Containment of invasive grey squirrels in Scotland: meeting the challenge

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Abstract Saving Scotland's Red Squirrels (SSRS), launched in 2009, is a project to stop the decline of core populations of Scotland's native red squirrel. It is a partnership project between Scottish Wildlife Trust, Scottish Natural Heritage, Forestry Commission Scotland, RSPB Scotland, Scottish Land & Estates and the Red Squirrel Survival Trust. The aim is the containment of the invasive non-native grey squirrel, which poses a dual threat to red squirrels through competition and disease transmission. Grey squirrels have replaced red squirrels over much of their former range in England, Wales, Ireland and central Scotland. SSRS controls grey squirrels at a landscape-scale in three strategically selected zones: in north-east Scotland, where the aim is eradication of an isolated grey squirrel population; coast to coast along the Highland Boundary Fault the aim is to prevent northwards incursion of grey squirrels into the Scottish Highlands and Argyll, where red squirrel is still the only species; and in southern Scotland, the aim is now to prevent replacement of priority red squirrel populations by focussing control in areas identified as having the best prospects for the long-term maintenance of red squirrel populations. Control methods involve live cage-trapping combined with humane dispatch. The control network comprises SSRS and Forestry Commission controllers, private landowners supported by EU/government funding and a large number of individual volunteers. The work is dependent on wide public acceptance and active volunteer support. To date SSRS has been successful at significantly reducing grey squirrel geographic range and occupancy in NE Scotland and as well as reducing the incidence of grey squirrels north of the 'Highland Line' to no more than the occasional occurrence. In southern Scotland grey squirrel control has contributed to the maintenance of red squirrel populations despite the continued spread of squirrelpox in grey squirrels. The major challenge now is sustaining the level of grey squirrel control needed to secure Scotland's red squirrel populations in the long term. A new project phase started in 2017, focused on building community action networks until such a time as alternatives means of controlling grey squirrel numbers and disease impacts become widely available.

Keywords: adaptive management, community engagement, land manager, sustainability, trapping effort, volunteer

INTRODUCTION

Grey squirrels (*Sciurus carolinensis*) were introduced into Britain in the 1890s from the US and Canada, including to several release sites in Scotland (Middleton, 1930; Middleton, 1931). The impact of grey squirrels on native red squirrel (*Sciurus vulgaris*) populations was documented relatively early after their introduction (Middleton, 1931; Shorten, 1962), but their range expansion was initially quite modest (Gurnell, 1987). The role of grey squirrels in the replacement of red squirrels was possibly not fully recognised until the 1980s (Lloyd, 1983; Skelcher, 1997; Reynolds, 1998), by which time grey squirrels occupied much of southern and central England and Wales and central Scotland (Lloyd, 1983).

The factors leading to the replacement of red by grey squirrels have been the subject of extensive research (reviewed by Gurnell, et al., 2014b). The evidence indicates that competition with grey squirrels for food resources alone can account for the loss of red squirrels from many forests (Bryce, et al., 2001; Wauters, et al., 2002). However, added to this is the threat of squirrelpox virus, which is carried by grey squirrels and is highly pathogenic to red squirrels (Sainsbury, et al., 2000, Thomas, et al., 2003), greatly enhancing the speed of replacement (Rushton, et al., 2006).

Red squirrels have been protected under UK law since the 1930s and bounty schemes were enlisted to combat increasing grey squirrel numbers in the 1950s (Sheail, 1999). However, low-level, sporadic control has failed to halt the spread of grey squirrels (Lawton & Rochford, 2007). Grey squirrels are already widespread and abundant throughout much of the UK and eradication is not considered to be a realistic option (Gurnell & Pepper, 1993; Pepper & Patterson, 1998). EU Regulation 1143/2014 on Invasive Alien Species lists grey squirrels as species of Union concern, hence Member States are required to take concerted management action to ensure they do not spread any further and to minimise the harm they cause to the environment.

Large-scale control and containment of grey squirrels was originally seen as an interim approach, whilst more sustainable, long-term control measures were developed (Scottish Squirrel Group, 2004; Scottish Natural Heritage, 2010). However, in the absence of a squirrelpox vaccine or immuno-contraceptive, there has been growing support for targeted grey squirrel control to protect red squirrel populations (Scottish Natural Heritage, 2010). Following public consultation, a draft strategy for grey squirrel control in Scotland was published (Scottish Natural Heritage, 2010), which focuses on targeted control to maximise the benefits for red squirrels.

A collaborative project under the heading 'Saving Scotland's Red Squirrels' (SSRS), was formalised in 2009. It is a partnership comprising the Scottish Wildlife Trust (SWT), Scottish Natural Heritage, Forestry Commission Scotland, RSPB Scotland, Scottish Land & Estates and the Red Squirrel Survival Trust. SSRS has become the principal means of coordinating red squirrel protection in Scotland. The focus of SSRS is on applied conservation action, but SSRS has made a concerted effort to collate records and monitor squirrel populations and has worked closely with researchers to inform an adaptive approach. A key challenge to SSRS has been to assess the efficacy and sustainability of control measures. This paper explores some of the work carried out to address these challenges and highlights some of the learning to date.

THE SSRS APPROACH

Co-ordination of grey squirrel control

The main focus of SSRS activity is the co-ordination of grey squirrel control. SSRS aims to co-ordinate grey

squirrel control across three strategic control zones (Fig. 1). The aims vary between zones reflecting the degree to which grey squirrels are already established. The Highlands of Scotland are currently free of grey squirrels; grey squirrels are long established in central Scotland (with introductions between 1892-1919) and had spread throughout much of the Central Lowlands by the 1980s; grey squirrels have spread into South Scotland from both the north and from northern England in recent years (Gurnell, et al., 2014a). The grey squirrel population in NE Scotland (Aberdeen and Aberdeenshire) has been recorded for about 30 years (Lloyd, 1983; Staines, 1986), and there is evidence it originates from a separate introduction rather than having spread from grey squirrels elsewhere in Scotland (Signorile, 2013). Squirrelpox was first reported to have crossed from northern England into Scotland in 2005, with the first cases in red squirrels observed in 2007 (McInnes, et al., 2009). The original SSRS aims are listed as follows, although these have been adapted in light of experience as is discussed later.

North-east (NE) Scotland – the original aim was to halt the spread of grey squirrels outwards from the city of Aberdeen;

Central Lowlands – SSRS's work in the Central Lowlands aims to contain the northward spread of grey squirrels into the Highlands and Argyll by carrying out control from coast to coast; along what is referred to as the 'Highland Line' a zone of control extending for some 160 km from just north of Glasgow to Montrose on the east coast.

Southern Scotland – the initial aim was to contain the spread of squirrelpox virus in south Scotland.

Grey squirrel control is currently carried out by a mixture of project staff, land managers and volunteers:

 Working with up to 197 landowners under five-year EU and Scottish Rural Development Programme funding (SRDP);

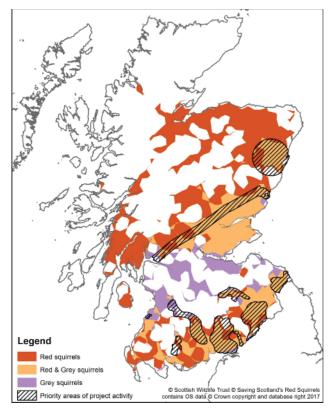


Fig. 1 Map of Saving Scotland's Red Squirrels project control zones.

- Co-ordination via five conservation officers, six fulltime and five part-time grey squirrel control officers;
- A trap-loan scheme involving up to 200 landowners, and 500 individuals.

Trapping is also carried out by Forest Enterprise Scotland at key sites on the National Forest Estate. Figure 2 illustrates the coverage of grey squirrel control initiated by SSRS by 2012 (from Tonkin, et al., 2015).

With a view to the long term, SSRS has sought to encourage land managers to carry out grey squirrel control on their own land. Regional conservation staff provide support to landowners applying for funding available through the SRDP to help cover the costs. SRDP contracts require land managers to operate an appropriate number of traps (as advised by SSRS staff) for a minimum number of sessions per year (usually five or six). All the traps are to be set for a minimum number of days (usually 10). SSRS control officers trap with landowner permission, in key gaps in the landowner protection network (Fig. 2). Most of the grey squirrel control occurs between April and the end of September, when grey squirrels are easier to catch. Due to the lack of specificity of other methods and animal welfare considerations (Central Science Laboratory, 2009), the SSRS Standard Operating Procedures specify the use of cage trapping and humane dispatch.

Trapping by SSRS control officers has typically followed the approach of five days pre-baiting and then trapping continuously until no or few further grey squirrels are caught. Traps are then revisited on a rotation. The traps are not located at a standardised density, but instead are grouped in areas of preferred grey squirrel habitats in the target zones. In South Scotland grey squirrel control by SSRS control officers was initially carried out in the area buffering known squirrelpox seropositive cases. The grey squirrels were then sent for laboratory testing for squirrelpox. Hence control effort was reactive and did not take place in the same locations across time.

In NE Scotland, in particular, SSRS is working in periurban and urban areas. Initially this created a challenge because large areas of wooded habitats in private gardens and parks were difficult to access, leaving reservoirs of grey squirrels. To address this challenge and to harness the community enthusiasm in other areas, SSRS has successfully instigated a trap-loan scheme. Under this scheme householders take responsibility for setting and monitoring traps (supplied by SSRS) in their garden. They

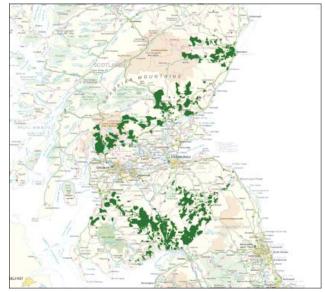


Fig. 2 Red squirrel protection network established across Scotland by 2012 (from Tonkin, et al., 2015).

are matched with a local trapper (gamekeeper or control officer) who is available to carry out humane dispatch. Project staff have also developed innovative trap designs for trapping grey squirrels in city parks to avoid drawing attention to traps.

Grey squirrel control in public spaces and, in particular, the involvement of volunteers requires a high degree of public acceptance, which is not guaranteed (Bertolino & Genovesi, 2003). A targeted approach to control was broadly supported in a public consultation (Scottish Natural Heritage, 2010) and public surveys in Aberdeen and Aberdeenshire have established that despite residents enjoying seeing grey squirrels, there is an appreciation of the need for grey squirrel control due to their impact on red squirrels (Ashbrook Research Consultancy Ltd, 2010).

Evaluation of control measures

Alongside establishing the network of grey squirrel control, SSRS has sought to collect evidence that this work is benefitting red squirrels. This has been critical for securing public funding for grey squirrel control. Three methods were employed by the SSRS in order to evaluate the efficacy of grey squirrel control:

- Evaluation of grey squirrel capture probability from trapping data;
- Annual (presence/absence) monitoring of red and grey squirrel occupancy in the three project areas, and
- Public sightings of squirrels across Scotland that have been catalogued since 2007.

Annual (presence /absence) monitoring of red and grey squirrels has been co-ordinated by SSRS in NE Scotland and the Central Lowlands since 2011 and since 2013 in South Scotland. The surveys are intended to assess if there are changes in squirrel distributions that can be attributed to the project. Nearly 200 volunteers have been mobilised to carry out these surveys. A sample of 2 km ×2 km grid squares or 'tetrads' are surveyed across each control zone. Four baited feeder-boxes are permanently located in woodland within each tetrad. Each feeder-box is checked by volunteers three times over a period of six weeks each spring. Hairs are identified under a microscope and each tetrad is consequently allocated to one of the following four categories: "red squirrels only", "grey squirrels only", "both species", or "neither" species (Fig. 3, Shikhorshidi & Tonkin, 2018). The number of tetrads has increased over time, but comparison of the same tetrads over time enables detection of changes in squirrel distributions. Changes between years have been explored using a replacement index as per Usher, et al. (1992). A positive index represents a change in tetrad occupancy in favour of grey squirrels and a negative index, a change in favour of red squirrels (Usher, et al., 1992).

A programme of squirrelpox surveillance has also helped guide the work in South Scotland. In 2012, grey squirrels were sampled from a systematic sample of locations across the whole of South Scotland to try and establish the full extent of exposure to the virus (10 grey squirrels are sampled from one 10 km square in every 20 km \times 20 km square across the region).

RESULTS

Evaluation of grey squirrel capture probability

The project initially aimed to gather data on grey squirrel trapping across all three control zones, however, inconsistencies in recording between the different project delivery models has made it problematic to fully assess the cumulative trapping effort that has been achieved. The control officers' data are the most reliable. The format of other records varies, effort is not always systematically recorded and problems have been encountered (data gathering and ownership) in accessing results of trapping from the land mangers supported by SRDP funding. Forestry Enterprise Scotland controllers' data are included with the control officers' data where this has been possible. The minimum total number of grey squirrels controlled and the trapping effort achieved have been estimated from collated data (SWT pers. comm.). It is estimated that between 2009 and 2016:

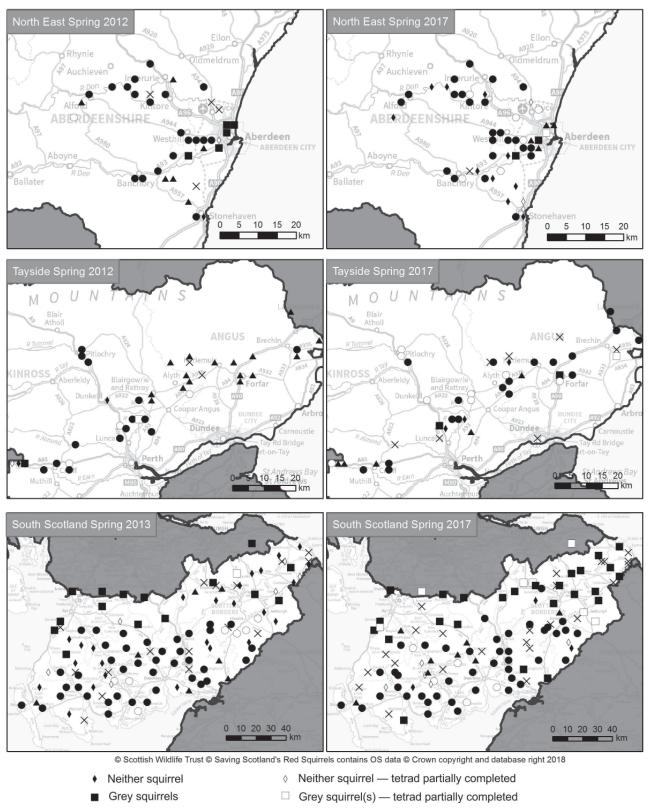
- Control officers provided c. 214,000 trap days (the number of traps multiplied by the number of days for which traps are set) and controlled c. 13,000 grey squirrels (Table 1); and
- Up to 197 SRDP contracts were established (Scottish Government Statistics, 2014), with those reporting accounting for 1.1 million trap days and having controlled c. 18,000 grey squirrels Table 1).

Those in receipt of trap loans have not consistently reported trapping effort, however, the trap loan scheme in NE Scotland has made a larger contribution to the red squirrel protection network than elsewhere, with trap loans here accounting for the removal of more than 1,700 grey squirrels between 2010 and 2016 (SWT pers. comm.).

Due to the scale of the task to follow up on missing trapping information, SSRS have sought to collect as complete trapping data as possible for four demonstration areas in order to assess the cumulative impact on grey squirrel capture probability (a proxy for abundance). The size of demonstration areas is not equivalent but as an illustration of control effort (control officer and landowner data), the total number of trap days in 2014 in NE Scotland demonstration area (55 km²) was 6,614 trap days, in Tayside (222 km²) was 15,004 trap days, in Argyll & Trossachs (278 km²) was 6,482 trap days and in South Scotland (604 km²) was 15,206 trap days (Table 2). Only the NE Scotland and Tayside demonstration areas had generated sufficient time series of data for detailed analysis by 2013 as reported in Tonkin, et al. (2013).

Using all the available trapping data for the NE Scotland Demonstration Area between 2007 and June 2013 and the Tayside Demonstration Area from 2010 to 2012, a GLMM was used to explore the relationship between the probability of grey squirrel capture and a range of explanatory variables including the cumulative control effort for each trap location, taking account of nearby captures. There was found to be a significant negative effect of cumulative control effort on the probability of grey squirrel capture in both areas (Tonkin, et al., 2013). In Tayside the GLMM coefficient was -1.54 (CI -1.99 -1.09), and in NE Scotland was -0.34 (CI -0.51 - -0.18) (both on link scale of logit model). Effects were found to be stronger in areas with the highest cumulative control effort. In these areas in Tayside the mean capture probability was close to zero and in NE Scotland was seven-fold lower than areas with relatively low effort (Tonkin, et al., 2013,). These results support the premise that trapping is having the desired effect of reducing grey squirrel abundance.

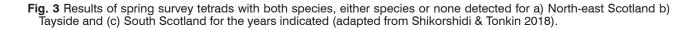
The reactive pattern of trapping in South Scotland in response to detecting squirrelpox, makes the data from this region problematic for assessing the impact of trapping on grey squirrel abundance. Added to this, despite the scale of trapping effort in South Scotland, it was apparent that the virus was still spreading (White & Lurz, 2014; Tonkin, et al., 2015). Hence SSRS sought the help of researchers to assess if containment of the virus was a realistic objective. White & Lurz (2014) used a spatially explicit population model to explore the spread of the disease under a range of control scenarios and levels of effort. Simulated control



- Red squirrel(s) tetrad partially completed
- Red and grey squirrels

Red squirrels

× Tedrad not surveyed



| | Grey Squirrel Of | fficer Control | SRDP supported land manger control | | |
|---|-----------------------|----------------------|------------------------------------|----------------------|--|
| Year | Total no of trap days | No of greys captured | Total no of trap days | No of greys captured | |
| 2009 | 6,610 | 471 | 7,610 | 71 | |
| 2010 | 18,615 | 1,637 | 41,365 | 510 | |
| 2011 | 34,150 | 2,191 | 76,906 | 2,817 | |
| 2012 | 40,783 | 2,797 | 237,738 | 3,630 | |
| 2013 | 42,991 | 1,690 | 256,456 | 3,730 | |
| 2014 | 32,889 | 1,819 | 222,031 | 2,713 | |
| 2015 | 27,833 | 2,013 | 172,222 | 3,293 | |
| 2016 | 9,776 | 490 | 89,316 | 1,029 | |
| Total | 213,647 | 13,108 | 1,103,644 | 17,793 | |
| Average grey squirrel capture rate/100TN 6.14 | | | _ | 1.61 | |

 Table 1 Grey squirrel control achieved in all SSRS regions by control officers and land managers supported by SRDP funding.

was parameterised to assess the impact of current control measures; approximating the number of grey squirrels removed and adjusting the intensity of control in the model to mirror these levels by varying the area over which control was applied (White & Lurz, 2014). An alternative control scenario involving control along key dispersal routes was also assessed. The projections highlighted that current levels of control would not prevent the spread of the disease across Southern Scotland. Targeted control could help slow the spread of the virus but was unlikely to halt its spread in areas where grey squirrels are already established. However, the modelling also indicated that co-ordinated grey squirrel control should allow local red squirrel populations to persist and their density can recover after disease outbreaks in conifer dominated landscapes (White & Lurz, 2014; White, et al., 2016).

Annual (presence/absence) monitoring red and grey squirrels

The programme of annual presence/ absence monitoring indicates that red squirrel distributions have remained stable and that there have been some reductions in the range of grey squirrels in north Scotland and conversely some expansion in south Scotland (Fig. 3, Shirkhorshidi & Tonkin, 2018). The 2017 results of the tetrads in the north of Scotland as a whole (NE Scotland and Central Lowlands) show a significant change in favour of red squirrels when compared with 2012 (RI=-0.17, P=0.02). Contributing to this is a significant decrease in grey squirrel occupancy across the north and an increase in red squirrel distribution in the north-east, particularly in areas close to the City of Aberdeen; meanwhile red squirrel occupancy has been stable across the Highland Line (Shirkhorshidi & Tonkin, 2018). Although not significant, the overall changes in the south of Scotland have been in favour of grey squirrels (2013-2017 RI = 0.19). This reflects an increase in grey squirrel occupancy (largely outside SSRS areas of operation), whilst red squirrel occupancy appears to have been maintained (Shirkhorshidi & Tonkin, 2018). Whilst noting that squirrel populations experience fluctuations between years relating to seed crops, we interpret the overall trends in occupancy as an indication that SSRS's actions are helping to meet the project aims.

Public sightings of squirrels

Although they do not represent a systematic sample, public sightings help to harness public support and provide an early warning of range expansion of both red and grey squirrels. Sightings are mapped on the SSRS website

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(SSRS, 2018). For example, public reports have helped illustrate where red squirrels have returned to areas where they had not been recorded in the last 20 or 30 years following grey squirrel control, such as Aberdeen city parks (SSRS, 2017).

There has also been some standardisation and analysis of public sightings of squirrels between 1991 and 2010 across different regions of the UK (Gurnell, et al., 2014a). The data suggest red squirrel occupancy is declining in all regions over this period (at different rates), with the exception of Central Lowlands (east) of Scotland which fluctuates showing little overall change. However, an upward turn in red squirrel occupancy in the last two or three years is noted across all regions, especially South Scotland. Gurnell, et al. (2014a) indicate it is too early to speculate if the apparent upturn in the fortunes of red squirrels is as a result of grey squirrel control or other factors.

DISCUSSION AND FURTHER DEVELOPMENTS

We have described the evidence showing that sustained grey squirrel trapping can reduce grey squirrel abundance and occupancy at a landscape scale (Tayside and NE Scotland). Trapping data from Wales around the same time, indicates that sustained trapping can bring about reductions in grey squirrel populations at a landscape scale (Schuchert, et al., 2014). However, it has also been demonstrated that recolonisation can occur following intensive grey squirrel control after between one and three months (Lawton & Rochford, 2007; Schuchert, et al., 2014). Hence, SSRS are involved in further work to better quantify the level of control that might need to be sustained and, in particular, to put in place more sustainable delivery models.

The collaboration with researchers that started in South Scotland is now focussed on addressing the question of how much control may be required along the Highland Line to prevent grey squirrels from extending their range to the north. A spatially explicit population model (White, et al., 2017) has examined the impact of three levels of trapping intensity on grey squirrel populations in the Central Lowlands. Projections include the presence of squirrelpox virus (as a worst-case scenario) even though it has not yet been detected in this region. The potential density of red and grey squirrels in each 1 km \times 1 km patch is derived based on average squirrel densities for the mixture of habitats encountered. Control is applied in targeted zones (typically 10 km \times 10 km) and, mirroring trapping practice, can occur from 1 April to 30 September

(183 days), which is split into three 61 day (2 month) control periods. Trapping is applied in a responsive way to grid squares in which grey squirrels are present and in grid squares in a 2 km buffer zone in each of the three control periods. The model was run for three levels of trap intensity (TD = 0.3 - low; 0.5 - medium; 0.75 - high). This equates to $0.3 \times 183 = 55$ trap days per year (in a 1 km ×1 km grid square) in the low intensity scenario, 92 trap days per year (medium) and 137 trap days per year per (high), respectively.

In the low intensity scenario, trapping represents a kind of harvesting; there are abundant greys to catch and greys persist indefinitely. At medium intensity, control appears to be largely effective at preventing the northwards spread along the Highland Line. The model also highlights key dispersal routes where high intensity trapping is likely to be required (White, et al., 2017). Taking the Tayside Demonstration area (a key dispersal route) as an example the average, annual control effort predicted to be required (regions 7, 8, 9 in White, et al., 2017) is c. 18,000 trap days under the high intensity scenario. Given the modelled control area includes a slightly larger area than the Tayside demonstration area in order to prevent recolonisation, the levels of control suggested by the model are of the same order as control on the ground between 2012 and 2014 (Table 2) suggesting that this level of control effort needs to be maintained (White, et al., 2017).

Having successfully reduced the range, abundance and occupancy of grey squirrel populations in NE Scotland (Tonkin, et al., 2013; Shirkhorshidi & Tonkin, 2018), eradication of this isolated population now seems like a realistic prospect. However, some of the locations remaining untrapped are more challenging (smaller, fragmented and increasingly urban habitats). In 2014, SSRS set up an additional layer of monitoring to establish grey squirrel occupancy across the entire wooded network in the region. Feeder-box squirrel hair traps (n=223) have been distributed through all the suitable grey squirrel habitat patches in urban Aberdeen and the surrounding area. These data will allow analysis of grey squirrel occupancy (MacKenzie, et al., 2006) and better projections for the time and effort required to eradicate this isolated population. The monitoring will be complemented by rapid-response grey squirrel control.

SSRS's approach in South Scotland has adapted following the continued spread of squirrelpox virus and the model outcomes reported in White & Lurz (2014). The modelling indicates that co-ordinated grey squirrel control can help to protect red squirrel populations from the threat of squirrelpox virus in conifer dominated landscapes,

Table 2Combined grey squirrel control effort (annual
trap days) achieved by control officers and landowners
supported by SRDP funding in the four demonstration
areas 2009–2016.

| | NE Scotland | Central Scotland | | Sau4h |
|------|----------------|-------------------------|-----------------------|---------------------|
| | | Tayside | Argyll & Trossachs | - South Scotland |
| 2009 | 2,465 | NA | NA | 4,987 |
| 2010 | 5,946 | 3,389 | 48 | 14,678 |
| 2011 | 7,878 | 8,201 | 360 | 17,912 |
| 2012 | 10,554 | 14,677 | 6,803 | 16,934 |
| 2013 | 6,178 | 16,158 | 6,721 | 20,079 |
| 2014 | 6,614 | 15,004 | 6,482 | 15,206 |
| 2015 | 7,500 | 9,780 | 6,590 | 5,114 |
| 2016 | 4,840 | 7,990 | 6,294 | 1,654* |

*Landowner data not available

where red squirrels typically occur at low densities, but importantly higher than those of grey squirrels. SSRS's control efforts have now shifted from the 'frontline' of squirrelpox detection to protecting identified priority areas for red squirrel conservation in South Scotland.

Sustaining the action

SSRS was initially funded for three years and eight months (2008–12), which was then extended by a further four years. The lead partner, SWT, secured a mixture of public and charitable funds to meet a project budget of just over £3 million covering the period 2008–16. In 2016, SWT secured a Heritage Lottery Fund Award of £2.46 million for the next 5 years (until 2022) towards a total project cost of £4.4 million. Hence, the costs have been roughly £0.5 million per annum to date. The piecemeal nature of project funding creates a challenge for sustaining co-ordinated grey squirrel control. Under the new SSRS phase, costs are anticipated to rise to c. £0.88 million per annum reflecting the additional activities aimed at ensuring the long-term sustainability of the control network and with a view to substantially reducing costs thereafter.

By September 2013, 197 landowners were in receipt of five-year SRDP funding at a cost of £4.5 million over the five-year period covered by the contracts. Although trapping by control officers is on average nearly four times more efficient (more captures per 100 trap days, Table 1) than SRDP-supported landowner grey squirrel control, landowner control provides five times more trapping effort than is provided by control officers (Table 1). Hence, being able to access public funding support has been hugely important. However, public funding is not without its challenges including: ease of access to the scheme for applicants; and ensuring trapping data are available to SSRS. Added to this there are uncertainties about the future of support upon leaving the European Union.

Quantifying the control effort needed to deliver SSRS's objectives has been challenging. However, SSRS's monitoring and associated modelling has supported that the levels achieved seem 'about right'. However, this equates to a substantial network of grey squirrel control that needs to be sustained.

Reflecting the successes to date and the challenges ahead, the next five-year phase is called Saving Scotland's Red Squirrels – Developing Community Action. This project's actions are geared towards long-term sustainability and how SSRS's work can be embedded in routine land management and community action, with a move away from reliance on project staff. Project funding at this level of investment is increasingly hard to find, hence there is an expectation that red squirrel conservation will increasingly rely on public delivery.

SSRS - Developing Community Action now aims to eradicate grey squirrels from NE Scotland within 10 years. In South Scotland the aims have been refined and focus on building the skills and resources available to local people and land managers working to control grey squirrels in identified priority areas. As part of this, a Community Hub information management system is being developed for staff and volunteers, which will better capture and integrate data from all sources and will allow improved feedback. For each priority area, an annual trapping programme is being developed that is capable of continuing to protect the red squirrel population. As yet it remains to be determined if the necessary levels of control can be sustained by these means. However, there is a shift in the focus of SSRS work from demonstrating the efficacy of control on to how can it be delivered.

Largely based on the evaluation of work co-ordinated by SSRS, the national policy position now recognises coordinated grey squirrel control as an integral part of the long-term approach to achieving the strategy aims (Scottish Squirrel Group, 2015).

The challenge of protecting Scotland's red squirrels remains significant given the scale and the ongoing nature of the work. However, the prospects for alternative/ or complementary approaches are also improving. Immunocontraceptives and squirrelpox vaccines are actively being explored with the support of parallel initiatives under the 'UK Squirrel Accord' but are likely to be some years in development. New research into the role of pine marten on the dynamics of red and grey squirrels also offers promising insights in that as pine marten populations recover their range and densities, grey squirrel populations appear to be suppressed in the presence of this novel (to them) native predator, thereby reducing the levels of management control required to promote red squirrel persistence (Sheehy, et al., 2018).

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REFERENCES

- Ashbrook Research Consultancy Ltd (2010). Assessment of Public Attitudes to Grey Squirrel Control in Aberdeen. Scottish Natural Heritage, Commissioned Report No. 384. Battleby, Perth: Scottish Natural Heritage
- Bertolino, S. and 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(3): 351-358.
- Bryce, J., Johnson, P.J. and Macdonald, D.W. (2001). 'Can niche use in red and grey squirrels offer clues for their apparent coexistence? Journal of Applied Ecology 39: 875-887.
- Central Science Laboratory (2009). Review of Methods of Humane Destruction of Grey Squirrels (Sciurus carolinensis). Scottish Natural Heritage Commissioned Report No, 317. Battleby, Perth: Scottish Natural Heritage.
- Gurnell, J. (1987). The Natural History of Squirrels. London: Christopher Helm
- Gurnell, J. and 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. and Bertolino, W. (2014a). 'The changing
- patterns in the distribution of red and grey squirrels in the north of England and Scotland between 1991 and 2010 based on volunteer Surveys'. Hystrix, the Italian Journal of Mammalogy 25 (2): 83–89. Gurnell, J., Lurz, P.W.W. and Wauters, L.A. (2014b). Years of Interactions
- and Conflict in Europe: Competition Between Éurasian Red Squirrels and North American Grey Squirrels'. In: C.M. Shuttleworth, P.W.W. Lurz and M.W. Hayward (eds.) *Red Squirrels: Ecology Conservation and Management in Europe*, pp. 19–37. Llangefni: European Squirrel Initiative.
- Lawton, C. and Rochford, J. (2007). 'The recovery of grey squirrel (Sciurus carolinensis) populations after intensive control programmes Biology and Environment: Proceedings of the Royal Irish Academy Vol.
- 107B, No. 1: 19–29. Lloyd, H.G. (1983). 'Past and present distributions of red and Grey
- Squirrels'. Mammal Review 13: 69–80.
 MacKenzie, D.I., Nichols, J.D., Royle, A.J., Pollock, K.H., Bailey, L.L. and Hines, J.E (2006). Occupancy Estimation and Modlling: Inferring Patterns and Dynamics of Species occurrence. Burlington, Massachusetts: Elsevier Academic Press
- Massachusetts: Elsevier Academic Press.
 McInnes, C.J., Coulter, L., Dagleish, M.P., Fiegna, C., Gilray, J., Willoughby, K., Cole, M., Milne, E., Meredith, A., Everest, DJ., and MacMaster, A. (2009). 'First cases of squirrelpox in red squirrels (*Sciurus vulgaris*) in Scotland'. *Veterinary Record* 164: 528–531.
 Middleton, A.D. (1930). 'The ecology of the American grey squirrel (*Sciurus carolinensis* Gmelin) in the British Isles'. *Proceedings of the Technology of the*
- Zoological Society of London 100: 809-843.
- Middleton, A.D. (1931). *The Grey Squirrel*. London: Sidgwick & Jackson. Pepper, H., and Patterson, G. (1998). *Red Squirrel Conservation*. Forestry
- Commission Practice Note 5. Edinburgh: Forestry Commission. <www. forestry.gov.uk/pdf/fcpn5.pdf/\$file/fcpn5.pdf>.

- Reynolds, J. (1998). 'Details of the geographic replacement of the red squirrel (*Sciurus vulgaris*) by the grey squirrel (*Sciurus carolinensis*) in Eastern England'. *Journal of Animal Ecology* 54: 149–162.
- Rushton, S.P., Lurz, P.W.W. Gurnell, J., Nettleton, P., Bruemmer, C. and Shirley, M.D.F. (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. Sainsbury, A. W., Nettleton, P., Gilray, J. and Gurnell, J. (2000). 'Grey
- squirrels have a high seroprevalence to a parapoxvirus associated with deaths in red squirrels'. *Animal Conservation* 3: 229–233.
- Schuchert, P., Shuttleworth, C.M., McInnes, C.J., Everest, D.J. and Rushton, S.P. (2014). 'Landscape scale impacts of culling upon a European grey squirrel population: Can trapping reduce population size and decrease the threat of squirrelpox virus infection for the native red squirrel?'. *Biological Invasions* 16: 2381–2391.
- squirrel?". Biological Invasions 16: 2381–2391.
 Scottish Government Statistics (2014) 'Number and value of Rural Development Contract: Rural Priorities Options funding under the 2007–13 SRDP'. [Statistics web resource]. <www.gov.scot/Resource/0044/00449780.pdf>. Accessed 20 February 2018.
 Scottish Natural Heritage (2010). Protecting Scotland's Red Squirrels. The Consultation Response. Battleby, Perth: Scottish Natural Heritage.
 Scottish Squirrel Group (2004). Scottish Strategy for Red Squirrel Conservation. Battleby, Perth: Scottish Natural Heritage.

- Scottish Squirrel Group (2015). Scottish Strategy for Red Squirrel Conservation. Battleby, Perth: Scottish Natural Heritage. https://www. nature.scot/scottish-strategy-red-squirrel-conservation-june-2015. Sheail, J. (1999). 'The grey squirrel (Sciurus carolinensis) – A UK
- historical perspective on a vertebrate pest species'. Journal of Environmental Management 55: 145–156.
- Sheehy, E., Sutherland, C., O'Reilly, C. and Lambin, X. (2018). 'The enemy of my enemy is my friend: native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations'. *Proceedings of the Royal Society B* 285: 20172603. <://dx.doi. org/10.1098/rspb.2017.2603>. Accessed 9 April 2018. Shorten, M. (1962). 'Squirrels, their biology and control'. *Ministry of Agriculture Fisheries and Food Bulletin* 184: 1–44.
- Shirkhorshidi, M. and Tonkin, M. (2018) Results of Spring 2017 Squirrel Surveys. Saving Scotland's Red Squirrels report. Edinburgh: Scottish Wildlife Trust. <www.scottishsquirrels.org.uk/docs/087_506_ ssrssquirrelsurvey2017_1517589214.pdf>. Signorile, A.L. (2013). 'Genetic Determinants of the Expansion of
- Eastern Grey Squirrel Populations Across Europe². PhD thesis. London: Imperial College London and Institute of Zoology, Zoological Society.
- Skelcher, G. (1997). 'The Ecological Replacement of Red by Grey Squirrels'. In: J. Gurnell and P.W.W. Lurz (eds.) *The conservation of Red Squirrels*, Sciurus vulgaris L., pp. 67–78. London: Peoples Trust
- for Endangered Species. SSRS (2017). 'New sightings signal red squirrels' return to Aberdeen city parks and gardens'. [website] (published 15/11/2017). <www. scottishsquirrels.org.uk/news/article/new-sightings-signal-red-
- squirrels squo-return-to-aberdeen-city-parks-and-gardens/>. SRS (2018). 'Map of squirrel sightings' [website] <www. SSRS (2018). scottishsquirrels.org.uk/squirrel-sightings/squirrel-sighting-map.>
- Accessed 20 February 2018. Staines, B. (1986). 'The spread of grey squirrels (*Sciurus carolinensis*) into north-east Scotland'. *Scottish Forestry* 40: 190–196.
- Thomas, K., Tompkins, D.M., Sainsbury, A.W. Wood, A.R., Dalziel, R., Nettleton, P.F and McInnes, C.J. (2003). 'A novel poxvirus lethal to red squirrels (Sciurus vulgaris)'. Journal of General Virology 84: 3337-3341
- Tonkin, M., Balmforth, L. and Ramoo, K. (2013). Evaluation of Grey Squirrel Control in the Saving Scotland's Red Squirrels Partnership Project (Phase Two) – Second Report 2009–2013. Unpublished Report to SSRS Steering Group Partners. Edinburgh: Scottish Wildlife Trust.
- Tonkin, M., Garritt, J., Bryce, J. and Cole, M. (2015). 'Species Management in Scotland 2007–2012: Red and Grey Squirrels'. In: M.J. Gaywood, P.J. Boon, D.B.A. Thompson and I.M. Strachan (eds.) The Strachan (eds.) Construction of the Strachan (eds.) The Species Action Framework Handbook, pp. 82-93. Battleby, Perth: Scottish Natural Heritage. Usher, M.B., Crawford, T.J. and Banwell, J.L. (1992). 'An American
- invasion of Great Britain: The case of the native and alien squirrel (Sciurus) species'. Conservation Biology 6: 108-115.
- Wauters, L.A., Gurnell, J., Martinoli, A. and Tosi, G. (2002). 'Interspecific competition between native Eurasian red squirrels and alien grey squirrels: does resource partitioning occur?'. Behavioural Ecology and Sociobiology 52: 332-341.
- White, A. and Lurz, P.W.W. (2014). A Modelling Assessment of Control Strategies to Prevent/Reduce Squirrelpox Spread. Scottish Natural Heritage Commissioned Report 627, Battleby, Perth: Scottish Natural Heritage.
- White, A., Lurz, P. W. W., Bryce, J., Tonkin, M., Ramoo, K., Bamforth, L., Jarrott, A. and Boots, M. (2016). 'Modelling disease spread in real landscapes: Squirrelpox spread in Southern Scotland as a case study Hystrix, the Italian Journal of Mammalogy 27 (1). DOI: 10.4404/ hystrix-27.1-11657.
- White, A. Lurz, P.W.W. and Boots, M. (2017). Grey Squirrel Control Along the Highland Line: A Model Analysis. NERC Innovation grant report (Ref: NE/M021319/1). <www.macs.hw.ac.uk/~awhite/SWT_ SNH HighlandLine_FinalReport.pdf>.