



Alien shades of grey: new occurrences and relevant spread of *Sciurus carolinensis* in Italy

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ABSTRACT

The eastern grey squirrel is listed among the worst invasive species throughout the world. This species of American origin is currently replacing the native Eurasian red squirrel in most of the Great Britain, as well as in parts of Ireland and Italy. It may debark trees and exert damages to woodlands and tree plantations. Therefore, its spread may be deleterious for biodiversity and environment, emphasising the need for a rapid detection in new areas of occurrence. In this work, we reported for the first time, the presence of new populations of this invasive species in Tuscany (Central Italy) and some updates and analyses regarding the status of this species in Veneto (North-Eastern Italy). Occurrences were collected through citizen-science contributory approach supported by photos, road-kills, and/or hair-tube sampling. Field investigations ad hoc were carried out in Veneto and Tuscany to confirm the repeated reports in the surroundings of Arezzo and in the province of Siena. Although records can be possibly related to erratic or single individuals escaped from captivity, reproductive nuclei have also been detected in both regions, with the observations of juveniles and/or lactating females. The occurrence of the species in these regions is still scarce and localised, but considering the surrounding favourable wooded habitats, a rapid removal of the animals would be required to prevent their spread.

KEYWORDS

Alien species, distribution range, Eastern grey squirrel, Eurasian red squirrel, impacts, *Sciurus vulgaris*

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INTRODUCTION

Alien species have to pass through three phases to become invasive: introduction, establishment, and spread (Allendorf & Lundquist 2003; Duncan et al. 2003; Lockwood et al. 2009). The establishment and spread of invasive alien species may alter the evolutionary processes as well as the relationships occurring within the indigenous biocoenosis (Mack et al. 2000; Colautti & Mclsaac 2004; Simberloff et al. 2013; Mazza et al. 2014).

A typical example of invasive alien species is represented by the Eastern grey squirrel *Sciurus carolinensis* Gmelin, 1788 (hereafter, grey squirrel), a rodent of North American origin, which has been introduced to the British Islands since the 19th century and to Northern Italy since 1948 (Gurnell & Pepper 1993; Martinoli et al. 2010).

The species is currently included among the 100 of the world's worst invasive alien species (Lowe et al. 2000). The main impact of the introduced grey squirrels is represented

by the competitive exclusion of the congeneric, smaller Eurasian red squirrel *Sciurus vulgaris* Linnaeus, 1758 (hereafter, red squirrel), the only European native tree squirrel (Gurnell & Pepper 1993; Bertolino et al. 2014; Čanádý et al. 2015). The competition between grey and red squirrels is mainly due to the higher ability of the introduced species to exploit trophic resources with respect to the native one (Wauters et al. 2002a, b). Grey squirrels have a mechanism of acorn tannin detoxification, which allows them to feed on unripe acorns (Kenward & Holm 1993; Chung-MacCoubrey et al. 1997) and deplete tree seeds hoarded by red squirrels (Wauters et al. 2002b). Grey squirrels also act as a reservoir for a squirrel *Poxvirus*, which affects the red squirrels (Gurnell et al. 2006); furthermore, the spillback (transmission of native parasites by the alien species) and spillover (transmission of alien parasites by the alien species) processes towards the native red squirrels may occur (Romeo et al. 2014). Although in Italy, the damage through bark-stripping seems to be limited (Signorile & Evans 2007),

the introduced species is responsible for severe damage to the timber industry and forestry in Great Britain and Ireland (Williams et al. 2010; Mayle & Broome 2013).

In Great Britain, grey squirrels were introduced many times between 1876 and 1929 – although Harris et al. (1995) reported the first record in 1828 – and rapidly spread, relegating the native red squirrel to few wooded areas in England and Scotland (Gurnell et al. 2008). The Italian situation is very worrying, since the range expansion of the introduced grey squirrel may threaten the conservation status of the red squirrel throughout the whole of Europe (Bertolino et al. 2014; Bertolino et al. 2015). The species is currently present and widespread in North-western Italy (Piedmont, Lombardy, and Liguria: Martinoli et al. 2010), while the population introduced in Rome (Villa Celimontana) went extinct possibly because of feral/stray cats (Monaco 2014). Since 2003, a population has been recorded in the surroundings of Perugia (Umbria, Central Italy: Gaggi & Paci 2014), and since 2012, other individuals were repeatedly observed in the surroundings of Città di Castello (Umbria), further threatening the red squirrel populations on the Apennines (Gaggi & Paci 2014).

In Veneto, the first occurrence was formally recorded in 2009 in Abano Terme (Padua), near the Euganean Hills, where two individuals were removed (Martinoli et al. 2010). In 2013, some individuals were repeatedly observed in Voltabarozzo, Padua (Battiston & Amerini 2013), but the distribution of the grey squirrels in Veneto is still not completely defined.

The aforementioned impacts underline the importance of a constant update of the distribution status of the grey squirrel, as once an alien species is established and has spread, eradication and control are generally hard activities to be carried out (Genovesi & Shine 2004). In this work, we summarised the first records of grey squirrels in Tuscany (Central Italy), and we updated the current situation in Veneto (North-Eastern Italy).

1. MATERIALS AND METHODS

Since 2012, an e-mail account was created to collect the records and photos of grey squirrels and other tree squirrels in the framework of a contributory citizen-science project carried out in Italy (saveredsquirrel@gmail.com: Mori & Menchetti 2014). Furthermore, an online project on iNaturalist was created to improve data collection on the distribution of alien and native squirrels in Italy (<http://www.inaturalist.org/projects/save-red-squirrel>). This project was sponsored through flyers and oral communications at universities, natural history museums, scientific congresses, main social networks, mailing lists, and blogs of photographers and hikers, to give maximum publicity to the idea and gather as much as data possible.

As for Tuscany, the records with photos were then validated through an expert-based approach, while those without pictures were included in the database, only if provided by the local experts. In the great majority of cases, photos were rapidly identified to the reference species, thus constituting undisputable records. Three road-kills were also included (one from Arezzo and two from Siena province, Table 1); carcasses are stored in freezer at the Natural History Museum of Maremma in Grosseto. The sightings and e-mail addresses of each detector were reported in a table to regularly inform the members of the network about the use of their data and photos. Furthermore, a description of the main habitat type surrounding the sighting place (e.g., deciduous woodland, conifer woodland, urban park) was noted. Occurrences from Palazzo del Pero (province of Arezzo) were not reported by experts, nor confirmed by the high resolution photos. We, thus, carried out a hair-tube survey in the woodland (*Corylus avellana*, *Juglans regia*, *Crataegus monogyna*, and *Pinus nigra*) surrounding the cemetery of this village, where the grey squirrel was observed, to verify its actual presence. A total of 20 plastic tubes (7.2 cm in diameter; 26 cm in length) were placed in the woodland, separated 25-30 m from one another. A plastic plate with adhesive material was placed on the upper side of the tube, to capture squirrel hairs. Nut-cream and sunflower seeds were

Table 1. Records of grey squirrels from Tuscany: N, the minimum number of individuals detected. The Records column follows the definition reported in the Materials and Methods section. The year of the first observation is also reported.

Year	Location (province)	Habitat type	Records	N
2012	Palazzo del Pero (Arezzo)	Deciduous woodland	Hair tubes	1
2012	La Pace (Arezzo)	Urban area	Single observation	1
2014	Panzano (Florence)	Deciduous woodland	Single observation	1
2014	Iesa (Siena)*	Deciduous woodland	Reproductive	8
2014	Monticiano (Siena)	Urban area	Continuative	3
2014	Quarata (Arezzo)*	Deciduous woodland	Single observation	1
2015	Scandicci (Florence)	Urban area	Single observation	1
2015	San Leo di Anghiari (Arezzo)	Deciduous woodland	Single observation	1

used as bait. Adhesive tapes were controlled for hair presence once every two weeks, between March and May 2012. The collected hair were stored in absolute ethanol and analysed at the microscope. A macroscopical observation allowed us to recognise hair of tree squirrels, which were long and band-coloured. Hairs of *S. vulgaris* and *S. carolinensis* show differences both in the macroscopical and in the microscopical structure (Dagnall et al. 1995; Signorile 2004). Long, straight, black- and white-tipped hairs are mainly typical of *S. carolinensis*, which also show a roundish section (kidney-shaped in *S. vulgaris*; Molinari et al. 2008). Red bands are more common on *S. vulgaris*. Cortex and medulla were analysed at the microscope. To analyse the cortex, the hair was placed on a glass slide, on a layer of nail polish. After the slide was completely dry, the hair was removed. Then, the mould was observed at the microscope and compared with specific atlases and reference collections (Debrot et al. 1982; Teerink 1991). To analyse the medulla, the hair was longitudinally sectioned and wet with cedar oil at the section level. The prepared slide was observed under the microscope to compare the structure of the medulla with atlases (Debrot et al. 1982; Teerink 1991) and reference collections. The macroscopical and microscopical analyses confirmed the presence of *S. carolinensis* in Palazzo del Pero; hairs of this species were found only in March, in one tube.

As for Veneto, most information was collected through two citizen-science projects: 'Piattoscoiattolo' (Amerini & Battiston 2016) and 'Atlante dei Mammiferi del Veneto' (www.mammiferiveneto.it). Relevant data were taken from the database of the Venetian Zoological Association (Associazione Faunisti Veneti) and from the observations by the authors (RA and RB). These observations were obtained through local surveys in the Padua countryside area, aimed to verify records from social media. Corn feeders and camera traps were placed on selected localities; nest counts and nine road-kills were also taken into account (Amerini & Battiston 2016).

Single, isolated, and non-continuative observations are reported as 'single observation'. We defined as 'occasional' those occurrences recorded in the urban park/wood patch and/or for only 1 year. As well, records involving more than one individual observed throughout > 1 year were classified as 'continuative'. We considered as 'reproductive'- only occurrences corresponding to juveniles or lactating females. Unconfirmed

observations (Quarto d'Altino, Venezia; Galliera Veneta, Padua; Barberino del Mugello, Firenze; Sovicille, Siena) were discarded from our results.

2. RESULTS

The first observation of the grey squirrel in Tuscany dates back to 2012 in the Province of Arezzo, where some observations were also occurred in 2014 and 2015. Reproduction has been ascertained only for the surroundings of Iesa (Municipality of Monticiano), where at least two litters have been detected (S. Balucanti, personal observation) and an immature individual killed by a cat was collected in September 2014 (Fig. 1; Fig. 2A). Dead individuals (two from Iesa, one from Quarata) are currently stored at the Maremma Natural History Museum, in Grosseto. The sites of observations are reported in Table 1 together with the typology of the record. Most observations (75%) occurred in deciduous woodlands (mainly mixed oak-woods with *Quercus cerris* and *Q. ilex* as predominant species) located at the immediate surroundings of cities and villages,



Figure 1. Records of grey squirrels from Tuscany (Provinces of Arezzo, Siena, and Florence). Map: Google, DigitalGlobe.

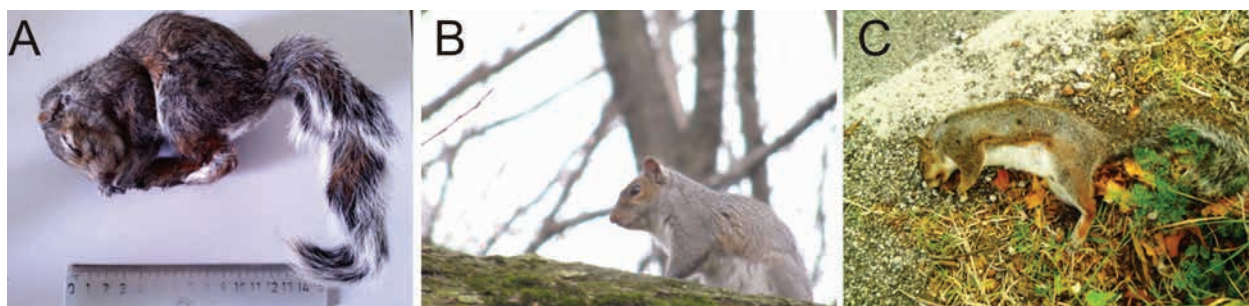


Figure 2. A) A young individual of grey squirrel killed by a cat found in September 2014 in the Village of Iesa (Municipality of Monticiano, Province of Siena, Tuscany: © Emiliano Mori); B) the adult grey squirrel observed in the surroundings of a farmhouse in Panzano (Province of Florence, Tuscany: © Jussara del Mastio); C) a road-killed grey squirrel in Montegrotto Terme (Province of Padua, Veneto: © Rachele Amerini).

while four individuals were observed in urban areas (urban parks or lined avenues).

As for Veneto, grey squirrels are continuously reported since 2008 (Table 2; Figs. 2-3). Two groups of individuals observed since more than 5 years are currently present in the Padua countryside (Abano and Montegrotto Terme) and East to Rovigo. In Abano Terme, a lactating female and her young were found in 2009 (Martinoli et al. 2010): this represents the only evidence of grey squirrel reproduction available for the region. Four groups of individuals were reported in separate gardens in the suburbs of Padua and in the near towns of Albignasego and Due Carrare. Three other nuclei are located at the edge of the known distribution in the Province of Padua and in/close to ecological corridors (see Fig. S1, Supplemental Material: www.mammiferiveneto.it). A free-ranging individual was observed in 2011 in Parco Faunistico Cappeller in Cartigliano (Province of Vicenza), where, at the present time, a group of five individuals is kept in captivity. Most of the localities (79%) are within urban areas, while only 21% of the locations are classified as deciduous (16%) or riparian (5%) woodlands. The Veneto plain is occupied by an almost continuous pattern of fragmented towns, interspaced by cultivated field, small isolated groves, gardens

or villas; thus, some locations, which included both rural and urban elements but with a significant anthropic impact, were classified as 'urban area'.

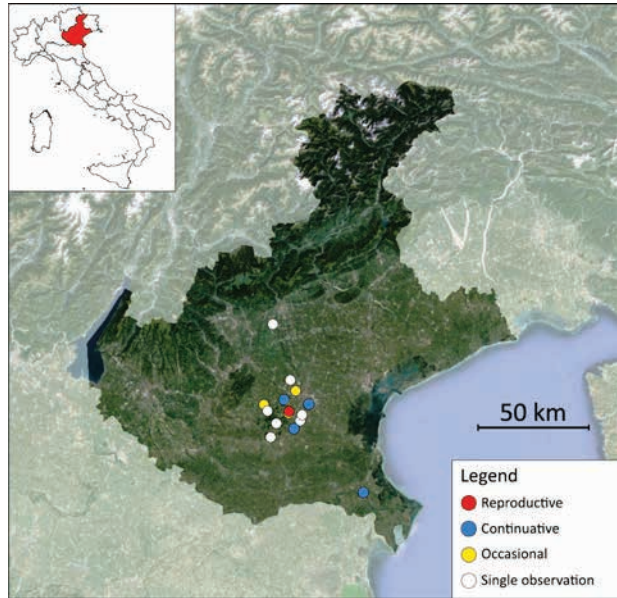


Figure 3. Records of grey squirrels from Veneto (Provinces of Vicenza, Padua, and Rovigo). Map: Google, DigitalGlobe.

Table 2. Records of grey squirrels from Veneto: N, the minimum number of individuals detected. The Records column follows the definition reported in the Materials and Methods section. The year of the first observation is also reported. (*), five individuals are still present in captivity.

Year	Location (province)	Habitat type	Records	N
2008	Porto Viro (Rovigo)	Urban area	Continuative	6
2009	Abano Terme (Padua)	Urban area	Reproductive	5
2010	Albignasego (Padua)	Urban area	Continuative	12
2011	Cartigliano (Vicenza)	Urban area	Single observation (*)	1
2012	Due Carrare (Padua)	Urban area	Continuative	2
2013	Padua	Urban area	Continuative	10
2013	Villafranca Padovana (Padua)	Urban area	Single observation	1
2013	Montegrotto Terme (Padua)	Urban area	Continuative	7
2013	Saccolongo (Padua)	Urban area	Continuative	2
2014	Maserà di Padova (Padua)	Urban area	Single observation	1
2014	Galzignano Terme (Padua)	Deciduous woodland	Single observation	1
2014	Baone (Padua)	Deciduous woodland	Single observation	1
2014	Canale Brentella, Rubano (Padua)	Riparian woodland	Occasional	3
2014	Selvazzano Dentro (Padua)	Urban area	Occasional	2
2014	Teolo (Padua)	Urban area	Single observation	1
2015	Rovolon (Padua)	Deciduous woodland	Occasional	2

3. DISCUSSION

This work represents an update of the grey squirrel distribution in Italy, with respect to the latest headcount performed by Martinoli et al. (2010). Given the impact of this species on the Italian biodiversity and environment (Bertolino et al. 2015), a comprehensive and continuously updated knowledge on its distribution is an indispensable tool to address management practices. Although just one evidence of reproduction is available up until now (Martinoli et al. 2010), more reproductive nuclei might be present in Veneto. Accordingly, the grey squirrel seems to be more widespread in this region, as it is observed at least since 2008 and with continuity in the provinces of Padua and Rovigo (16 total municipalities) with respect to Tuscany (8 locations), where continuous observations are only available for the province of Siena (Municipality of Monticiano). In the latter area, two litters have been observed (S. Balucanti, personal observation 2016). The population in the province of Siena needs rapid investigations, as it is located near protected areas of conservation concern (Riserva Naturale Alto Merse, Riserva Naturale Basso Merse, Riserva Naturale Farma, and Riserva Statale di Tocchi), and in continuity with extensive densely wooded areas.

The fragmented distribution and the lack of systematic records of grey squirrels in Veneto, where individuals have been observed in urban parks, country villas, and even hilly forests, depict a situation with many potential critical localities, which may be the source of a significant future expansion. The range expansion of the grey squirrel in Veneto represents a serious threat for the red squirrel, in the Alpine and pre-Alpine area and in urban areas recently colonised by the native species (Battiston & Amerini 2013). Furthermore, the spread of this invasive species highlights the more than likely risk of invasion of the Balkan peninsula and Eastern Europe.

On the other hand, the Tuscan population may increase the risk of spread throughout the Apennine range, together with the one expanding from Umbria (Martinoli et al. 2010). Both Tuscany and Veneto host populations made up by an apparently small number of grey squirrels, but located in the areas potentially suitable for their expansion. Thus, small nuclei described in this work may join to large populations, thus increasing the risk of range expansion towards new areas; this emphasises the importance to monitor these populations and start addressed management plans (Genovesi & Shine 2004).

A rapid removal intervention would be desirable to avoid further expansion of this species, as it happened in the case of North-western Italy and UK (Reynolds 1985; Bertolino et al. 2008; Bertolino et al. 2014). Adriaens et al. (2015) showed how eradication of small and isolated populations of potentially invasive tree squirrels may be feasible with a small amount of funds and energies. Citizen-science represents a useful, cheap method to obtain the species distribution occurrences (Conrad & Hilchey 2011), especially when the available funds for research are low (Cagnacci et al. 2012). By contrast, although effective with tree squirrels (Mori & Menchetti 2014; Bartolomei et al. 2016), data collected by non-expert citizens require verification through photo analysis and on-the-spot investiga-

tions. In this context, *S. carolinensis* may be confused with grey morphs of *S. vulgaris* as well as with the edible dormouse *Glis glis*. The verification of photos discarded the reported occurrences, which belonged to the last species. As well, observations not confirmed by unequivocal data need field surveys created *ad hoc*.

Although since January 2013, the Italian law has banned trade, breeding, and possession of the grey squirrel in the whole country, we cannot exclude that squirrels kept in captivity could be released and establish new breeding colonies in Italy. For example, single individuals have been also observed in the provinces of Rimini and Forlì-Cesena in the Emilia-Romagna region (A. Laurenzi and C. Gontero, personal communication 2015). Multi-regional or national coordinated action plans, including an early detection and rapid response system, should be encouraged to provide a timely reaction, together with local education, to prevent future releases in other localities. A well-structured, citizen-science-based warning system may also serve the double purpose of recording new data and involving the public in the problems related to invasive squirrels' management.

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References

- Adriaens, T., Baert, K., Breyne, P., Casaer, J., Devisscher, S., Onkelinx, T., Pieters, S. & Stuyck, J. (2015) Successful eradication of suburban Pallas' squirrel *Callosciurus erythraeus* (Pallas 1779) (Rodentia, Sciuridae) population in Flanders (northern Belgium). *Biological Invasions*, 17, 2517-2526.
- Allendorf, F.W. & Lundquist, L.L. (2003) Introduction: population biology, evolution, and control of invasive species. *Conservation Biology*, 17, 24-30.
- Amerini, R. & Battiston, R. (2016) La sottile linea di confine tra lo scoiattolo rosso *Sciurus vulgaris* e lo scoiattolo grigio *Sciurus carolinensis* in Veneto: problematiche annunciate e prospettive di sviluppo (Rodentia: Sciuridae). In: Bonato, L., Trabucco, R., Bon, M.

- (eds.) Atti 7° Convegno Faunisti Veneti. Bollettino del Museo di Storia Naturale di Venezia, suppl. 66, 292.
- Bartolomei, R., Sgrasso, S. & Aloise, G. (2016) Espansione recente di *Sciurus meridionalis* Lucifero, 1907 in Basilicata. *Hystrix, the Italian Journal of Mammalogy*, suppl. 2016, 68.
- Battiston, R. & Amerini, R. (2013) Distribuzione dello scoiattolo comune *Sciurus vulgaris* (Rodentia: Sciuridae) nella provincia di Vicenza: sinurbazione e colonizzazione di aree pianiziali in contesti antropizzati. *Natura Vicentina*, 16, 17-27.
- Bertolino, S., Lurz, P.W., Sanderson, R. & Rushton, S.P. (2008) Predicting the spread of the American grey squirrel (*Sciurus carolinensis*) in Europe: a call for a co-ordinated European approach. *Biological Conservation*, 141, 2564-2575.
- Bertolino, S., Di Montezemolo, N.C., Preatoni, D.G., Wauters, L.A. & Martinoli, A. (2014) A grey future for Europe: *Sciurus carolinensis* is replacing native red squirrels in Italy. *Biological Invasions*, 16, 53-62.
- Bertolino, S., Colangelo, P., Mori, E. & Capizzi, D. (2015) Good for management, not for conservation: an overview of research, conservation and management of Italian small mammals. *Hystrix, the Italian Journal of Mammalogy*, 26, 25-35.
- Cagnacci, F., Cardini, A., Ciucci, P., Ferrari, N., Mortelliti, A., Preatoni, D.G., Russo, D., Scandura, M., Wauters, L.A. & Amori, G. (2012) Less is more: a researcher's survival guide in time of economic crisis. *Hystrix, the Italian Journal of Mammalogy*, 23, 1-7.
- Čanádý, A., Mošanský, L. & Krišovský, P. (2015) Are there sex differences in the body size of the Eurasian red squirrel in Slovakia? *European Journal of Ecology*, 1, 5-12.
- Chung-MacCoubrey, A.L., Hagerman, A.E. & Kirkpatrick, R.L. (1997) Effects of tannins on digestion and detoxification activity in gray squirrels (*Sciurus carolinensis*). *Physiological Zoology*, 70, 270-277.
- Conrad, C.C. & Hilchey, K.G. (2011) A review of citizen science and community-based environmental monitoring: issues and opportunities. *Environmental Monitoring and Assessment*, 176, 273-291.
- Colautti, R.I. & MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. *Diversity and Distribution*, 10, 135-141.
- Dagnall, J.L., Duckett, J.G. & Gurnell, J. (1995) A simple negative staining technique for the identification of mammal hairs. *Journal of Zoology, London*, 237, 670-675.
- Debrot, S., Fivaz, G., Mermoud, C. & Weber, J.M. (1982) Atlas des pois de mammifères d'Europe. Institut de Zoologie de l'Université de Neuchâtel, Paris, France.
- Duncan, R.P., Blackburn, T.M. & Sol, D. (2003) The ecology of bird introductions. *Annual Review of Ecology, Evolution and Systematics*, 34, 71-98.
- Gaggi, A. & Paci, A.M. (2014) Atlante degli Erinaceomorfi, dei Soricomorfi e dei piccoli Roditori dell'Umbria. Dimensione Grafica Snc Edizioni, Spello (Perugia), Italy.
- Genovesi, P. & Shine, C. (2004) European Strategy on Invasive Alien Species. *Nature and Environment*, n. 137. Council of Europe publishing (eds), Strasbourg, France.
- Gurnell, J. & Pepper, H. (1993) A critical look at conserving the British red squirrel *Sciurus vulgaris*. *Mammal Review*, 23, 125-136.
- Gurnell, J., Lurz, P.W.W., Shirley, M.D.F., Cartmel, S., Garson, P.J., Magris, L. & Steel, J. (2004) Monitoring red squirrel *Sciurus vulgaris* and grey squirrel *Sciurus carolinensis* in Britain. *Mammal Review*, 34, 51-74.
- Gurnell, J., Rushton, S.P., Lurz, P.W.W., Sainsbury, A.W., Nettleton, P., Shirley, M.D.F., Bruemmer, C. & Geddes, N. (2006) Squirrel *Pox-virus*: landscape scale strategies for managing disease threat. *Biological Conservation*, 131, 287-295.
- Gurnell, J., Kenward, R.E., Pepper, H. & Lurz, P.W.W. (2008) Grey squirrel *Sciurus carolinensis*. (eds S Harris & DW Yalden. *Mammals of the British Isles: handbook*, 4th edn), pp 66-72. The Mammal Society, Southampton, UK.
- Harris, S., Morris, P., Wray, S. & Yalden, D. (1995) A review of British mammals: population estimates and conservation status of British mammals other than cetaceans. Peterborough: The Joint Nature Conservation Committee.
- Kenward, R.E. & Holm, J.L. (1993) On the replacement of the red squirrel in Britain. A phytotoxic explanation. *Proceedings of the Royal Society of London B: Biological Sciences*, 251, 187-194.
- Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distribution*, 15, 904-910.
- Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. The Invasive Species Specialist Group (ISSG), Gland, Switzerland.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications*, 10, 689-710.
- Martinoli, A., Bertolino, S., Preatoni, D.G., Balduzzi, A., Marsan, A., Genovesi, P., Tosi, G. & Wauters, L.A. (2010) Headcount 2010: the multiplication of the grey squirrel populations introduced to Italy. *Hystrix, the Italian Journal of Mammalogy*, 21, 127-136.
- Mazza, G., Tricarico, E., Genovesi, P. & Gherardi, F. (2014) Biological invaders are threats to human health: an overview. *Ethology, Ecology and Evolution*, 26, 112-129.
- Mayle, B.A. & Broome, A.C. (2013) Changes in the impact and control of an invasive alien: the grey squirrel (*Sciurus carolinensis*) in Great Britain, as determined from regional surveys. *Pest Management Science*, 69, 323-333.
- Molinari, A., Wauters, L.A. & Tosi, G. (2008) Monitoraggio dello scoiattolo comune (*Sciurus vulgaris* L.) con l'utilizzo di *hair-tubes* in foreste di conifere della provincia di Sondrio. *Il Naturalista Valtellinese*, 19, 113-124.
- Monaco, A. (2014) Alieni. La minaccia delle specie alloctone per la biodiversità del Lazio. Palombi Editori, Roma, Italy: 251 pp.
- Mori, E. & Menchetti, M. (2014) "Sometimes they come back": citizen science reveals the presence of the Italian red squirrel in Campania. *Quaderni del Museo di Storia Naturale di Ferrara*, 2, 91-94.
- Reynolds, J.C. (1985) Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*) in eastern England. *The Journal of Animal Ecology*, 54, 149-162.

- 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, e88002.
- Signorile, A.L. (2004) Spreading and behaviour of the grey squirrel (*Sciurus carolinensis* Gmelin): a comparison between the Italian and the British situations. MSc Thesis, Imperial College London, UK.
- Signorile, A.L. & Evans, J. (2007) Damage caused by the American grey squirrel (*Sciurus carolinensis*) to agricultural crops, poplar plantations and semi-natural woodland in Piedmont, Italy. Forestry, 80, 89-98.
- Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pysek, P., Sousa, R., Tabacchi, E. & Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution, 28, 58-66.
- Teerink, B.J. (1991) Hair of West-European Mammals. Cambridge: Cambridge University Press.
- Wauters, L.A., Gurnell, J., Martinoli, A. & Tosi, G. (2002a) Interspecific competition in tree squirrels: Eurasian red squirrels and alien grey squirrels: does resource partitioning occur? Behavioral Ecology and Sociobiology, 52, 332-341.
- Wauters, L.A., Tosi, G. & Gurnell, J. (2002b) Interspecific competition in tree squirrels: do introduced grey squirrels (*Sciurus carolinensis*) deplete tree seeds hoarded by red squirrels (*S. vulgaris*)? Behavioral Ecology and Sociobiology, 51, 360-367.
- Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., Shaw, R.S., Varia, S., Lamontagne-Godwin, J., Thomas, S.E. & Murphy, S.T. (2010) The economic cost of invasive non-native species on Great Britain. CABI report, 198 pp.