by Wauters *et al.* (2007) (winter: December–February, spring: March–May, summer: June–August, autumn: September–November). Model selection was carried out based on the minimum value of AIC. We checked model fit for overdispersion and through visual inspection of residuals (Zuur *et al.* 2009). Statistical analysis were carried out

using the R software (R Core Team 2013) and in particular the *lme4* package ver. 1.1-7 for fitting and analysing mixed models (Bates *et al.* 2014). We decided to analyse presence/absence rather than abundance because the number of ectoparasites on an individual host showed a reduced variability with low values (*see* Table 1).

Results

Endoparasites

A total of 74 squirrels (females = 34, males = 40) were examined for gastrointestinal parasites. This sample size allowed for parasite detection with a confidence of 95%, with an expected prevalence greater than 4% from a population of 1000 individuals (Thrusfield 2013).

Overall, 16 specimens belonging to five nematode species were identified (Table 1). Four hosts harboured the Oxyurid nematode *Rodentoxyuris (Trypanoxyuris) sciuri* (Cameron 1932) with intensity of infection ranging from one to six helminths per squirrel (Table 1). Four other hosts had a single specimen of *Trichuris muris* each. One specimen of *Strongyloides callosciureus* was found in the small intestine of a squirrel, and a female belonging to the genus *Strongyloides* was found in the small intestine of another individual. A single immature female of an unidentified Spirurid nematode was found in the stomach of a squirrel. Also, an immature

Table 1. Macroparasite species hosted by Pallas's squirrel, *Callosciurus erythraeus*, in Italy. Ectoparasite counts are set in italic when the number of infected hosts < 10.

Macroparasite species	Prevalence (%)	Intensity ± SE
Helminths (total number of examined hosts = 73)		
<i>Trypanoxyuris (R.) sciuri</i>	5	<i>1, 1, 1, 6</i>
<i>Trichuris muris</i>	4	<i>1, 1, 1</i>
<i>Strongyloides callosciureus</i>	1	<i>1</i>
<i>Strongyloides</i> sp.	1	<i>1</i>
Capillariinae	1	<i>1</i>
Spiruridae	1	<i>1</i>
Arthropods (total number of examined hosts = 135)		
<i>Ceratophyllus (M.) s. sciurorum</i>	50	1.0 ± 0.1
<i>Ixodes (I.) ricinus</i>	47	3.0 ± 0.7
Trombiculidae	7	–
<i>Ctenophthalmus (C.) agyrtes sardiniensis</i>	1	<i>1</i>
<i>Ctenophthalmus</i> sp.	1	<i>1</i>

female of a Capillariinae was found in the small intestine of another squirrel. There were no co-infections.

Ectoparasites

We found three species of ectoparasites in a sample of 497 ectoparasite specimens collected from the fur of 135 Pallas's squirrels (females = 61, males = 74): two species of fleas and one hard-tick species (Table 1). Of these specimens, 48 Ixodids could not be identified to the species level (43 larvae and five nymphs). Both the common hard tick *Ixodes (Ixodes) ricinus* (131 larvae, 212 nymphs) and the flea *Ceratophyllus (Monopsyllus) sciurorum sciurorum* (51 females and 53 males) were the most prevalent parasitic arthropods with the prevalence of 47% and 50%, respectively (Table 1). Other arthropods found were a single unidentified female of a flea from the genus *Ctenophtalmus sensu stricto*, and a single male of *Ctenophtalmus (Ctenophtalmus) agyrtes sardiniensis*. Acarid mites belonging to the family Trombiculidae were found on ten squirrels and only their presence/absence on each squirrel was recorded. Species richness ranged from 0 to 3 (mean = 1.0 ± 0.1 species per host).

The minimal model describing ectoparasite prevalence retained as explanatory factors only trapping season for *C. (M.) s. sciurorum*, and trapping season and sex for *I. (I.) ricinus* (Table 2). However, in the model for *I. (I.) ricinus*, sex was not statistically significant ($p = 0.13$). These results suggest that body mass, sex and the presence of the other parasite did not affect the prevalence of the two main ectoparasites. Pairwise comparisons between seasons showed that the prevalence of fleas was significantly higher in autumn than in spring (Wald's test: $p < 0.01$), whereas the prevalence of ticks was significantly higher in spring than in all the other seasons (Wald's test: all $p < 0.05$) and also higher in summer than in winter (Wald's test: $p < 0.01$) (Fig. 1).

Discussion

Pallas's squirrels introduced to Italy harbour

a very few macroparasite species: two main ectoparasite species, and a few helminth species all occurring with prevalence below 10%. Moreover, all the recorded parasite species, with the exception of the nematode *S. callosciureus*, are European, and were acquired locally. This agrees with the previous analyses of macroparasites of *C. erythraeus s.l.* introduced elsewhere (Japan: Shinozaki et al. 2004a, France and Belgium: Dozières et al. 2010, Argentina: Gozzi et al. 2013, 2014).

In the present study, the gastro-intestinal helminth with the highest prevalence was *T. (R.) sciuri*, an Oxyurid species specific to the native Eurasian red squirrel (Hugot 1984, Romeo et al. 2013, Santicchia et al. 2015). In our study area, Pallas's squirrels co-occur with Eurasian red squirrels and no other squirrel species are present in the area. Hence, it is likely that the alien species acquired the local parasites for example by using red-squirrel nests where helminth eggs were present. Moreover, from one host we recovered gravid *T. (R.) sciuri* females, indicating that the worm can fulfil its reproductive cycle in *C. erythraeus*. However, its prevalence remained very low, suggesting that this parasite is still not fully adapted to Pallas's squirrel since it does not reach abundances observed in its natural host (Romeo et al. 2013). Moreover, the reported low prevalence may have resulted from both low environmental contamination and reduced direct contact between the native and alien species, as supported by radio-tracking data (authors' unpubl. data).

In this study, *S. callosciureus* was found in one animal only. This nematode primarily infects sciurids (Sato et al. 2007) and was originally found in Pallas's squirrels introduced to Japan, where its prevalence of infection is high (i.e., 73%, $n = 100$; Sato et al. 2007). Additionally, Sato et al. (2007) revealed that differences in the prevalence of *S. callosciureus* in Japanese *C. erythraeus* populations are associated with the host's genetic variability, which could also explain the low prevalence of *S. callosciureus* in the Italian population.

The other species of helminths reported in this study were likely acquired through accidental infections. For example, *T. muris* was most likely acquired from terrestrial small rodents

(Murid and Arvicolid, *see* also Feliu *et al.* 2000) co-existing with Pallas's squirrels (Dozières *et al.* 2010, Gozzi *et al.* 2014).

The other most prevalent ectoparasite species found on Pallas's squirrels in Italy was the hard tick *I. (I.) ricinus*, which infests a wide variety of terrestrial vertebrate hosts (lizards, birds and mammals, e.g. Pérez-Eid 2007) in many Italian habitats (Dantas-Torres and Otranto 2013). It was found on both native and introduced squirrels in France (Vourc'h *et al.* 2007, Pisanu *et al.* 2010, 2014), but not on *S. vulgaris* and *S. carolinensis* in Italy (Romeo *et al.* 2013, 2014).

Such a discrepancy in infestations by *I. (I.) ricinus* between sciurids in France and Italy has been explained by the low densities or absence of ungulates, that are the key hosts species for *I. (I.) ricinus* (e.g., Ruiz-Fons *et al.* 2006, Pérez-Eid 2007, Tagliapietra *et al.* 2011) in the Italian sites where squirrels were collected (e.g. Romeo *et al.* 2013). In contrast, in our study area where Pallas's squirrels were sampled, roe deer is present. The tick prevalence in our Pallas's squirrel population peaked in spring as in other sciurids in France (i.e. Siberian chipmunks: Pisanu *et al.* 2010, Eurasian red squirrel: Pisanu *et al.* 2014).

Table 2. Model selection in the logistic regression to investigate the effects of Pallas's squirrels' sex and body mass, season of sampling, and the presence/absence of *Ixodes (I.) ricinus* on the presence/absence of *Ceratophyllus (M.) s. sciurorum*, and of Pallas's squirrels' sex and body mass, season of sampling, and the presence/absence of *Ceratophyllus (M.) s. sciurorum* on the presence/absence of *Ixodes (I.) ricinus*. Random term for all models: "year of sampling"; + = presence of the term in the model.

	Body mass	Presence of ticks	Season	Sex	AIC	ΔAIC
Presence of fleas			+		186.6	–
		+	+		188.5	1.88
			+	+	188.5	1.90
	+		+		188.6	1.99
		+	+	+	190.4	3.73
	+	+	+		190.5	3.87
	+		+	+	190.5	3.89
					101.1	4.50
			+		192.3	5.61
	+	+	+	+	192.4	5.72
	+				192.9	6.28
				+	193.1	6.49
	+	+			194.0	7.39
			+		194.2	7.60
	+			+	194.9	8.27
	+	+		+	196.0	9.38
Presence of ticks			+	+	137.7	–
			+		138.0	0.31
		+	+	+	139.3	1.52
	+		+	+	139.4	1.64
	+		+		139.4	1.69
		+	+		139.6	1.83
	+	+	+	+	140.9	3.16
	+	+	+		140.9	3.21
			+		164.2	26.49
			+	+	164.3	26.58
				+	165.2	27.43
				+	165.2	27.51
	+	+			165.8	28.12
	+	+		+	166.1	28.38
	+				167.0	29.27
	+			+	167.2	29.45

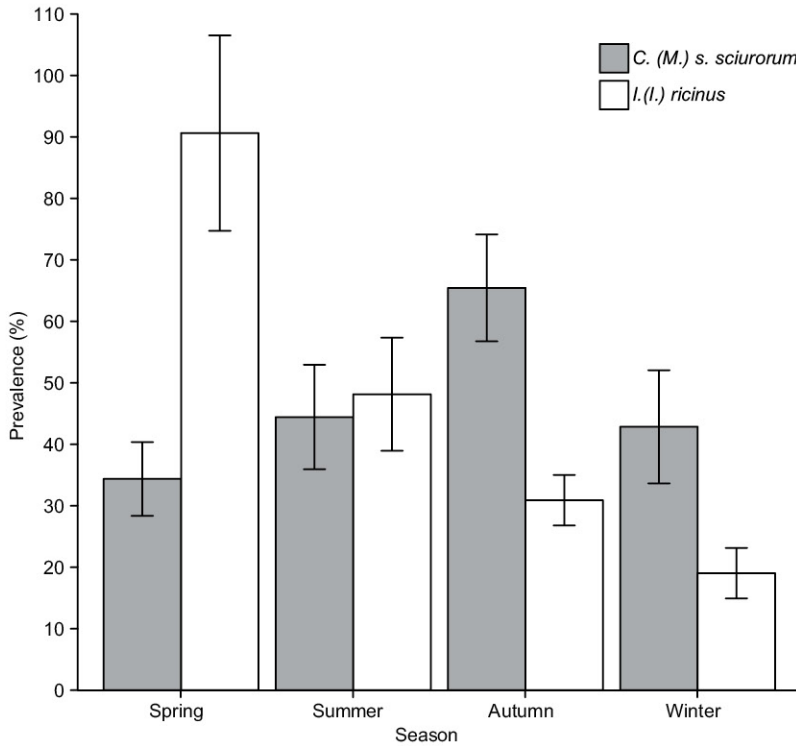


Fig. 1. Prevalence (percentage of infected hosts \pm SE) of *C. (M.) s. sciurorum* and *I. (I.) ricinus* in different seasons.

This peak coincided with the wettest season of temperate climates to which *I. (I.) ricinus* could be sensitive. Interestingly, the nymph-to-larvae ratio on Pallas's squirrel was close to 2:1, which is similar to observations made on *S. vulgaris* in Switzerland and France (Humair & Gern 1998, Pisanu *et al.* 2014). This ratio is much higher than the one usually observed for ground-foraging rodents with smaller body size (e.g. 1:80 for bank voles *Myodes glareolus*, and 1:10 for Siberian chipmunks *Tamias sibiricus*, Pisanu *et al.* 2010). This pattern of infestation could be related to the arboreal behaviour and wider home ranges of these larger body-sized sciurids, which may lead to a more frequent pick-up of nymphs from the undergrowth than larvae occurring on the ground.

We did not find any gender-related differences in arthropod infestation of Pallas's squirrel, and this lack was also found for *S. vulgaris* in France and Italy (Romeo *et al.* 2013, Pisanu *et al.* 2014) and *S. carolinensis* in Italy (Romeo *et al.* 2014). These findings deserve further attention, as sex-biased infestations by ectoparasites

are critically related to behavioral processes associated with reproduction in small rodents (e.g. Krasnov *et al.* 2005, 2012, Ferrari *et al.* 2007). The complex interactions prevailing in this context can be difficult to assess (Le Coeur *et al.* 2014), especially for parasite species that do not have a long co-evolutionary history with a new host.

In contrast to what has been reported for *C. erythraeus* from other European countries and from Japan (Shinozaki *et al.* 2004b, Dozières *et al.* 2010, Lurz *et al.* 2013), we did not find any sucking lice infesting the Italian population.

The low richness of macroparasite species found in our survey could be attributed to the history of this introduction. Despite the lack of precise information, the Italian population was likely founded by few individuals during just one or few introduction events. Such a small subset of founding individuals reduces the probability of parasites being introduced along with the founding hosts due to sampling effects (Torchin *et al.* 2003). Moreover, some parasites may have arrived in the new area, but they may

have been lost during the first steps of establishment of the new population because of low host densities or adverse environmental conditions (Shinozaki *et al.* 2004a, MacLeod *et al.* 2010, Romeo *et al.* 2014). Finally, the founders likely originated from pet shops where antiparasitic treatments could have been applied. However, we must stress that this limited parasite fauna could also be transitory because this population is still young and new host–parasite associations need time to establish (Torchin & Mitchell 2004, Gozzi *et al.* 2014).

Our findings suggest that, even though tree squirrels are in general poorly parasitised because of their arboreal habits, which reduce the probability of acquiring infective, free-living stages in the environment (Aprile & Chicco 1999, Lurz *et al.* 2013), the loss of native parasites might indeed have contributed to successful invasion of squirrels (parasite release or enemy release hypothesis, Torchin *et al.* 2003).

We also showed that *C. erythraeus* acquired the flea *C. (M.) s. sciurorum* and the oxyurid nematode *T. (R.) sciuri* from red squirrels and introduced the nematode *S. callosciureus* with potential impacts on native red squirrels because of spill-back and spill-over processes (Kelly *et al.* 2009). The low prevalence of *T. (R.) sciuri* seems however to preclude, at least at present, any premises for parasite spill-back. On the other hand, further studies are needed to better understand the potential consequences of *C. (M.) s. sciurorum* spill-back and *S. callosciureus* spill-over to red squirrels (*see also* Romeo *et al.* 2014) and the role of the ongoing parasite colonisation process on the invasion success of *C. erythraeus*. It must be stressed that, despite the fact that the parasite fauna of Pallas's squirrel in its native range has recently been reviewed (e.g., Gozzi *et al.* 2013, 2014, Lurz *et al.* 2013), effects of parasites at the host-population level (e.g. Torchin *et al.* 2003) are unknown. Finally, special attention should be paid to vector-borne diseases, especially pathogens transmitted by *I. (I.) ricinus* in Europe, since the high nymph-to-larvae ratio might indicate that Pallas's squirrels actually play a significant role in the circulation and transmission of such pathogens in the vertebrate community (*see* Pisanu *et al.* 2014), humans included.

Acknowledgments

Many thanks to Provincia di Varese for allowing field collections. Special thanks to Federica Turba, Mattia Panzeri and all the other students involved in sampling and lab analysis. We are grateful to the two anonymous reviewers for their helpful and constructive comments and suggestions. This is paper number 8 of the LIFE09 NAT/IT/000095 EC-SQUARE Project.

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