Grey squirrel control along the highland line: A model analysis

By Andrew White¹, Peter Lurz² and Mike Boots³

1. Department of Mathematics and the Maxwell Institute for Mathematical Sciences, Heriot-Watt University, Edinburgh, EH14 4AS.
2. Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Midlothian, UK.
3. Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall, TR10 9EZ.

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## Contents

**Executive Summary**  
Page 3

**1. Background**  
Page 4

**2. Mathematical Model**  
Page 6
  
  *2.1. Determining Potential Density*
  *2.2. Model Framework*
  *2.3. Initial Conditions*

**3. Baseline results without grey squirrel control**  
Page 8
  
  *3.1. Grey expansion in the absence of squirrelpox (with no grey squirrel control)*
  *3.2. Grey expansion with squirrelpox (with no grey squirrel control)*
  *3.3. Grey expansion with squirrelpox and with conifer as a poor habitat for grey squirrels (with no grey squirrel control)*

**4. Results with grey control along the highland line**  
Page 12
  
  *4.1. Low intensity trapping \((T_D = 0.3)\)*
  *4.2. Medium intensity trapping \((T_D = 0.5)\)*
  *4.3. High intensity trapping \((T_D = 0.75)\)*
  *4.4. A comparison on trap effort for different trapping intensity*

**5. Long term expansion of grey squirrels in northern Scotland in the absence of grey squirrel control.**  
Page 18

**6. Conclusions**  
Page 19

**7. References**  
Page 20

**8. Supplementary Information**  
Page 21
Executive Summary

This report details the findings from a mathematical modelling study to examine the realistic, spatial dynamics of red and grey squirrels and squirrelpox when grey squirrels are subject to population control through trapping and removal. In particular the report assesses the viability of grey squirrel control along the ‘highland line’ which runs from Loch Lomond in the west to Montrose in the east of Scotland and which represents the northern interface between red and grey squirrels in Scotland. The key findings from the study are:

• Grey squirrel control along the highland line is an effective method of preventing northwards grey squirrel range expansion.

The model highlights key control regions and indicates the level of control that is required to prevent the range expansion of grey squirrels. The suggested successful levels of control in the model are in line with current estimates of the control effort on the ground (SWT pers. comm.) and therefore indicates that the current effort should be continued if the red – grey squirrel interface at the highland line is to be maintained.

• Medium to high intensity grey squirrel control should be applied in response to grey squirrel observations (where medium equates to 92 and high 137 trap days per 1km by 1km per year – see main text for full details).

This has the effect of (largely) clearing the control region of grey squirrels and focussing control on the southern boundary of the control region (although control is still required in the interior of the control regions in response to grey squirrel observations and sporadic grey squirrel dispersal).

• Squirrelpox does not impact on red squirrel conservation to the north when grey squirrels are controlled at the highland line.

When control is applied to prevent grey squirrels from expanding their range beyond the highland line then squirrelpox is also contained to the south of the highland line. Here, since trapping and removal of grey squirrels in the control regions prevents grey squirrel establishment it also prevents the establishment of squirrelpox. In line with previous research (Lurz et al. 2015) the model predicts that squirrelpox will not spread through established red squirrel populations along or to the north of the highland line.

• If resources for grey squirrel control in Scotland are reduced, preventing the range expansion of grey squirrels in Angus and Aberdeenshire should be a priority, but a watching brief should be instituted in other potential areas of dispersal.

The model evaluation indicates that much of the region north of the highland line is disconnected from regions where red squirrels are currently observed in Highland Scotland. Therefore, red squirrel populations in the Cairngorm National Park (and further north and west) may not be threatened by a direct northwards expansion of grey squirrels beyond the highland line. However, dispersal through Angus and Aberdeenshire could offer a long-term route for grey squirrel dispersal and establishment in the Highlands. This therefore highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. Expansion of grey squirrels into Argyll over the very long term may still be a possibility, particularly if new habitat networks are established or habitat restructured to favour native woodland.
1. Background

The native red squirrel is under threat as a result of the expansion of the introduced North American grey squirrel. Scotland has a special responsibility for red squirrels in a UK context, as an estimated 75% of the remaining UK populations are thought to live in Scotland. The red squirrel has already disappeared from a large part of its former Scottish range in central and south-eastern Scotland. Replacement of red squirrels by grey squirrels takes the form of disease-mediated competition and decline is significantly faster in areas where grey squirrels act as carriers of squirrelpox virus (Tompkins et al. 2003). The virus is currently present in some parts of southern and central Scotland and efforts to stem its spread in the south of Scotland managed to slow but not prevent SQPV spread. In southern Scotland, the virus persists at endemic levels in the widespread and established grey squirrel populations. Red squirrels still persist widely across the region and the conservation strategy is to defend prioritised red squirrel populations from the threat of replacement by grey squirrels (SNH 2015). Recent research (Chantrey et al. 2014, Lurz et al. 2015) and modelling work, by Heriot-Watt University (White et al. 2014, White and Lurz 2014) has provided insights and valuable lessons on how to manage red squirrel populations to potentially "live" with the threat of the virus in priority regions for the conservation of red squirrels (see Fig. 1.1).

In northern Scotland red squirrel conservation is aimed at protecting red squirrel populations in the Highlands, Argyll, north-east Scotland, northern Tayside and Stirling where there are currently no grey squirrels (SNH 2015). To do this grey squirrel control is implemented at the interface between red and grey squirrels, currently running approximately along the Highland Boundary Fault. This major fault zone cuts across Scotland like a geological knife, north-east to south-west from coast to coast. A few narrow passes and river or coastal corridors create potential routes for grey squirrel dispersal between the lowlands and highlands. Along the highland red squirrel protection line, (see Fig. 1.1) grey squirrel control is implemented with the aim of preventing the northwards range expansion of grey squirrels. The ‘highland line’ is extensive, from Helensburgh in the west to Montrose in the east and therefore grey control along the highland line is a resource intensive task. Mathematical modelling can be used as a tool to improve the coordination and effectiveness of this control and in this study we undertake large-scale model simulations to predict the likely rate of the future invasion of greys into red squirrel-only populations north of the highland line. The mathematical model includes grey squirrel control and can therefore indicate the location and level of control required to maintain the red-grey squirrel interface along the highland line. This will help answer a key question of ‘where and how much’ control should be applied and therefore inform future policy and resource utilisation of ongoing conservation projects.
Figure 1.1: A map highlighting key areas for red squirrel protection in Scotland (SNH 2015). Priority areas for conservation of red squirrels in southern Scotland are shown in red. The highland line, which is an interface with red squirrel populations in the absence of greys to the north of this line and red and grey squirrel populations to the south, is shown in yellow.
2. Mathematical Model

The modelling framework represents the abundance of red and grey squirrels and squirrelpox infection in 1 km by 1 km grid squares. Grid squares are linked by dispersal and the potential squirrel density in each grid square is based on landcover data and therefore approximates the real heterogeneous habitat of Scotland. Following discussions with Saving Scotland's Red Squirrels (SSRS) and Scottish Natural Heritage (SNH), we focus on the region of Scotland above the central belt that includes the highland grey squirrel protection line (Fig. 2.1).

![Figure 2.1: An OS map of the region considered in model simulations on which we examine the level of grey control required along the highland line (© Digimaps).](image)

2.1. Determining Potential Density

Using GRASS GIS software ([https://grass.osgeo.org/](https://grass.osgeo.org/)) we used National Forestry Inventory Scotland 2014 and Forest Estate Scotland 2014 digital landcover datasets (supplied by the Forestry Commission) to extract coniferous, broadleaf, shrub and Sitka spruce (*Picea sitchensis*) habitat types and used the Scottish Natural Heritage 2007 dataset to extract urban habitat types at a 25 m by 25 m scale. This data was combined with estimates of squirrel densities in different habitat types (Table 2.1) and summed to obtain the potential density of red and grey squirrels at a 1km x 1km patch level that could be supported in the landscape. This scale and approach have been used successfully to model the UK squirrel system in previous studies (Macpherson et al. 2016; White et al. 2015, 2016).
Table 2.1: The default parameters used to generate the potential density for red and grey squirrels at the 1km by 1km patch level in the model simulations (and the lower potential density for grey squirrels if we assume that conifer offers a poor habitat, see section 3.3 later).

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<th>Default (density /ha)</th>
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</tr>
<tr>
<td>Broadleaf</td>
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<tr>
<td>Conifer</td>
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<tr>
<td>Sitka</td>
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</tr>
<tr>
<td>Shrub</td>
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</tr>
<tr>
<td>Urban/suburban</td>
<td>0.14</td>
</tr>
</tbody>
</table>

2.2. **Model Framework**

We base our model framework on previous mathematical models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al. 2003) to consider a spatial, stochastic model, (Macpherson et al 2016; White et al. 2014, 2015, 2016). Here, the deterministic underpinning allows the key population dynamical processes to be understood and the stochastic adaptation provides essential realism when squirrel numbers become low and therefore the chance of extinction and the fade-out of infection are represented.

To generate the stochastic model, the rates in the deterministic model are converted to probabilities of events that account for changes in individual grid cell level abundance. We consider the abundance of susceptible, infected and recovered grey squirrels, $(S_G, I_G, R_G)$, and susceptible and infected reds, $(S_R, I_R)$, respectively. The probabilities are given in Table 2.

2.3. **Initial Conditions**

The model was initialised with observed data for the presence of red and grey squirrels between 2012-2014 (using the National Biodiversity Network's (NBN) Gateway, http://data.nbn.org.uk/). In regions where only one squirrel species was predicted the model was initialised at the respective potential density based on available habitat types. In regions where both squirrel species were predicted the model was initialised by assuming that reds and greys had access to half the habitable area in each grid cell. In model runs that included the impact of squirrelpox, infected grey squirrels were introduced each year in grid cells near Strathblane and Denny in central Scotland (to represent the spread of infection from central Scotland, where infected grey squirrels have been observed).
Table 2.2: The stochastic model within each 1km by 1km grid square indicating the probability of different events. In particular the parameters representing control and dispersal were fitted with observed data on the Island of Anglesey (Jones et al. 2017). Here $R = \sum \text{rates}$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (6 months from the start of April to the end of September) and are set to zero otherwise. Transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells due to daily movement within a core range of radius, $\theta = 0.15$ km. The dispersal term is shown for the class $S_G$ only but is similar for all other classes. The model assumes density dependent dispersal such that squirrel dispersal increases as density increases and the dispersal rate is $m=2b$ when the patch density is equal to the potential density. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of 2km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). The control of squirrels is shown for class $S_G$ only but is similar for all other classes (although when a red squirrel is caught there is no change in red squirrel abundance to reflect the fact that it is released unharmed). Here, $c$ represents the rate of trapping a squirrel and $T_D$ is the trap intensity (trap effort per gridcell per day). Further details of the model framework and the calculation of parameter values can be found in Jones et al. (2017).

3. Baseline results without grey squirrel control

We initially undertook simulations of the model without grey control. This allowed an assessment of the potential spatial expansion of grey squirrels in the absence of control (and what would happen if the grey control programme was ended). We undertake simulations for 3 scenarios: in the absence of squirrelpox, with squirrelpox introduced in the central Scotland, and with squirrelpox introduced in central Scotland and with grey squirrel density at poor levels in conifer.
3.1. Grey expansion in the absence of squirrelpox (with no grey squirrel control)

Figure 3.1 shows the model results for default parameters (Table 2.1) in the absence of squirrelpox. Results at time zero indicate the initial conditions as taken from the NBN observed data. After 5 years grey squirrel expansion has occurred to regions of nearby suitable habitat and the ‘highland line’ is indicated by the northern extent of the light orange gridcells. It is clear that without grey control grey squirrels expand their range northwards into regions previously occupied by red squirrels only, causing loss of red squirrel range to the north of the highland line. The expansion is most pronounced in eastern regions to the north of Montrose and in the central Highlands north of Dunkeld and Blairgowrie. The expansion is less pronounced in the west in Argyll, around Loch Lomond, Loch Earn and the western extent of Loch Tay, but is possible over a longer timescale.

3.2. Grey expansion with squirrelpox (with no grey squirrel control)

Figure 3.2 shows the model results for the occupancy of red and grey squirrels for default parameters when squirrelpox is included and Figure 3.3 shows the associated spread of squirrelpox. The expansion of grey squirrels beyond the highland line initially occurs at a similar rate to that in the absence of squirrelpox (Fig. 3.1), but then occurs at a slightly faster rate from year 20 onwards, with grey range expansion increased in central highlands from year 25 onwards (compare Fig. 3.1 and 3.2). This is due to the absence of squirrelpox in central Highlands regions until year 20 (Fig. 3.3) and so prior to this red replacement has been due to competitive effects only (and therefore Fig. 3.1 and Fig. 3.2 are very similar till year 20 in these regions). After year 20 the expansion of greys in the central Highlands is more rapid when squirrelpox is present and therefore further highlights that squirrelpox plays a key role in the rate of replacement of red squirrels by greys. In regions around Loch Lomond and the Trossochs squirrelpox is present after approximately 10 years (Fig. 3.3). However the expansion of grey squirrels in these regions does not seem to be enhanced by the presence of squirrelpox. This is likely to be due to the relatively poor habitat at the north of Loch.
Lomond that makes grey squirrel establishment difficult, potentially keeps densities low and makes the persistence of squirrelpox within grey populations unlikely.

Figure 3.2: Model simulations under default parameter values with squirrelpox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

Figure 3.3: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 3.2.
3.3. Grey expansion with squirrelpox and with conifer as a poor habitat for grey squirrels (with no grey squirrel control)

Results for grey squirrel expansions when we assume that conifer offers a poor habitat for grey squirrels are shown in Figure 3.4, with the associated spread of squirrelpox in Figure 3.5. Under this scenario the expansions of grey squirrels is slightly reduced (compare Fig. 3.4 with Fig. 3.2). Moreover, there is an increase in the regions in which red and grey squirrels coexist. Some of these regions reflect areas where red squirrels are currently observed in central Scotland (e.g. north east Fife, Kinross and Perthshire) and suggests that more information on the suitability of coniferous habitat in Scotland for grey squirrels is required (the empirical data for grey squirrel potential density on conifer largely comes from studies in English and Welsh habitat, see Smith 1999, Cartmel 2000).

Figure 3.4: Model simulations under parameter values in which conifer offers a poor habitat for grey squirrels and with squirrelpox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations). Notice the persistence of reds as far south as Clackmannanshire and Fife.

Squirrelpox spread is contained in central Scotland when conifer offers a poor habitat for grey squirrels (Fig. 3.5). This is due to grey squirrel density being suppressed to levels that do not support endemic persistence of squirrelpox in grey squirrel populations between central Scotland and northern Fife, Kinross-shire and southern Stirlingshire. This has implications if future woodland management favours restructuring towards native woodland species.
Figure 3.5: Model simulations showing the percentage chance of seropositive grey squirrels under the model set-up of Figure 3.4.

4. Results with grey control along the highland line

The results in the absence of control were used to isolate key regions in which control should be included in an attempt to prevent the northwards expansion of grey squirrels beyond the highland line. The control regions are shown in Figure 4.1. The control regions were determined by studying the grey squirrel expansion paths in Figure 3.2 and by undertaking model simulations with a range of control regions to determine their best size and location (results not shown). We chose to undertake the model simulations that include control for the default parameter setting (Table 2.1) and in which squirrelpox is included. This represents a worst case scenario and should provide an upper bound on the level of grey control required to maintain red squirrel protection along the highland line.

To understand the results that follow, it is important to understand the method in which grey squirrel control is implemented in the model. Control is only applied in the regions (typically 10km by 10km) outlined in Figure 4.1. In specified 1km by 1km gridcells within these regions control is applied with a trap intensity of $T_D$ traps per day. An analysis of when control was applied in the field was undertaken for a reduced region in Tayside (data for the Tayside demonstration area was provided by SWT, results not shown). This indicated that the majority of grey squirrel control occurs between 1 April and 30 September. Therefore in the model we assume control can occur for up to 6 months, from 1 April – 30 September (183 days) which is split into three 61 day (2 month) control periods. At the start of the first control period trapping is applied in gridsquares in which grey squirrels are present and in gridsquares in a 2km buffer zone around these gridsquares. Control is maintained at this level for 61 days. The same procedure is applied to determine the gridcells in which greys squirrels are present (and the buffer zone) at the start of the second and third control period. This way trapping can react to grey squirrel dispersal and observations of grey squirrels throughout the trapping period. This means that within any control region the level of trapping can increase or decrease from year to year as it depends on the grey squirrel presence within the control regions (which varies over time and in response to previous trapping). We run the model for three
levels of trap intensity \( T_D = 0.3 \) – low; 0.5 – medium; 0.75 – high). To aide interpretation, a low intensity of trapping equates to a maximum of \( 0.3 \times 183 = 55 \) trapdays per year in a 1km by 1km gridsquare (and equates to 92 and 137 trap days per year per gridsquare for medium and high intensity trapping respectively).

Figure 4.1: The initial distribution of red and grey squirrels and the regions in which control is applied in the model along the highland line (see Table 8.1 for further details of the location of the control regions).

4.1. Low intensity trapping \( (T_D = 0.3) \).

Low intensity trapping fails to prevent the expansion of grey squirrels beyond the highland line (Fig. 4.2). The highland line is breached in the north east (between Montrose and Brechin) and in the central Highlands (around Dunkeld) after 10 years, potentially threatening the Red Squirrel Stronghold forest at Rannoch, and by year 30 also north of Blairgowrie and Kirriemuir in the Highlands and Strathyre in the Trossachs. By the end of the 35 year model simulation greys are present to the north of all the control regions. Note, however, that grey expansion was significantly reduced when a low level of control was applied compared to when no control was applied (compare Fig. 4.2 with Fig. 3.2).
4.2. Medium intensity trapping ($T_D = 0.5$).

A medium intensity level of control prevents grey expansion beyond the highland line in the majority of simulations. However, in some control regions greys manage to evade capture and spread northward (this happens in 1 out of the 10 realisations after 10 years and in a further realisation after 30 years). This occurs in regions north of Dunkeld and north of Blairgowrie (as seen by the orange colour above the control regions in Figure 4.3). This suggests that medium intensity control would suffice in most regions but additional control may be required in regions around Dunkeld and Blairgowrie.
Figure 4.3: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a medium trapping intensity. Maps show the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).

4.3. High intensity trapping ($T_D = 0.75$).
High intensity trapping prevented grey squirrels from expanding beyond the highland line in all model realisations (Fig. 4.3). This therefore suggests that a combination of medium intensity trapping in most control regions with high intensity trapping around Dunkeld and Blairgowrie (regions 7-10, see table 4.1 below) would prevent the northward expansion of grey squirrels and protect red squirrels above the highland line.

Figure 4.3: Model simulations under default parameter values with squirrelpox when grey squirrel control is applied with a high trapping intensity. Maps show the percentage occupancy of red and grey squirrels at 5 year intervals (based on ten model realisations).
4.4. A comparison on trap effort for different trapping intensity

Table 4.1 shows the trap effort, in trap days per year, for three different levels of trap intensity. The modelling results suggest that if medium trapping intensity is undertaken in regions 1-6 and 11-14 and high trapping intensity in regions 7-10 then grey squirrel range expansion beyond the highland line will be prevented. This implies that the number of trap days per year in each region should range from 1831 to 7494. The associated number of grey squirrel caught in each region is shown in Table 4.2. Note, in general as the intensity of trapping is increased the number of grey squirrels caught (from year 5 onwards) decreases. This is because at low intensity trapping grey squirrels can disperse throughout the control regions and so trapping is required across the whole control region and there are abundant greys to catch. Trapping, in effect, represents a kind of harvesting and greys persist indefinitely. As trap intensity increases the control regions are cleared of grey squirrels and so most grey captures will occur at the interface with regions in which greys are not controlled (typically at the southern boundaries of the control regions). This also explains why the trap effort in control regions can decrease over time. For example there is a decrease in trap effort in region 14 (Montrose) as greys are removed from the majority of the region and therefore control becomes focussed on the southern boundary. These results highlight the importance of undertaking grey squirrel control with a sufficient trap intensity to prevent their dispersal within and beyond the control regions. In practical terms this involves employing traps in the highland line control zone in locations where grey squirrels are observed (and in a buffer zone around these regions). According to model results the trap intensity should be either 92 (medium) or 137 (high) trap days per 1km by 1km per year.
Table 4.1: The average trap effort for a model realisation (trap days per year) for the different control regions for the low, medium and high intensity trapping scenarios. The 14 trap regions are indicated in Figures 4.1-4.4 starting on the left with region 1 and moving to region 14 on the right. To aid interpretation of the trap regions we provide approximate geographical location as follows. Region 1 – Garelochhead, Region 2 – Arden, Region 3 – Rowardennan forest, Region 4 – Loch Ard/Achray forest, Region 5 – Strathyre forest, Region 6 – Eastern Loch Earn, Region 7 – Dunkeld (west), Region 8 – Dunkeld (east), Region 9 – Blairgowrie, Region 10 – Alyth, Region 11 – Kirriemuir, Region 12 – Finavon, Region 13 – Brechin, Region 14 – Montrose. Note, in some regions trapping is initially low as there is a low initial presence of grey squirrels (see Figure 4.1).
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Table 4.2: The average trap number of grey squirrels caught for a model realisation for the different control regions for the low, medium and high intensity trapping scenarios. For a description of the location of each of the control regions see Table 4.1.
Long term expansion of grey squirrels in northern Scotland in the absence of grey squirrel control.

A key question for red squirrel conservation management is what would be the impact of a reduction or removal of grey squirrel control along the highland line? In Figures 3.2 and 3.4 we highlight the medium term impact (over 35 years) of grey expansion in regions beyond the highland line. In this section we consider grey squirrel expansion over a longer time scale and assess the impact on currently thriving populations of red squirrels in the Highlands of Scotland. To achieve this we extended the region over which the model simulations were undertaken (see Fig. 8.1) and expand the time scale to 70 years (for the default model parameters, see Table 2.1, and where squirrlepox was included). The results are shown in Figure 5.1. This indicates that much of the region north of the highland line is disconnected from regions where red squirrels are currently observed in Highland Scotland. For instance, the Grampian Mountains north of Blair Athol, Glen Shee, Glen Isla, Glen Prosen and Glen Clova prevent grey squirrel expansion into suitable habitat in the Cairngorm National Park (which is home to well-established populations of red squirrels). However, grey squirrel expansion through Angus and into Aberdeenshire does provide a potential long-term route for grey squirrels to enter the Cairngorm National Park. This could occur via a route north of Aberdeen, through Huntly, Dufftown and then along the river Spey valley. This confirms the rationale and highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. In the west of Scotland grey squirrel range expansion is less rapid, taking approximately 30 years to spread beyond Crianlarich, the north of Loch Long and Loch Lomond. Red squirrel control (at a medium intensity) could be employed in these regions to protect red squirrel populations in the West Highlands, on the Cowal Peninsula and the Mull of Kintyre.

Figure 5.1: Model simulations under default parameter values with squirrlepox in the absence of grey squirrel control showing the percentage occupancy of red and grey squirrels at 10 year intervals (based on ten model realisations). Results are comparable to Figure 3.2 but here we have expanded the geographical region over which the model simulations are undertaken and show results over a longer time period.
6. Conclusions

In this report we used have shown how mathematical modelling that represents realistic, spatial dynamics of red and grey squirrels can be used as a tool to improve the coordination and effectiveness of grey squirrel control to prevent the range expansion of grey squirrels into Highland Scotland. The key findings from the study are:

- Grey squirrel control along the highland line is an effective method of preventing northwards grey squirrel range expansion.

  The model highlights key control regions and indicates the level of control that is required to prevent the range expansion of grey squirrels. The suggested successful levels of control in the model are in line with current estimates of the control effort on the ground (SWT pers. comm.) and therefore indicates that the current effort should be continued if the red – grey squirrel interface at the highland line is to be maintained.

- Medium to high intensity grey squirrel control should be applied in response to grey squirrel observations (where medium equates to 92 and high 137 trap days per 1km by 1km per year – see main text for full details).

  This has the effect of (largely) clearing the control region of grey squirrels and focussing control on the southern boundary of the control region (although control is still required in the interior of the control regions in response to grey squirrel observations and sporadic grey squirrel dispersal).

- Squirrelpox does not impact on red squirrel conservation to the north when grey squirrels are controlled at the highland line.

  When control is applied to prevent grey squirrels from expanding their range beyond the highland line then squirrelpox is also contained to the south of the highland line. Here, since trapping and removal of grey squirrels in the control regions prevents grey squirrel establishment it also prevents the establishment of squirrelpox. In line with previous research (Lurz et al. 2015) the model predicts that squirrelpox will not spread through established red squirrel populations along or to the north of the highland line.

- If resources for grey squirrel control in Scotland are reduced, preventing the range expansion of grey squirrels in Angus and Aberdeenshire should be a priority, but a watching brief should be instituted in other potential areas of dispersal.

  The model evaluation indicates that much of the region north of the highland line is disconnected from other regions in Highland Scotland where red squirrels are currently observed. Therefore, red squirrel populations in the Cairngorm National Park (and further north and west) may not be threatened by a direct northwards expansion of grey squirrels beyond the highland line. However, dispersal through Angus and Aberdeenshire could offer a long-term route for grey squirrel dispersal and establishment in the Highlands, potentially threatening several red squirrel stronghold forests. This therefore highlights the need for the continued effort to remove grey squirrels from Aberdeenshire and for grey control to prevent their expansion through Angus. In addition, expansion of grey squirrels into Argyll over the very long term may still be a possibility, particularly if new habitat networks are established or habitat restructured to favour native woodland.
7. References


8. Supplementary Information

8.1 Locations of the grey squirrel control regions along the highland line

We provide easting and northing reference locations for the grey squirrel control regions used in this study.

<table>
<thead>
<tr>
<th>Control Region</th>
<th>Lower left</th>
<th>Upper right</th>
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</tr>
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</tr>
<tr>
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<td>241000</td>
</tr>
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<td>Strathyre forest</td>
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<td>252000</td>
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</table>

Table 8.1: The lower left and upper right grid location for the control regions used in this study (see Fig. 4.1).

Figure 8.1: A map of the extended region considered in Section 5 (© Digimaps).