Evolving grey squirrel management techniques in Europe

Craig M. Shuttleworth*, Nikki Robinson1, Elisabeth C. Halliwell1, Rebecca Clews-Roberts4, Holly Peek1, Gala Podgornik5, Michael Stinson3, Shanna Rice1, Caroline Finlay5, Conor McKinney6, David J. Everest7 and Karl W. Larsen8

1School of Natural Sciences, Bangor University, Bangor, Gwynedd LL57 2UW, United Kingdom
2The Wildlife Trusts, The Kiln, Waterside, Mather Road, Newark, Nottinghamshire, NG24 1WT, United Kingdom
3Natural Resources Wales, Maes y Ffynnon, Bangor, LL57 2DW, United Kingdom
4Red Squirrels Trust Wales, Ty Cross, Anglesey, LL63 2TF, United Kingdom
5Ulster Wildlife, McClelland House, 10 Heron Road, Belfast, BT3 9LE, United Kingdom
6Queens University Belfast, University Rd, Belfast BT7 1NN, United Kingdom
7Animal and Plant Health Agency-Weybridge, Woodham Lane, New Haw, Addlestone, Surrey, KT15 3NB, United Kingdom
8Department of Natural Resource Sciences, Thompson Rivers University, 805 TRU Way, Kamloops, British Columbia, V2C 0C8, Canada

Author e-mails: craig.shuttleworth@rsst.org.uk (CMS), njr2510@gmail.com (NR), Rebecca.Clews-Roberts@cyfoethnaturiolcymru.gov.uk (RCR), Liz.Halliwell@cyfoethnaturiolcymru.gov.uk (LH)
*Corresponding author

Abstract

The North American Eastern grey squirrel (Sciurus carolinensis) is a highly invasive mammalian species adversely affecting forest ecosystems worldwide, notably in Europe. The species extirpates sympatric red squirrel (Sciurus vulgaris) populations through resource competition and the spread of pathogenic squirrelpox virus (SQPV) infection. In the United Kingdom (UK), the Red Squirrels United (RSU) project empowered volunteers with the skills, equipment and protocols needed to undertake the proactive detection and subsequent removal of grey squirrels at local, regional and national scales as an aid to red squirrel conservation. The establishment of local volunteer groups to undertake this provided a strong post-project legacy where bespoke local management approaches reflected regional variation in woodland isolation and invasion pathways. Here we highlight valuable lessons for international invasive species management via an adaptive volunteer-based approach to monitoring and control. This included the development of non-invasive techniques to determine the presence of pathological infections in wild squirrels, the provision of evolving approaches to grey squirrel control and where appropriate, red squirrel conservation translocation.

Key words: invasive species, red squirrel, control, volunteers, Canada

Introduction

The North American Eastern grey squirrel (Sciurus carolinensis Gmelin, 1788) is a highly invasive species introduced to parts of western Canada (Larsen 2016), Italy (Bertolino and Genovesi 2003), Great Britain and Ireland (Gurnell et al. 2016) and other locations. Geographical range expansion is the result of both natural dispersal (Teangana et al. 2000; Shuttleworth et al. 2016) and accidental and/or deliberate translocation (Larsen 2016; Signorile et al. 2016). Its impacts upon European forest landscapes are particularly well documented (Gurnell et al. 2016).
bark stripping by grey squirrels can result in serious stem deformity and crown death (Kenward et al. 1988). This can lead to a substantial reduction in timber yields, with associated serious economic impacts to commercial hardwood production (Mayle and Broome 2013; Nichols et al. 2016).

In Europe, grey squirrels cause regional native Eurasian red squirrel (*Sciurus vulgaris* Linnaeus, 1758) extirpation. They compete for resources and pilfer cached autumn food supplies (Wauters et al. 2002). Grey squirrel presence acts to suppress juvenile recruitment rates, reduce adult fitness (Gurnell et al. 2004) and elevate stress levels in red squirrels (Santicchia et al. 2018). In the British Isles, grey squirrels are the immune reservoir hosts for squirrelpox virus (SQPV) (Chantrey et al. 2019), an infection that produces pathogenic outbreaks in their congener (Romeo et al. 2018; Tomkins et al. 2003) where it is invariably fatal. Infection presence greatly accelerates the rate of sympatric red squirrel decline (Rushton et al. 2006). In Europe, grey squirrels also regionally carry a range of murine infections (Greenwood and Sanchez 2002) and squirrel adenovirus (Everest et al. 2014). In Italy they carry the North American nematode *Strongyloides robustus*, and they increase rates of native oxyurid *Trypanoxyuris sciuri* (Cameron, 1932) infection in sympatric red squirrels (Romeo et al. 2015).

As a result of negative effects upon European forest biodiversity, the grey squirrel is listed within the EU Regulation 1143/2014 on Invasive Alien Species. This places a legal responsibility on Member States to act to prevent spread into, and establishment within, states where the grey squirrel is currently absent. In parallel, those Member States where grey squirrels are widely spread, must put in place management measures so that their impact on biodiversity, the related ecosystem services and on the economy are minimised (e.g. Welsh Government 2018). Early detection, before or during, the invasion lag phase of population growth, is essential and is the most cost-effective management option (Barbara et al. 2018).

Here, we describe an element of work carried out by the Red Squirrels United (RSU) project co-funded by LIFE14 NAT/UK/000467 and the National Lottery Heritage Fund (HG-14-10510) in the period 2016–2020. This partnership collaboration involved The Wildlife Trusts, Forest Research, Newcastle University, Northumberland Wildlife Trust, Red Squirrels Trust Wales, Ulster Wildlife, Wildlife Trust of Lancashire, Manchester and North Merseyside and the Wildlife Trust of South and West Wales. The work programme was supported by Natural Resources Wales (NRW) and in addition, the Animal and Plant Health Agency (APHA) provided both information and advice regarding appropriate tissue sample selection for viral infection surveillance. APHA were also contracted to undertake the polymerase chain reaction (PCR) analyses of a proportion of the subsequent samples collected. RSU principally sought to increase community awareness of the invasive grey squirrel, facilitate increased volunteer participation in its management and establish co-ordinated local squirrel control groups, aided
by new approaches to detection and control. These enhanced grey squirrel early detection approaches aimed to rapidly respond to incursions in order to prevent population establishment and retard associated geographical spread.

We report on applied management outcomes in north Wales and Northern Ireland (NI), two regions containing remnant red squirrel populations that are either sympatric with, or in close proximity to, grey squirrels.

**Materials and methods**

We quantified data on community participation in grey squirrel early detection and control. These included assessing the intensity and spatial distribution of surveying effort at a progressive forest, regional and country-wide scale across a series of case-studies in the United Kingdom (UK) (Figure 1). In parallel, we evolved methods of grey squirrel dispatch and investigated public opinion regarding red and grey squirrels. How individual views change in relation to the amount of subject information made available was also an area of investigation.

**Early detection in remote forest areas**

Halliwell et al. (2016) provide a detailed overview of grey squirrel colonisation of Clocaenog Forest, a remote 5,500 hectare upland commercial plantation in north Wales that is dominated (69%) by Sitka spruce (*Picea sitchensis* (Bong.) Carrière). Although grey squirrels have less of a competitive advantage over red squirrels in such coniferous habitats (Kenward et al. 1998; Lurz et al. 1998), continual invasion pressure led to population establishment within Clocaenog Forest. Here, Shuttleworth and Hayward (2015) found grey squirrel presence was associated with a red squirrel
population decline to perhaps 10% of the 251 and 330 adults that Gurnell et al. (2002) had historically projected would persist in 2015.

RSU in collaboration with NRW, recruited and trained local volunteers to remove grey squirrels via live-trapping from within the forest and adjacent woodlands, having first detected them using a network of remote wildlife-cameras. This complemented ongoing contractor based control operations. Volunteers were also involved in a parallel red squirrel population reinforcement translocation programme (Natural Resources Wales 2017). The translocation adhered to international guidelines (IUCN/SSC 2013) and was undertaken following independent external review (Shuttleworth and Hayward 2015), internal NRW review and consultation with The Office of the Chief Veterinary Officer (OCVO) in the Welsh Government. The population reinforcement used PiT tagged captive-bred animals donated from the UK breeding programme which is co-ordinated by the Welsh Mountain Zoo. Animals were housed for several weeks in 3 m × 4 m forest enclosures. Post-release monitoring used radio-frequency identification (RFID) equipment, radio-telemetry for welfare purposes and post mortem and histological examination of dead red squirrels.

Disease and viral infection surveillance

APHA used PCR assays and negative contrast stain transmission electron microscopy (TEM) as tools to screen suspected pathogenic infection cases e.g. where visible lesion presence was observed and squirrelpox disease suspected in red squirrels. The PCR platform was in the form of a nested qPCR assay as reported by Everest et al. (2019) and a TEM assay as described by Everest et al. (2010). The collection of hair samples as a non-invasive means of viral surveillance was also available (see Everest et al. 2019).

Preventing reinvasion of landscape from which grey squirrels were eradicated

Grey squirrels were eradicated from the 720 km² island of Anglesey, UK in 2013 (Schuchert et al. 2014; Jones et al. 2017) following a control programme using live-capture traps which started in 1998. The population had first spread from the mainland in the mid 1960s and by the late 1990s grey squirrels had colonised all of the suitable woodland habitats. The island is home to 67,000 people and is separated from the mainland by a narrow sea channel called the Menai Strait. The channel is spanned by two bridges linking Anglesey with the Gwynedd mainland where established grey squirrel populations have been present since the late 1960s. Grey squirrel eradication facilitated the restoration of red squirrels through natural population recovery (Shuttleworth 2003) and reinforcement translocations (Halliwell et al. 2015). A limited mainland red squirrel recolonisation also occurred. During the eradication, genetic studies demonstrated grey squirrel movement between the island and mainland was occurring (Signorile and
In the autumn of 2015, three grey squirrels were successfully removed from Anglesey following sighting reports received from citizens (Shuttleworth et al. 2016); a fourth animal was later shot by a local citizen. The RSU project built on these foundations and developed a reactive reinvasion contingency plan (Shuttleworth and Halliwell 2016). Local citizens were proactively recruited to monitor fixed garden or woodland squirrel feeding stations creating a low cost, sustainable and co-ordinated surveillance network. They were provided with detailed guidance on squirrel management written in laymen’s terms (Shuttleworth and Halliwell 2018). A parallel grey squirrel control programme was put in place within coastal mainland woodlands to limit red and grey squirrel contact.

**Establishing a country-wide network**

Grey squirrels are widely established in Northern Ireland (Lawton et al. 2015) and in 2016 there were seven well established citizen groups dedicated to control of the species (Shuttleworth et al. 2015): Ards, Ballygally, Fermanagh, Glens, North West, Ring of Gullion and Tollymore red squirrel groups. RSU initially funded spatial modelling research to identify key squirrel dispersal routes in the country and to highlight the best national geographical deployment of resources to reverse or halt grey squirrel spread (Flaherty and Lawton 2016). A regional grey squirrel eradication campaign focussed upon an isolated coastal plain inland from the Mourne Mountains. The RSU project also facilitated the creation of new red squirrel conservation volunteer groups at geographically strategic locations.

**Understanding and maintaining community support**

To understand public views on native and invasive squirrel species management, RSU undertook a nationwide citizen consultation (reported by Dunn et al. 2018). Parallel research examined public opinion plasticity and whether people alter their views when provided with new information (Shrubbs 2019) and the key relevant findings are reported here.

**Developing novel approaches to grey squirrel control**

Historically, grey squirrels caught alive in single-capture cage traps were either shot or killed by a blow to the head (Mayle et al. 2007). These dispatch methods rely upon operator confidence and skill, factors that are a barrier to some citizen volunteers actively controlling grey squirrels. RSU explored alternative dispatch methods, in particular the use of a Kania 2000 spring-trap (Watson 2018) which could be firmly attached to the exterior of the inwards-opening door of a live-capture ALBI™ 079 Squirrel trap. When the ALBI door was opened, a confined squirrel would exit into the Kania 2000 where it would release a trigger and be killed by a bar held under high tension.
Results

Grey squirrel early detection in remote forest areas

Out of 83 recruited volunteers (representing 69% of those who attended introductory project training courses), it became apparent that a core group of 25 volunteers were regularly active and delivering most of the conservation work in Clocaenog Forest. This core group of volunteers was established from communities located as far as 22.7 km from the Clocaenog Forest edge (mean 10.5 ± 1.9 s.e. km) (Figure 2). The remaining 58 volunteers were only occasionally involved in RSU activities. The project provided training on grey squirrel control methods, carcass tissue sampling and remote wildlife surveillance camera use for monitoring squirrel feeding stations established in the forest (Figure 3). Volunteers worked together to undertake proactive trapping of conifer/hardwood forest edge interface areas to reduce immigration pressure and reactive trapping in internal forest stands. Grey squirrels were detected by remote wildlife-cameras forming a key early warning network (Table 1). Citizen volunteers were also involved in every aspect of the Clocaenog Forest red squirrel population reinforcement. A cumulative total of 18 red squirrels were used across phased releases during 2017 and 2018. Monitoring revealed annual breeding, successful weaning of young, the continued presence of wild remnant population animals and significant predation events by both avian (Goshawk, Accipiter gentilis) and mammalian predators (potentially either pine marten, Martes martes or red fox Vulpes vulpes).

Gross post-mortem, associated histological studies and analytical analyses using both PCR and TEM undertaken by APHA revealed an absence of squirrelpox infection in two dead red squirrels retrieved from Clocaenog Forest. Careful monitoring of camera images similarly indicated
Evolving grey squirrel management techniques in Europe

Figure 3. Image recorded on a remote wildlife camera of a grey squirrel feeding at a live-capture trap in Clocaenog Forest. Cameras can be placed at wooden squirrel feeding stations.

Table 1. Clocaenog Forest volunteer hours and activity.

| Year | Number of grey squirrels removed | Number of hours voluntary time | Workshops and group co-ordination |
|------|----------------------------------|--------------------------------|----------------------------------|
|      |                                  | Grey squirrel control | Camera monitoring | Community education | Workshops and group co-ordination |
| 2017 | 339                              | 907                       | 902.5               | 150.75             | 403.75                       |
| 2018 | 406                              | 1116.75                   | 2335                | 243.75             | 403.75                       |
| 2019*| 178                              | 661.25                    | 1309                | 110.75             | 398                           |

* January to September data only

no signs of infection in free-ranging animals. Pathogenic adenovirus was detected and was a significant factor in pre-release mortality.

Preventing reinvasion of landscape from which grey squirrels were eradicated

A citizen-monitored network of over 230 garden/woodland feeding stations was established across Anglesey by Red Squirrels Trust Wales. This regional surveillance network provided proactive monitoring for squirrelpox signs in red squirrels and the early detection of grey squirrel reinvasion (Figure 4). The production of an associated bilingual (Welsh/English) e-book guide empowered citizens with detailed knowledge of squirrel ecology, guidance on how to differentiate between squirrel species and how to identify squirrelpox signs (e.g. skin lesion appearance) in red squirrels.

In parallel, we implemented contingency planning that highlighted the major grey squirrel incursion pathways. These included accidental international passage via sea-ferry traffic, heavy-goods vehicles, railway freight and domestic passage via vehicles. In addition, the ability of animals to cross the Menai Strait using either of the bridges or by swimming the sea channel were also deemed as highly likely. An ongoing social media campaign
raised wider public awareness of invasion pathways, threats posed by grey squirrels and the importance of reporting suspected island sightings.

This combined awareness and surveillance approach resulted in a number of annual “possible” grey squirrel sightings being reported including nine in 2017. Remote camera footage and trapping subsequently identified two animals that were both caught. Squirreelpox was not detected in island red squirrels, and although a small mainland outbreak was detected by volunteers and confirmed via histology in 2017, the infection was successfully contained to the mainland and limited to a small number of animals. This was achieved by taking down point food sources such as feeding stations, removing carcasses of infected red squirrels and imposing a stringent disinfection protocol whilst trapping for sick red squirrels and sympatric grey squirrels.

*Establishing a country-wide network*

The RSU project in NI expanded the initial seven local squirrel groups to 13 by autumn 2019 (Figure 5). It provided funding (£1,000–£2000) through a support scheme to each of 10 local squirrel management groups to purchase additional equipment such as live traps and remote wildlife-cameras. Several of the groups work on a cross-border basis and RSU also supported the creation of the first squirrel group in the Republic of Ireland (Donegal Red Squirrel Group). Volunteer groups demonstrate variable levels of expertise (not all undertake grey squirrel management) and the RSU project was a valuable support structure for them.

Additionally, during the spring and summer months in the period 2017 to 2019, 200+ woodlands were surveyed by citizen volunteers across Northern
Ireland in a national squirrel survey. Overall, 33.5% of forests surveyed were found to contain red squirrels, representing an increase of 8.2% from 2017. The percentage of woodlands surveyed containing pine marten (*Martes martes* Linnaeus, 1758), a mustelid predator associated with grey squirrel population decline, also increased from 21.2% in 2017 to 26.1% in 2018. In the west in County Fermanagh, there was no evidence of grey squirrel populations based on the survey and this landscape continued to support the highest density recordings of both red squirrel and pine marten.

**Understanding and maintaining community support**

The RSU project observed that whilst 36% of respondents to a public survey disagreed or strongly disagreed that “there should be no management of grey squirrels and nature should be allowed to take its course”, only 25% agreed or strongly agreed with this statement. The published public survey also revealed a strong preference for those control methods considered the most humane. Subsequent public consultation found that the general public will alter their opinion when given additional information. For example, preference increased for lethal trap use and decreased for live traps when citizens were provided with detailed texts describing the relative effectiveness and potential humaneness of each.

To maximise community engagement, the RSU project convened a Project Advisory Group which included citizen volunteers alongside academics, Government representatives, researchers and conservation professionals to ensure strong stakeholder representation. In addition, the RSU Programme Manager spent approximately 5–10% of their annual time facilitating
meetings with national agencies and parallel invasive species partnerships. An archived online document library of webinars, e-books, best practice downloads and an annual national public “knowledge fair” were developed and hosted to facilitate future collaboration and wider knowledge sharing.

Despite ongoing formal training and mentoring of volunteers by RSU project staff, some citizens did not remain active in the project. Some individuals never gave reasons; the younger volunteers in secondary or higher education often found employment and could no longer offer time; one volunteer who had dispatched a high number of grey squirrels in a short amount of time found this affected them to the extent that they had to stop helping. We found that many volunteers had never trapped or culled animals before, yet once trained they were willing to get directly involved in grey squirrel control. Volunteers benefitted from ongoing mentoring especially when attempting to catch individual “trap-shy” grey squirrels or when plentiful natural food reduced squirrel trapping efficiency. Because unpaid volunteers only were active when they had available spare time, it was sometimes difficult to ensure efficient squirrel monitoring surveillance. Additionally, due to a wind-farm construction project in Clocaenog, large areas of that forest were inaccessible to the public and simply could not be monitored by volunteers.

Developing novel approaches to grey squirrel control

Devolved administrations across the UK stated that providing the conditions of use set out in the Spring Traps Approval Order (STAO) were met, a Kania trap 2000 fitted to a live-capture trap so that a confined grey squirrel could enter the kill-trap and be humanely discharged is permissible (Figure 6). Narrowing the entrance of the live-capture trap from a central 15 × 15 cm to 10 × 10 cm hole prevented any confined animal bolting too quickly into the Kania 2000 (behaviour which would lead to the trap striking the shoulders rather than the neck) and also acted to perfectly position the squirrels so the dispatch mechanism was triggered uniformly. This method of dispatch is now widely used by local squirrel management groups in Northern Ireland. Participation in RSU also facilitated amplification of this approach to other parts of the UK.

Discussion

The RSU project successfully galvanised strong community support for proactive invasive mammal surveillance, detection and removal. This was based upon regionally adaptive and bespoke approaches that reflected variation in geographical isolation, invasion pressure and spatial distribution of identified incursion pathways. Local volunteer recruitment was fundamental to this strategy. Citizens were not only trained so they had the confidence, skills, equipment, protocols and support to contain or prevent
volunteer groups that actively led regional invasive species management. Volunteer groups in both Wales and NI primarily undertook grey squirrel control alongside professional control in order to safeguard residual red squirrel populations. As the Clocaenog Forest population reinforcement in particular demonstrated, the opportunity for citizens to monitor red squirrels not only led to more intensive grey squirrel control in the immediate vicinity, but was a catalyst for control across a wider area. This reduced the threat posed to red squirrels by grey squirrel dispersal. This control intervention would lead to significant parallel landscape benefits in terms of tree protection.

Where squirrelpox presents a threat to endemic red squirrels (Everest et al. 2017), it is now possible to amplify viral DNA from hair (Everest et al. 2019). This means that a non-invasive method of determining viral presence in residual grey squirrel populations is available to squirrel management projects. As an example, testing hair collected via sticky tape placed on squirrel feeding stations gives an indication of an infection present in any particular area at a given time point, thus providing for a potential early warning infection system. Technological genetic advances now mean that research could determine haplotype (mtDNA) and genotype (nDNA) from hair samples collected from grey squirrels found on Anglesey and Clocaenog Forest, allowing comparison against a UK/Ireland genebank to try and determine whether origins of incursion were local, regional or international source populations. RSU volunteers welcomed skill development and earlier citizen-science projects (e.g. Bright et al. 1996; https://www.vwt.org.uk/projects-all/mise/) have demonstrated that the public happily collect biological samples to aid scientific research.
We note that although the establishment of self-sustaining volunteer groups provides a strong post-project legacy, it is well documented that historically, similar established groups frequently state they benefit from the support of paid regional co-ordinators (Shuttleworth et al. 2015). This highlights the further need for Governments to secure ongoing funding to ensure country-wide or regional staffing. In addition, the geographical woodland access restrictions experienced in Clocaenog Forest reinforce the need for projects to minimise geographical access restrictions via negotiation.

The RSU project encompassed rural, suburban and urban areas containing extant red squirrel populations. In locations where red squirrels are extinct and local people have little recollection of their presence, it is likely that fewer citizens would get involved in grey squirrel control as public support for culling is depressed in such circumstances (Dunn et al. 2018). Where red squirrels persist, volunteer efforts have been proven to be frequently sustained and long-term (see Parrott et al. 2009; Shuttleworth et al. 2015; http://www.northernred squirrels.org.uk/). Elsewhere, where red squirrels are absent, it is likely that non-lethal methods of control such as gene-drive (Whitelaw and McFarlane 2019) or chemical contraception (Yoder et al. 2011) would be more attractive to the public than lethal control methods.

The shared project lessons and archived online resources (www.redsquirrels united.org.uk) will assist agencies managing mammalian invasive species internationally, including within Austria, France, Slovenia and Switzerland that are threatened by grey squirrel spread from neighbouring Italy (Lurz et al. 2001). In particular, the evidence gathered that demonstrates proactively providing information about different approaches to grey squirrel control can influence public opinion and support. Greater knowledge about pest species is a key determinant of control acceptability (Bremner and Park 2007).

RSU also provides transferable inter-continental lessons valuable for western Canada and any site of newer grey squirrel introductions. Of particular note are the benefits of model-based grey squirrel incursion pathway prediction (e.g. Flaherty and Lawton 2016) and the central role citizen volunteers have and will continue to play in reporting and removing grey squirrels in both remote upland, rural and urban localities. The westernmost province in Canada, British Columbia, has expansive mountainous terrain with climate and forests (e.g. serotinous pine, Douglas-fir) likely inhabitable or at least suboptimal for grey squirrels (Gonzales 2005). However, the key centres of grey squirrel establishment in the province all are relatively-large cities e.g. Vancouver, Victoria and Kelowna (Nagorsen 2005), in low-elevation regions that contain natural or planted hardwood stands associated with adjacent agricultural landscapes. Deciduous woodland including heavily forested neighbourhoods in these locations create optimal habitat that facilitates grey squirrel establishment;
these new populations in turn increase the potential for even wider spread of the species, as evidenced by the detection of grey squirrels in other communities not directly linked to the above-mentioned cities (e.g. Williams Lake 400 km north of Kelowna – Larsen 2016). Our recommendation, to all agencies battling the expansion of the invasive grey squirrel, is to develop local management approaches, integrated with topographical and habitat barriers to grey squirrel movement. As demonstrated by the RSU project in the UK, local and regional networks of volunteers can cull existing populations and provide a low-cost early detection system to prevent spread (Robinson and Shuttleworth 2019).

Acknowledgements

This article is a part of the conference “Detection and control of forest invasive alien species in a dynamic world” organised by the project LIFE ARTEMIS (LIFE15 GIE/SI/000770), co-funded by the EU LIFE programme, Ministry of Environment and Spatial planning of the Republic of Slovenia and the Municipality of Ljubljana. The article processing charges were covered by the project LIFE ARTEMIS. The paper reports upon outputs from LIFE14 NAT/UK/000467, HG-14-10510 Red Squirrels United and collaboration between Canada and the UK researchers supported by the Winston Churchill Memorial Trust. Project documents and resources are available online www.redsquirrelunited.org. We wish to thank the reviewers whose input greatly improved the original draft manuscript.

Funding Declaration

The studies were funded via LIFE14 NAT/UK/000467, HG-14-10510 Red Squirrels United. The EU LIFE programme and the National Lottery Heritage Fund had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

References

Barbara F, La Morgia V, Parodi V, Toscano G, Venturino E (2018) Analysis of the Incidence of Poxvirus on the Dynamics between Red and Grey Squirrels. *Mathematics* 6: 113, https://doi.org/10.3390/math6070113

Bertolino S, Genovesi P (2003) Spread and attempted eradication of the grey squirrel (*Sciurus carolinensis*) in Italy, and consequences for the red squirrel (*Sciurus vulgaris*) in Eurasia. *Biological Conservation* 109: 351–358, https://doi.org/10.1016/S0006-3207(02)00161-1

Bremner A, Park K (2007) Public attitudes to the management of invasive non-native species in Scotland. *Biological Conservation* 139: 306–314, https://doi.org/10.1016/j.biocon.2007.07.005

Bright PW, Morris P, Mitchell-Jones T (1996) A new survey of the dormouse *Muscardinus avellanarius* in Britain 1993-94. *Mammal Review* 26: 189–195, https://doi.org/10.1111/j.1365-2907.1996.tb00153.x

Cameron TW (1932) On a new species of *Oxyuris* from the grey squirrel in Scotland. *Journal of Helminthology* 10: 29–32, https://doi.org/10.1017/S0022149X00001279

Chantrey J, Dale T, Jones D, Begon M, Fenton A (2019) The drivers of squirrelpox virus dynamics in its grey squirrel reservoir host. *Epidemics* 28: 100352, https://doi.org/10.1016/j.epidem.2019.100352

Dunn M, Marzano M, Forster J, Gill RMA (2018) Public attitudes towards “pest” management: perceptions on squirrel management strategies in the UK. *Biological Conservation* 222: 52–63, https://doi.org/10.1016/j.biocon.2018.03.020

Everest DJ, Stidworthy MF, Milne EM, Meredith AL, Chantrey J, Shuttleworth C, Blackett T, Butler H, Wilkinson M, Sainsbury AW (2010) Retrospective detection by negative contrast electron microscopy of faecal viral particles in free-living wild red squirrels (*Sciurus vulgaris*) with suspected enteropathy in Great Britain. *Veterinary Record* 167: 1007–1010, https://doi.org/10.1136/vr.c4111

Everest DJ, Shuttleworth CM, Stidworthy MF, Grierson SS, Duff PJ, Kenward RE (2014) Adenovirus infection: An emerging factor in red squirrel conservation programmes. *Mammal Review* 44: 225–233, https://doi.org/10.1111/mam.12025

Everest DJ, Floyd T, Donnachie B, Irvine RM, Holmes JP, Shuttleworth CM (2017) Confirmation of squirrelpox in Welsh red squirrels. *Veterinary Record* 181: 514–515, https://doi.org/10.1136/vr.j5132
Robinson N, Shuttleworth CM (2019) Invasive Alien Species Colonisation Prevention: Your guide to early detection and rapid response. The Royal Society of Wildlife Trusts, 204 pp

Romeo C, Ferrari N, Lanfranchi P, Saino N, Santicchia F, Martinoli A, Wauters LA (2015) Biodiversity threats from outside to inside: effects of alien grey squirrel (Sciurus carolinensis) on helminth community of native red squirrel (Sciurus vulgaris). Parasitology Research 114: 2621, https://doi.org/10.1007/s00436-015-4466-3

Romeo C, McInnes C, Dale T, Shuttleworth CM, Bertolino S, Wauters L, Ferrari N (2018) Disease, invasions and conservation: no evidence of squirrelpox virus in grey squirrels introduced to Italy. Animal Conservation 22: 14–23, https://doi.org/10.1111/acv.12433

Rushton SP, Lurz PWW, Gurnell J, Nettleton P, Bruenmer C, Shirley MDF, Sainsbury AW (2006) Disease threats posed by alien species: The role of a poxvirus in the decline of the native red squirrel in Britain. Epidemiology and Infection 134: 521–533, https://doi.org/10.1017/S0950268805005303

Santicchia F, Dantzer B, van Kesteren F, Palme R, Martinoli A, Ferrari N, Wauters LA (2018) Stress in biological invasions: Introduced invasive grey squirrels increase physiological stress in native Eurasian red squirrels. Journal of Animal Ecology 87: 1342–1352, https://doi.org/10.1111/1365-2656.12853

Signorile AL, Shuttleworth CM, Hayward M (2015) Future Red Squirrel Conservation In Clocaenog Forest. Natural Resources Wales Contract Report P21018-00026

Signorile AL, Shuttleworth CM (2016) Genetic evidence of the effectiveness of grey squirrel control operations: lessons from the Isle of Anglesey. In: Shuttleworth CM, Lurz PWW, Gurnell J (eds), The grey squirrel: ecology & management of an invasive species in Europe. European Squirrel Initiative, Woodbridge, Suffolk, 120 pp

Shuttleworth CM, Hayward M (2015) Future Red Squirrel Conservation in Clocaenog Forest. European Squirrel Initiative, Woodbridge, Suffolk, UK, 220 pp

Shuttleworth CM, Hayward M (2015) Red Squirrel (Sciurus vulgaris) Conservation Plan for Anglesey and Gwynedd. A report prepared for Natural Resources Wales and Royal Society of Wildlife Trusts. EU LIFE14 NAT/UK/000467

Shuttleworth CM, Halliwell EC (2018) Red squirrels in my garden: Guidance and tips to help encourage and conserve local populations. European Squirrel Initiative, Woodbridge, Suffolk, 120 pp

Shuttleworth CM (2003) A tough nut to crack: red squirrel conservation in Wales. The Ecologist 33: 231–235

Shuttleworth CM, Lurz PWW, Halliwell EC (2015) Shared Experience of Red Squirrel Conservation Practice. European Squirrel Initiative, Woodbridge, Suffolk, UK, pp 475–494

Shuttleworth CM, Lurz PWW, Gurnell J (2006) Interspecific competition in tree squirrels: do introduced grey squirrels (Sciurus carolinensis) deplete tree seeds hoarded by red squirrels (Sciurus vulgaris)? Animal Conservation 9: 360–367, https://doi.org/10.1017/S0950268805005303

Stress in biological invasions: Introduced invasive grey squirrels increase physiological stress in native Eurasian red squirrels. Journal of Animal Ecology 87: 1342–1352, https://doi.org/10.1111/1365-2656.12853

Teangana DO, Reilly S, Montgomery WI, Rochford J (2000) Distribution and status of the Red Squirrel (Sciurus vulgaris) and Grey Squirrel (Sciurus carolinensis) in Ireland. Mammal Review 30: 45–56, https://doi.org/10.1046/j.1365-2907.2000.00054.x

Welsh Government (2018) Grey squirrel management action plan for Wales (WG35495). https://gov.wales/grey-squirrel-management-action-plan-for-wales

Whitelaw B, McFarlane G (2019) Accelerating evolution. The Biologist 66: 18–21

Yoder CA, Mayle BA, Furcolow CA, Cowan DP, Fagerstone KA (2011) Feeding of grey squirrels (Sciurus carolinensis) with the contraceptive agent Diazac®-TM effect on cholesterol, hematology, and blood chemistry. Integrative Zoology 6: 409–419, https://doi.org/10.1111/j.1749-4877.2011.00247.x