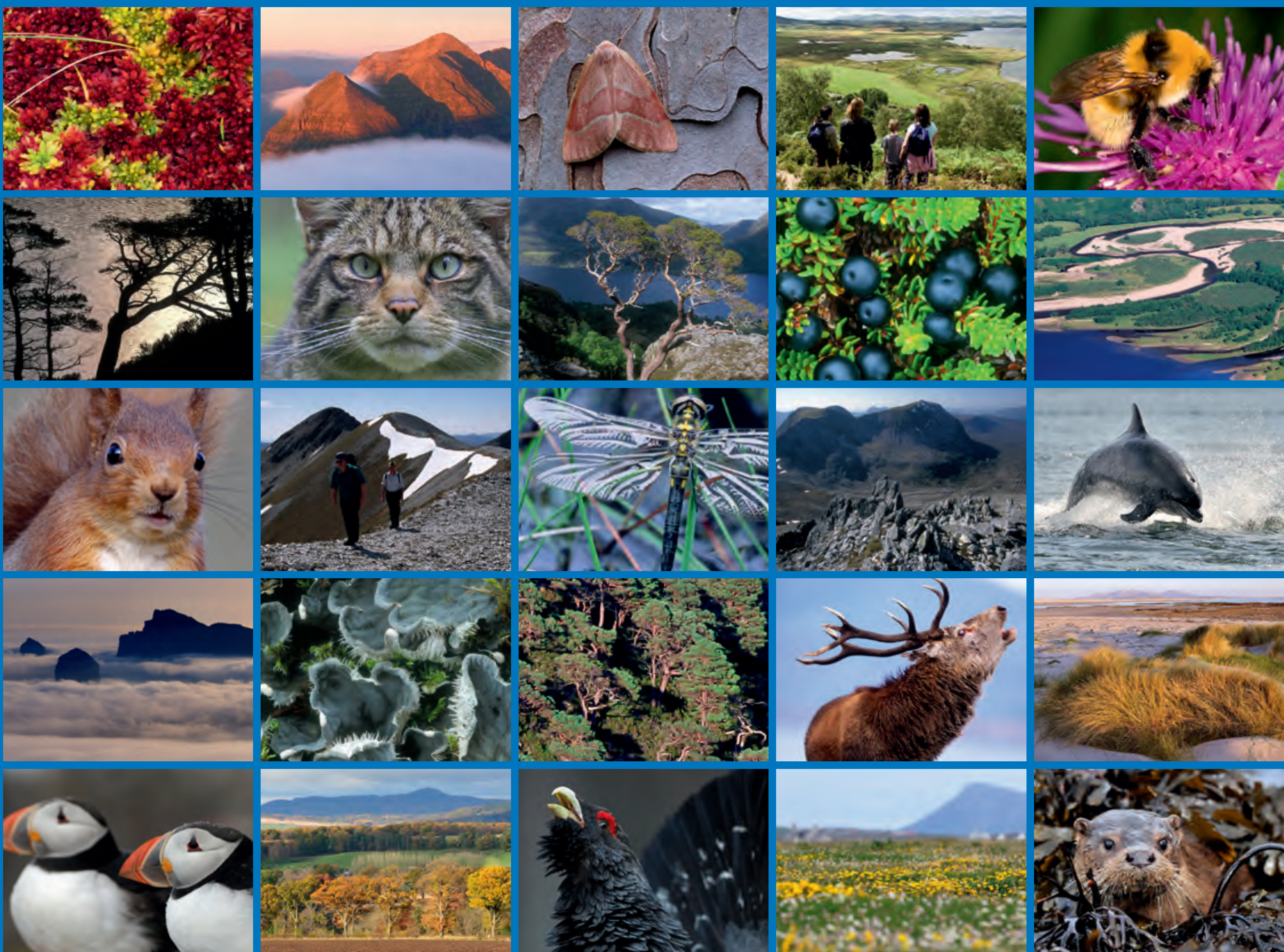
Scottish Natural Heritage
Commissioned Report No. 627

A modelling assessment of control strategies to prevent/reduce Squirrelpox spread



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COMMISSIONED REPORT

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A modelling assessment of control strategies to prevent/reduce Squirrelpox spread

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COMMISSIONED REPORT

Summary

A modelling assessment of control strategies to prevent/ reduce Squirrelpox spread

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Project no: 14749
Contractor: Dr Andrew White & Dr Peter Lurz
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Background

This report is the outcome of a partnership agreement between Scottish Natural Heritage, Andrew White (Heriot-Watt University) and Peter Lurz (Ecological Consultant). The team worked closely with the staff and steering group of the Saving Scotland's Red Squirrels Project with a view to informing strategic approaches to red squirrel conservation.

The objectives of the project are to undertake a modelling assessment of how the current level of grey squirrel control has impacted on the spread of squirrelpox in the South of Scotland and to explore if there are control strategies that can reduce its further spread. The model framework is then extended to assess the effectiveness of grey squirrel control should squirrelpox spread into Central/Northern Scotland and to predict the impact of squirrelpox at the interface between red and grey populations in Highland Scotland. The model is also used to assess the success of control strategies to protect red squirrel populations in Stronghold forests from extinction and disease outbreaks using Fleet basin as an example.

A spatially explicit, individual-based, stochastic model was developed to represent the population and epidemiological dynamics of red and grey populations based on the deterministic model of Tompkins *et al.* (2003). The carrying capacity at a 1km grid square scale was calculated from the proportion of suitable habitat types in the landscape; determined from digital landcover maps following the methods of Lurz *et al.* (2003).

Main findings

- Squirrelpox (SQPV) can spread rapidly through high density grey populations in the absence of control.
  - SQPV is predicted to spread rapidly through established grey populations in Southern Scotland.
  - Spread from Southern to Central populations occurs through distinct corridors that connect high density regions. The disease persists in extant high density areas and can cross between such areas via (rare/occasional) spread along low density corridors. The model identified several such potential corridors through forest and urban habitat, and all corridors would need to be targeted for control to prevent spread from Southern to Central grey squirrel populations.
  - Grey squirrel populations in Central Scotland are at high density and well connected and therefore should SQPV reach a local area of Central Scotland, it is predicted to spread rapidly throughout the whole region.

  - Spread from Central to Northern Scotland similarly occurs through establishment in high density areas and onward spread through corridors. High density areas for grey squirrels in Northern Scotland are more fragmented and therefore the spread of SQPV occurs along more isolated and fewer distinct corridors.
  - In the absence of control, SQPV will continue to spread and its distribution is predicted to (ultimately) coincide with the distribution of grey squirrels in Scotland with potential outbreaks and subsequent burn outs in connected, adjacent 'red squirrel only' populations.

- The model predicts that SQPV outbreaks in red squirrel populations only occur in areas where red and grey squirrels are sympatric or adjacent to each other.
  - Based on limited current veterinary knowledge and data on SQPV infection, transmission and mortality in reds squirrels, the model predicts that spread through 'red only' populations will be restricted and localised to the interface of the two species. Therefore a Scotland wide epidemic of SQPV is not predicted in 'red only' areas and beyond the interface with grey squirrels, 'red only' areas remain disease free.
  - Disease outbreaks in reds cause population crashes making red population more vulnerable to replacement and extinction.

- Targeted control may help to stop or slow the progress of the disease, but will require that very low densities of grey squirrels are achieved.
  - In much of Southern Scotland simulated control to prevent SQPV spread between areas with established grey populations is not viable as there are many possible interconnected routes that allow SQPV to 'jump' from one region of high density greys to the next.
  - The model suggests that there are clear breaks between high density squirrel habitats connected by distinct corridors (pinchpoints). In model simulations targeted, intensive, control along pinchpoints was successful in preventing local SQPV spread.
  - The model identifies potential pinchpoints between Southern and Central populations which may allow SQPV spread to be contained. The locations of these pinchpoints are based on simplified available habitat data and so ground-truthing is required to determine the precise location and viability of pinchpoints in the field. There are numerous predicated pinchpoints between Southern and Central populations and the containment of SQPV may be difficult.
  - There are fewer pinchpoints connecting Central to Northern populations and the number of pinchpoints further decreases northwards. Should SQPV spread into Central populations these may offer viable alternative pinchpoints where control could limit SPQV spread.
  - Where red populations are sympatric or adjacent to greys, SQPV can cause epidemic outbreaks in reds leading to population crashes. This makes red populations more vulnerable to extinction (through stochastic processes) and allows greys to invade and replace reds more rapidly.
  - We would predict that grey control at the interface between grey and red only populations will reduce outbreaks in reds and reduce the competitive advantage of greys and therefore allow reds to persist within their current distribution.

- Simulated control of grey squirrels within and around strongholds can prevent extinction of reds and therefore conserve viable populations of reds in strongholds.
  - The level of control depends upon the habitat quality in the woodlands surrounding a stronghold. For the Fleet basin stronghold the model predicted that the level of control was achievable (with the removal of approximately 100 greys per year in simulations).
  - If squirrelpox is endemic in populations surrounding a stronghold, then control of grey squirrels may not prevent periodic outbreaks of SQPV within the stronghold.

However, reds are predicted to recover to pre-outbreak levels (provided grey control is continued).

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Table of Contents **Page**

Acknowledgements

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1. BACKGROUND

Since its introduction into the UK, the grey squirrel (*Sciurus carolinensis*) has replaced the native red squirrel (*S. vulgaris*) throughout most of England and Wales, and in parts of Scotland and Ireland. There are now only certain regions in which the red squirrel survives and maintaining these populations is a major conservation priority. Squirrelpox (SQPV), carried by but avirulent to the greys, yet lethal to reds, is unequivocally linked to the rapid replacement of red populations (e.g. Tompkins *et al.* 2003). Squirrelpox is observed at high seroprevalence (average of 62%) in the established grey populations in England and Wales (Sainsbury *et al.* 2000). Grey squirrels are also abundant in Southern and Central Scotland but until recently these populations were largely disease-free (albeit with outbreaks in the most southern Scottish populations; see McInnes *et al.* 2009. Here, a disease outbreak implies that individuals become infected and can transmit the disease. Following an outbreak infected greys recover (and are assumed to be seropositive) while infection is fatal for red squirrels). As part of the Saving Scotland's Red Squirrels (SSRS) initiative grey numbers have been controlled in Southern Scotland and routine sampling has been undertaken to assess the distribution of SQPV. Recently there has been shift in the northward limit of the SQPV distribution in grey squirrels (Figure 1.1 and Appendix A) and therefore there is a need to reassess current control strategies and determine whether they are sufficient to prevent the further spread of SQPV. The aim of this assessment is to use mathematical modelling approaches to assess the effectiveness of grey control on SQPV spread.

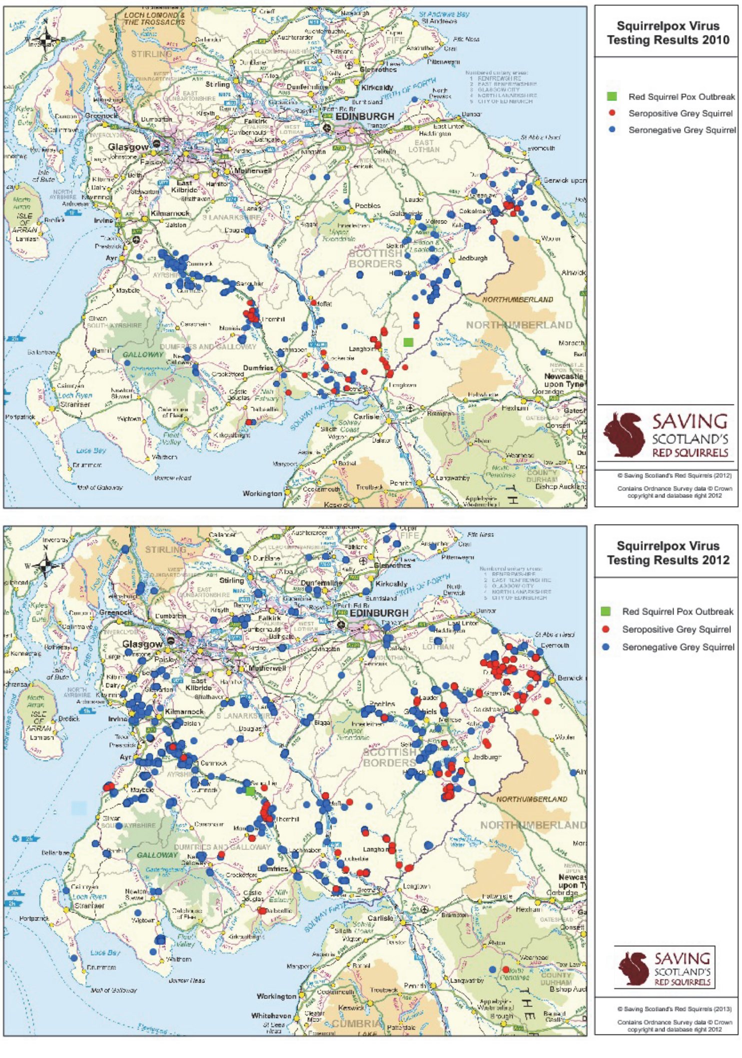

Figure 1.1. The recorded incidence of squirrelpox in the south of Scotland in 2010 and 2012.

2. MATHEMATICAL MODELLING

Based on the deterministic model of Tompkins et al (2003) a spatially explicit, individual-based, stochastic model was developed to represent the population and epidemiological dynamics of red and grey populations. The model represents the dynamics in a 1km x 1km patch with patches linked by dispersal to create a grid of interlinked subpopulations. The habitat composition in each patch was determined from digital landcover maps (following the methods of Lurz *et al.* 2003) with an estimate of carrying capacity determined by the proportion of suitable habitat types (this estimate will be verified using available trapping data from the SSRS project). The model can be used to understand the spread of SQPV through grey populations and to test the effectiveness of a range of control strategies on reducing SQPV spread (for full details of the model set-up and parameterisation see Appendix B).

2.1 Key Model Assumptions

- Grey densities in conifer are based on limited studies of mixed pine, larch and spruce in England and Wales. This may over estimate grey densities in the simplified landcover data available for large scale model runs which defines forest type only as 'conifer'.
- Greys squirrels out-compete reds in most habitat types used in large scale simulations.
- The disease transmission rate is derived from seroprevalence data for grey squirrels (Tompkins *et al.* 2003) and corresponds to grey-grey transmission. Lack of additional data requires that we use this rate for red-grey and red-red transmission.

3. SOUTHERN AND CENTRAL SCOTLAND

The model framework has been developed to represent real and large scale landscapes that simulate the current distribution of red and grey squirrels in Southern Scotland.

3.1 Determining Gridded Habitat Composition and Red/Grey Squirrel Carrying Capacities

The Forestry Commission Scotland forest inventory maps for 2011 (http://www.forestry.gov.uk/datadownload) were analysed using GRASS GIS (Version 6.4, http://grass.osgeo.org/) to determine the proportion of each 1km x 1km grid square that was occupied by coniferous forest, broadleaved forest, shrub or that was inhabitable (see Appendix A, Figure A.2). Published densities for red and grey squirrels in each habitat type (Table 3.1) were consolidated to provide best estimate parameters for two levels of squirrel density (Table 3.2). The gridded habitat data and best estimate squirrel density were then combined to produce carrying capacities at the 1km x 1km grid square level (Figure 3.1).

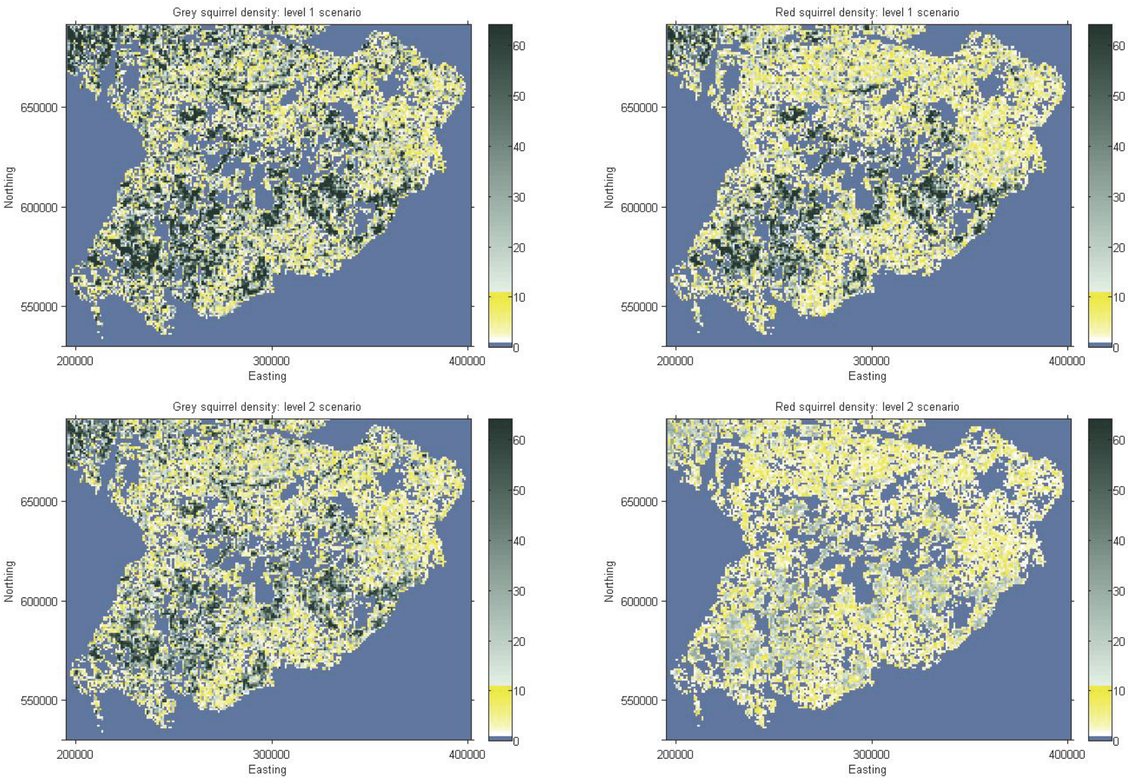

Figure 3.1. Estimates of densities in 1km x 1km grid squares used in the model assessments. Habitat composition was derived using the Forestry Commission Scotland forest inventory maps and combined with the density estimates of Table 3.2. The top graphs show estimates using level 1 densities and the bottom graphs level 2 densities for grey squirrels (left) and reds (right).

Table 3.1. Grey and red squirrel densities in different habitat types.

Density Squirrels/ha	Habitat	Method	Reference
Grey Squirrel			
0.92-1.1	Pine, Beech	Trapping	Wauters *et al.* 2000
1.9-3.4	Oak, hazel	Trapping	Gurnell 1983
0.8-1.3	oak, hazel (young)	Trapping	Gurnell 1983
0.67-1.53	Oak-ash*1	Trapping	Kenward 1985
3.0-18.0	Oak	Trapping	Gurnell 1996
2.44±0.11	CP, oak	Trapping	Kenward *et al.* 1998
0.66±0.15	SP, SS, L, (some oak)	Trapping	Kenward *et al.* 1998
0	SS	Trapping	Lurz (unpublished)
1.49	SY, oak, beech	Trapping/shooting	Don 1985
0.06-0.89	NS, SP, L, SS, beech	Trapping	Cartmel 2000
0.07-0.79	NS, SS	Trapping	Cartmel 2000
0.31-0.79	CP, SP, L	Trapping	Smith 1999
0.43-0.88	CP, SP, L, beech, oak	Trapping	Smith 1999
Red Squirrel			
0.42-0.83	Scots pine	Trapping	Tittensor 1970
0.33	Scots pine	Trapping	Moller 1986
0.02-0.032	SP, LP,L, SS	Trapping	Halliwell 1997
0.12 -0.19	SP, L, NS, SS	Trapping	Halliwell 1997
0.17 -0.21	Lodgepole	Trapping	Lurz *et al.* 1998
0.02-0.20	Sitka spruce	Trapping	Lurz *et al.* 1998
0.12-0.41	NS	Trapping	Lurz *et al.* 1998
1.1	Pine (SP, CP, LP)	Trapping	Reynolds 1981
0.7	Mixed deciduous	Trapping	Tonkin 1983
0.62 -0.87	Mixed deciduous	Trapping	Magris 1998
1.0	Mixed deciduous	Trapping	Holm 1991

*1 densities for winter Dec-March over 3 years; SP=Scots pine, CP=Corsican pine, SS=Sitka spruce, L=Larch, NS=Norway spruce, SY=Sycamore.

Table 3.2. Estimates of squirrel density used in the model assessment. Note that densities for grey squirrels used for conifer woodland are based on studies in pine and larch with deciduous species present to reflect the presence of both deciduous and conifer in 1 km grid cells. Studies of densities of grey squirrels in Sitka spruce dominated areas are not available and abundance in these areas is likely to be low to zero.

Grey Density per Ha	**Level 1**	**Level 2**
Conifer	0.9	0.7
Broadleaf	3.0	2.0
Shrub	0.2	0.15
Red Density per Ha		
Conifer	0.83	0.33
Broadleaf	1.0	0.62
Shrub	0.2	0.15

The gridded data on squirrel carrying capacities was used in conjunction with a stochastic model that represents red and grey squirrel competition and the transmission of squirrelpox.

Initial conditions were chosen to reflect the observed distribution of squirrels in 2005 (see Appendix B). SQPV spread was simulated through the South of Scotland following its introduction from the North of England in approximately 2005 in Dumfries and Galloway and 2010 in the Scottish Borders based on SSRS blood sample data (see Appendix A and B).

3.2 The spread of SQPV in Southern and Central Scotland without control

Model simulation were undertaken to determine the rate and extent of squirrelpox spread in the absence of any control measures that reduce grey squirrel density. These simulations provide baseline results to which the impact of control measures can be compared. They also indicate the likely progression of squirrelpox should control measures be stopped. Model simulations were replicated ten times and below we present results of typical individual model simulations (Figure 3.2-3.6) and also combine the output to convey the average behaviour (Figure 3.7). Results are presented for the level 1 density estimates of Table 3.2. The level 2 estimates showed little disease spread with the disease failing to establish in the long-term in 8 out of the 10 simulations (see Appendix C). Thereby level 1 appears to be a better match for the observed spread and is adopted in subsequent simulations.

Figure 3.2 shows that there is rapid epidemic spread of squirrelpox from its initial point of entry in south-west Scotland (Solway area); and by 2012 squirrelpox is established in much of Dumfries and Galloway and the Scottish Borders. The seroprevalence varies spatially from around 30%-80% and reflects the underlying distribution of squirrel density as shown in Figure 3.1 (level 1) where high density regions can support the disease at higher seroprevalence. In this (single) simulation the disease spread remains contained from around 2013 onwards (although there is a small expansion of the distribution in 2020) and in particular squirrelpox does not manage to spread and establish in the high density grey populations of Central Scotland. This pattern is reflected in 5 of the 10 simulations and arises due to the difficulty of infectious spread through extended regions of poor (low density) habitat.

In the remaining 5 simulations squirrelpox successfully spreads and establishes in Central Scotland. In the example simulation in Figure 3.3 squirrelpox spreads through a dispersal route in north-east Ayrshire which (in the figure) can be seen as the expansion in the region of seropositive greys in 2017. Once squirrelpox reaches the grey squirrel population in Central Scotland it rapidly spreads. Squirrelpox reaches central Scotland via this route in 2 of the 10 simulations. In another run in Figure 3.4, squirrelpox spreads through a dispersal route in the northern Scottish Borders, which can be seen as the expansion in the region of seropositive greys in 2015/2016. Squirrelpox reaches central Scotland via this route in 2 of the 10 simulations. In Figure 3.5 squirrelpox spreads through a dispersal route in the eastern Scottish Borders and East Lothian, which can be seen as the expansion in the region of seropositive greys in 2014. Squirrelpox reaches central Scotland via this route in 1 of the 10 simulations. Note that seroprevalence is either low or zero in these regions outside 2014-2019 and highlights that relatively poor habitats can still act a dispersal corridor for squirrelpox.

To determine the likelihood of squirrelpox spread into different regions we combine the data from the 10 individual simulations to present a map of the percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% (e.g. one in five grey squirrels have antibodies to squirrelpox) in a 1km grid square. Figure 3.6 shows the spread and establishment of squirrelpox across Southern and Central Scotland between 2005-2028. By 2013 squirrelpox is present in 100% of model simulations in Southern Scottish regions that can support a reasonable density of grey squirrels. The pattern in Southern Scotland remains largely fixed from 2014 onwards and also reflects the current observations for the occurrence of squirrelpox in this region (see Figure 1.1 and

Appendix A). From 2014 onwards the occurrence of squirrelpox in Central Scotland increases and by 2019 occurs in 30% of the model runs and by 2024 in 50% of the model runs. The slow spread to central Scotland is due to regions of poor connectivity in habitat between Southern and Central Scotland through which infection spread rarely occurs. These population bottlenecks and potential dispersal routes from Southern to Central Scotland are highlighted in Figures 3.2-3.5. If the model simulations were continued for a longer time period there would be more opportunity for the (rare) spread of infection through dispersal corridors and so the probability of the occurrence of squirrelpox in Central Scotland would continue to increase.

To summarise, in the absence of control measures to reduce grey squirrel density the model simulations suggest that:

1. Squirrelpox will rapidly spread and be present across much of Southern Scotland by 2013, remaining endemic with seroprevalence levels between 20-80% thereafter.
2. Spread from Southern to Central Scotland is limited to specific dispersal routes through which disease spread is rare.
3. Once disease reaches Central Scotland it spreads rapidly through the high density populations of greys throughout this region.
4. Due to the stochastic nature of the simulations the timing of disease spread can vary, but in the absence of control of grey squirrels and thus squirrelpox, the disease could already be present in Central Scotland or arrive there with increasing probability in the near future.

In the next section we will examine the impact that grey squirrel control has had on limiting the spread of squirrelpox.

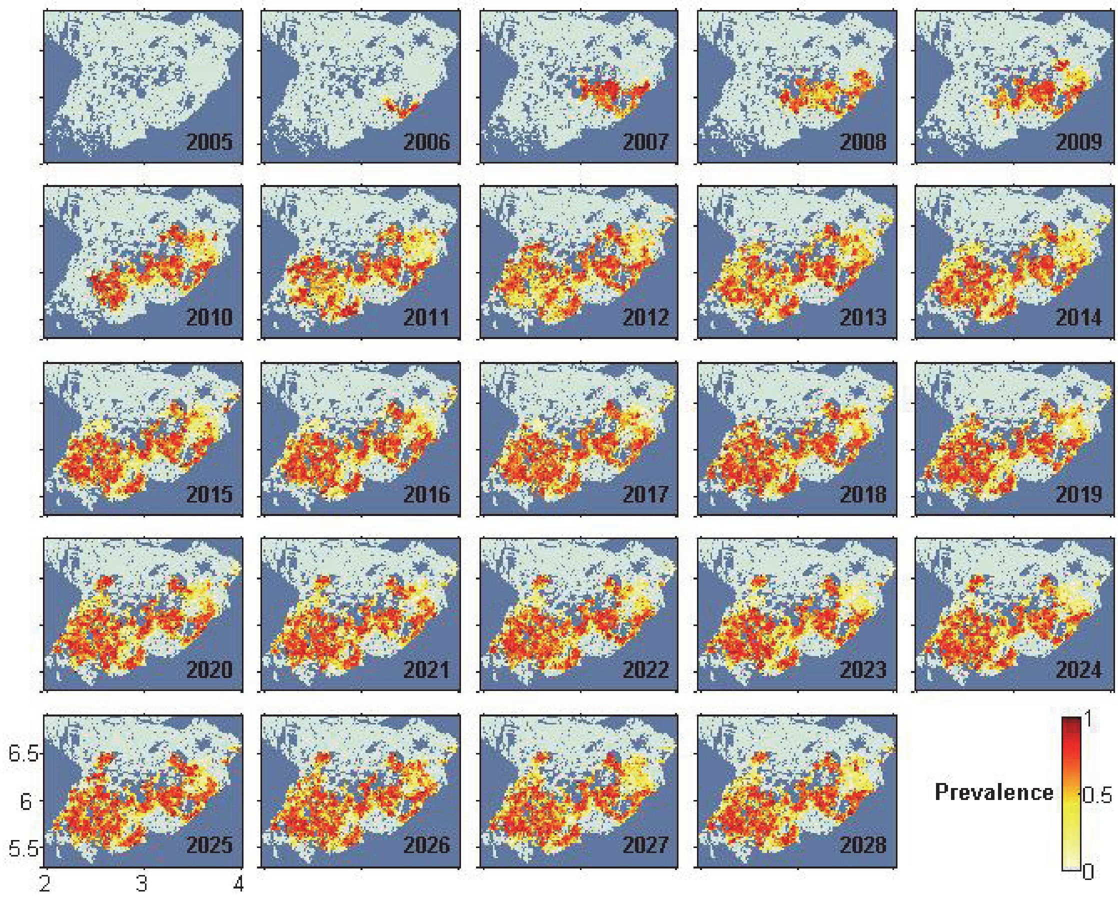

Figure 3.2. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). The extent of disease remains relatively fixed from 2013 onwards. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

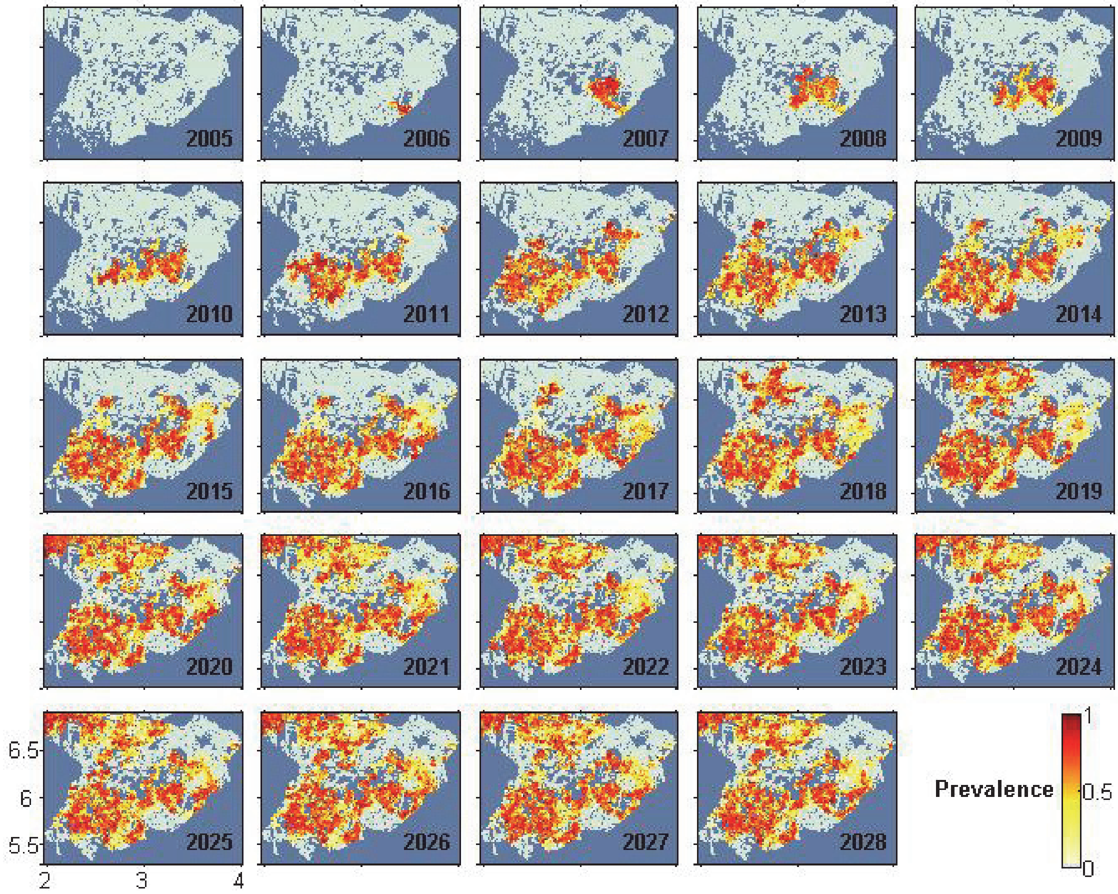

Figure 3.3. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). The disease expands into Central Scotland through a dispersal route in north east Ayrshire which can be seen as the expansion in the region of seropositive greys in 2017. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

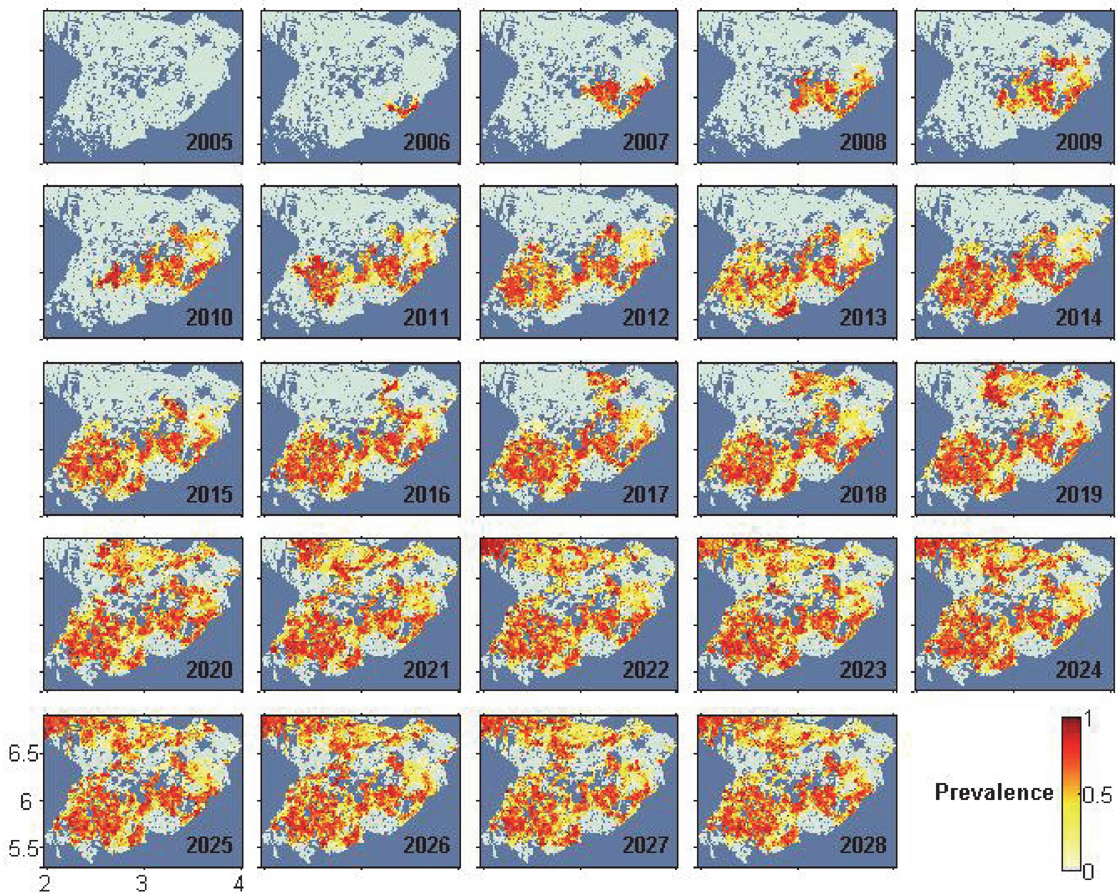

Figure 3.4. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). The disease expands into Central Scotland through a dispersal route in the northern Scottish Borders which can be seen as the expansion in the region of seropositive greys in 2015 and 2016. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

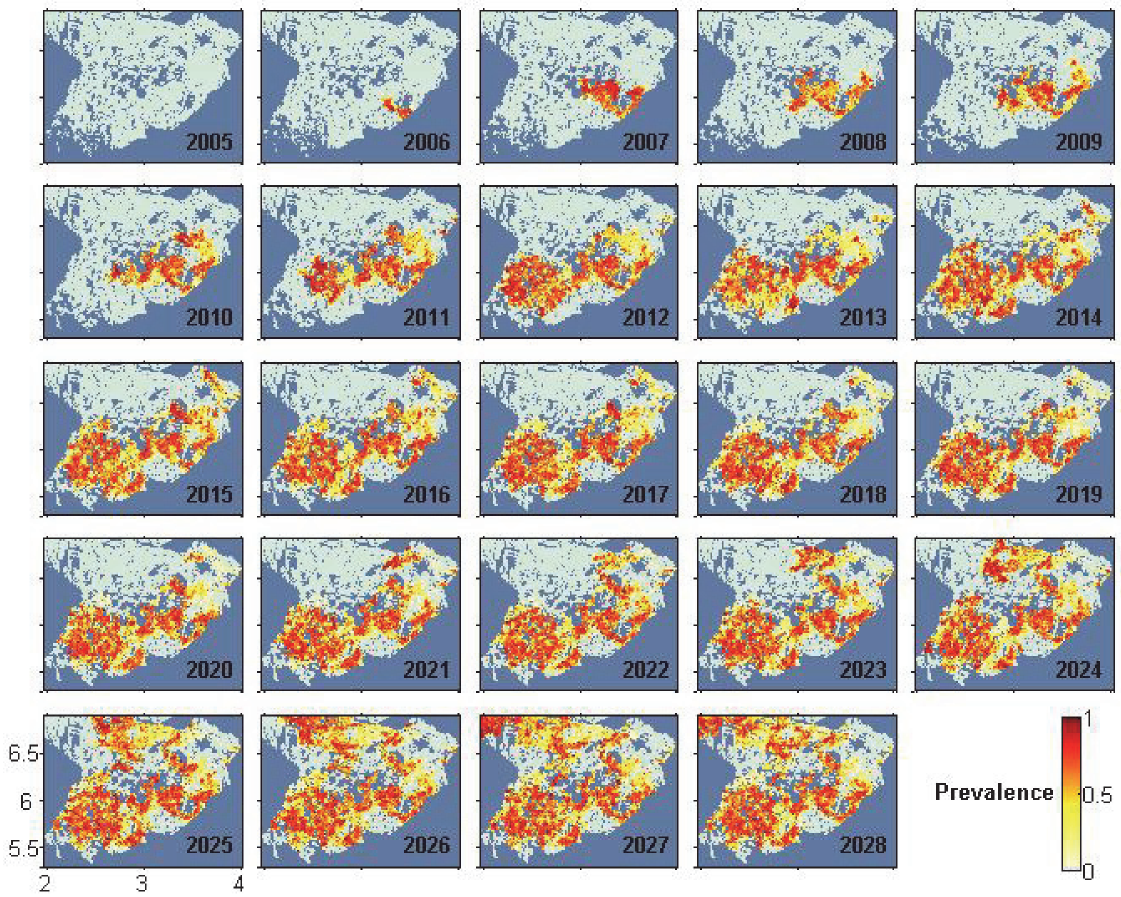

Figure 3.5. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). The disease expands into Central Scotland through a dispersal route in the eastern Scottish Borders and East Lothian which can be seen as the expansion in the region of seropositive greys in 2014. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

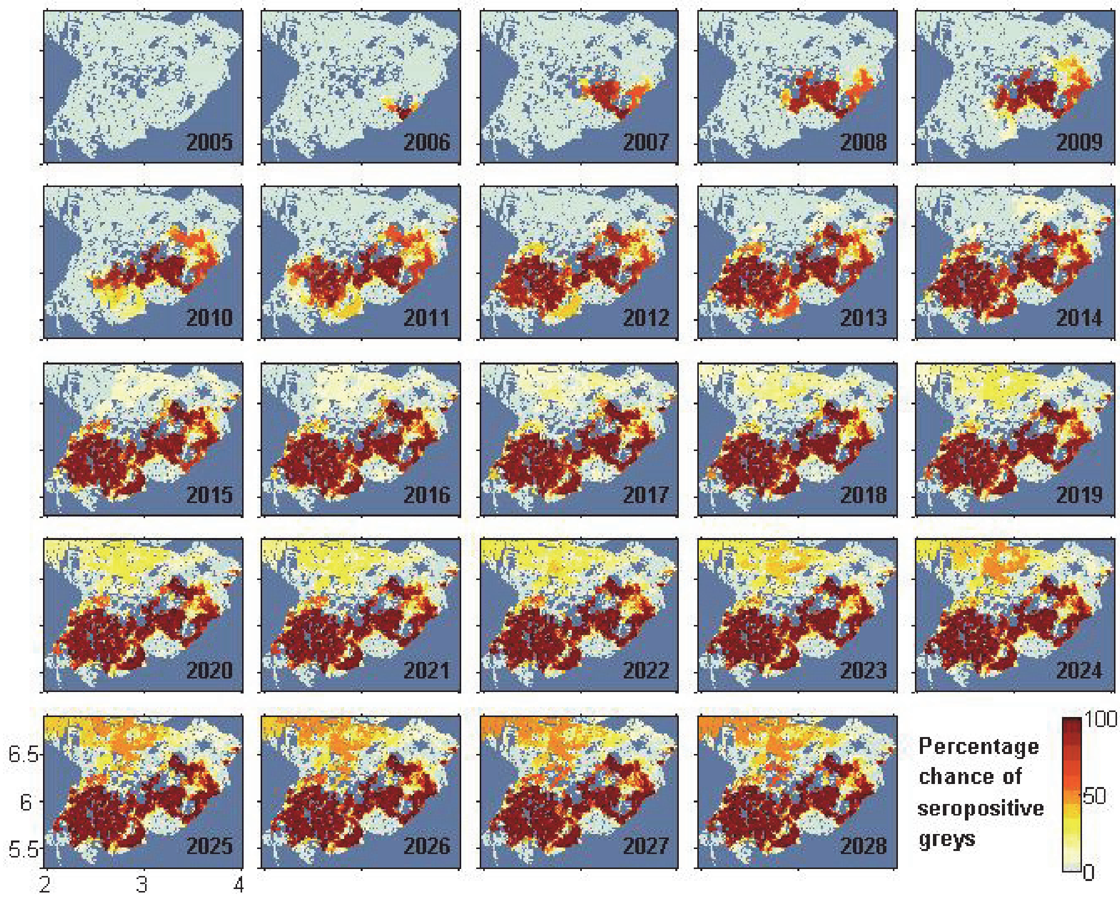

Figure 3.6. The percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

3.3 The spread of SQPV in Southern and Central Scotland under current control strategies

In an attempt to prevent or slow down the spread of squirrelpox through Southern Scotland there has been a programme of targeted control of grey squirrels via the Saving Scotland's Red Squirrels Project. In particular grey squirrels are trapped and removed in regions where squirrelpox outbreaks are detected. There are three main approaches to grey squirrel control. The use of a trap loan scheme and volunteers, Scottish Rural Development Programme (SRDP) funding to landowners to carry out control and the use of grey squirrel control officers. These control measures began in 2005 and have over time become more coordinated and extensive. Since 2012 they have been supplemented by systematic, strategic surveys to determine the extent of squirrelpox spread with the output from the surveys informing trapping regions. Between 2005 and 2011 approximately 4500 grey squirrels have removed through trapping with around 1500 greys caught in each of 2010 and 2011 (see Red Squirrels in South Scotland Project Report, 2012). However, the actual number of greys removed is likely to be larger than this due to unrecorded removals.

For this project data have been provided by SNH and SSRS to allow the temporal and spatial trapping effort to be approximated (see Appendix D, Figure D.2). This data can then be used to develop control procedures to remove grey squirrels in model simulations. The procedure is outlined in Appendix D (original control procedure). The objective is to assess the impact of current control measures on the spread of SQPV and determine whether the scale of current efforts is sufficient to slow or prevent further disease spread. By comparing the results in which grey control is applied to the baseline results without control (section 3.2) it will indicate how control has slowed/prevented the spread of SQPV.

The data from 10 individual simulations in which the control procedure is applied are combined to present a map of the percentage occurrence of squirrelpox in Figure 3.7. Initial simulations of current levels of grey squirrel control were based on a combination of various data, but also some assumptions about the intensity and area over which control is carried out. Using these levels and distribution of control (Figure 3.8) SQPV is not predicted to spread out of South Scotland (Figure 3.7). However, from Figure 3.9 it is clear that the simulated control procedure is removing approximately ten times the number of greys than that reported (around 17000 per year from 2010 onwards rather than the reported amount of around 1500). This will clearly have an impact on the results and the effectiveness of control at reducing squirrelpox spread. To better reflect the reported number grey squirrels that are removed while still retaining the spatial locations over which control is applied, the control procedure in the model was adjusted by reducing the intensity of control (the proportion of a 10km grid square in which control is applied) while retaining the same removal level (when control occurs in a grid cell 40% of greys are removed - see Appendix D, adjusted control procedure).

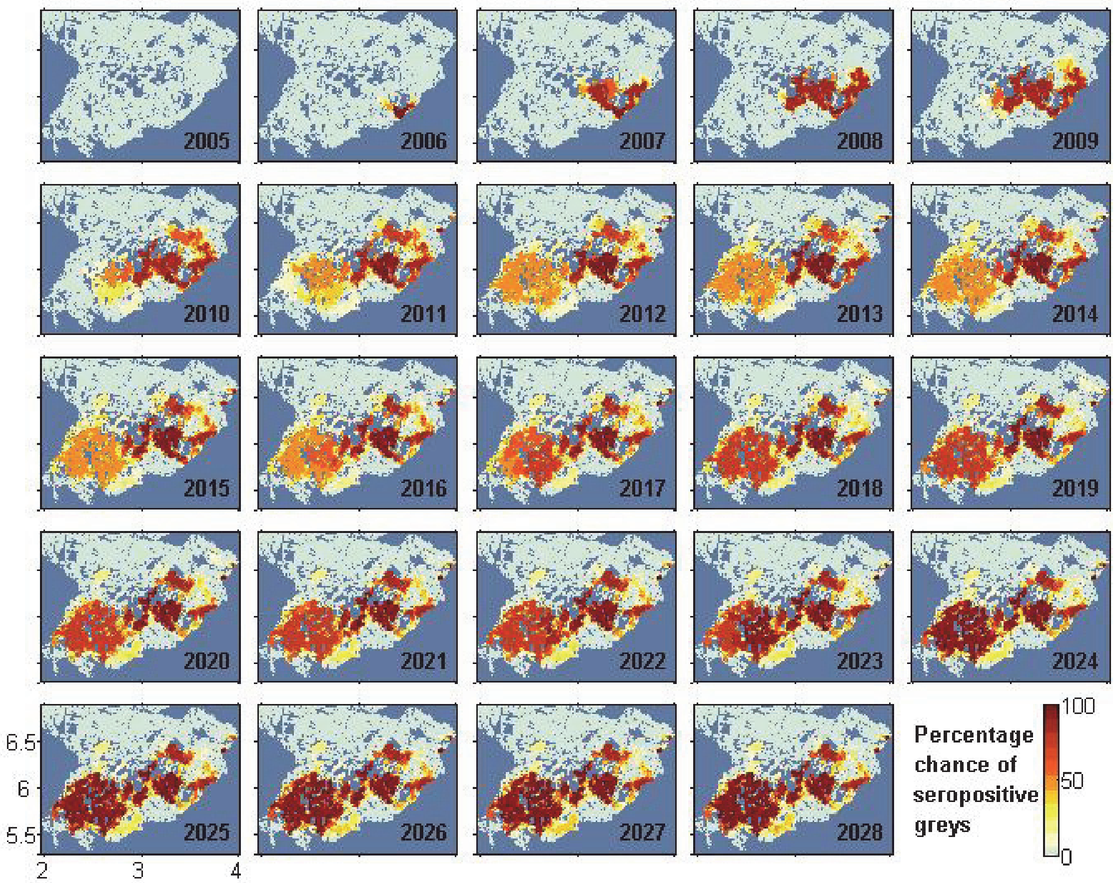

Figure 3.7. The percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2) and the original control procedure is applied (see Appendix D). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

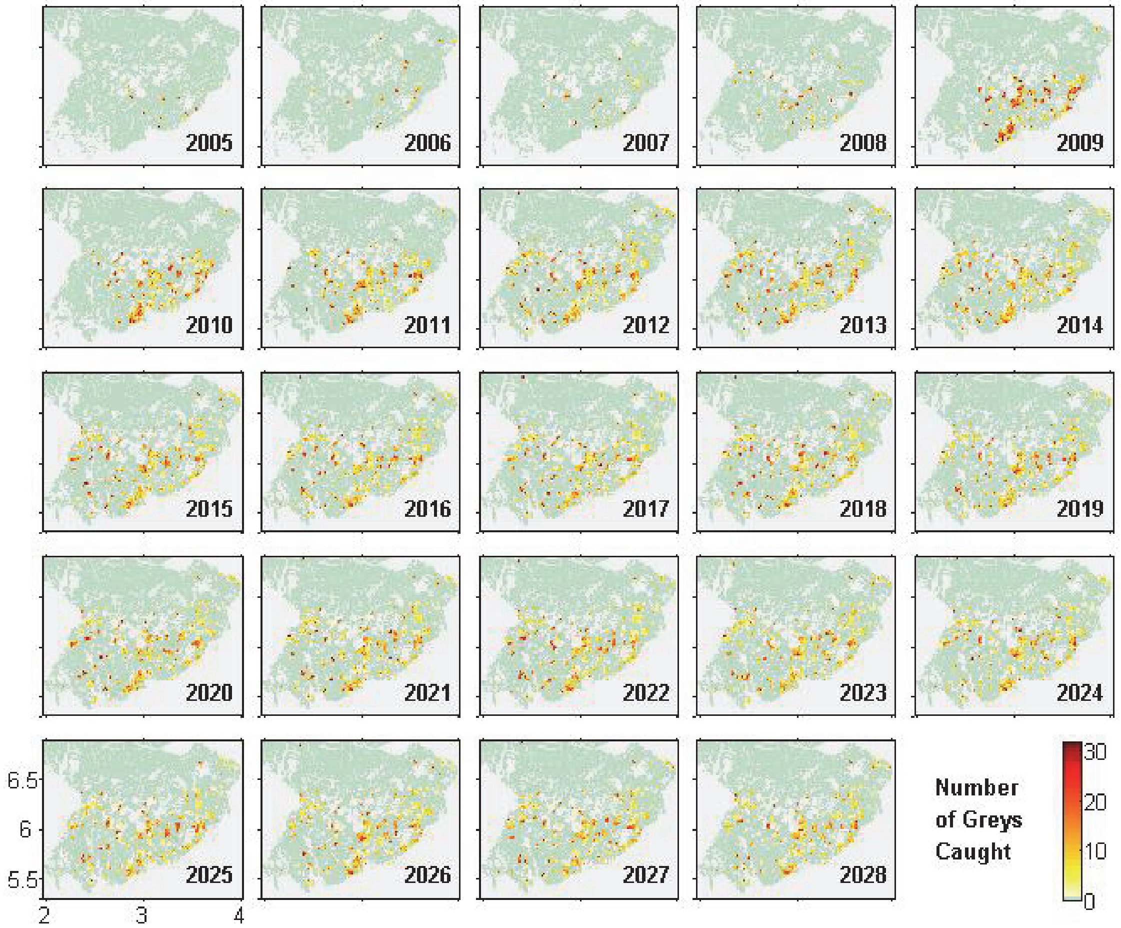

Figure 3.8. The spatial distribution of number of grey squirrels removed each year using the original control procedure. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

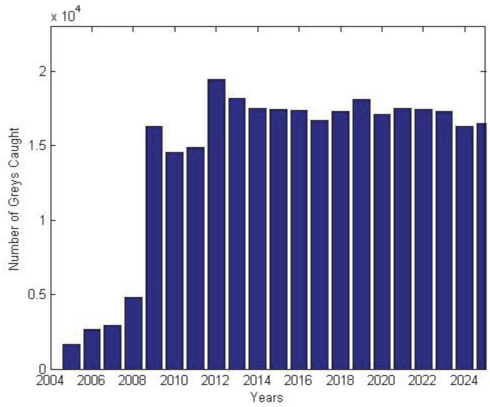

Figure 3.9. The total number of grey squirrels removed each year using the original control procedure.

The adjusted control procedure retains the spatial location over which control is applied and uses the same level of grey removal (40%) when control occurs in a 1km grid cell but reduces the intensity at which control is applied at the 10km grid square level (a 10km grid square that would have been subject to control in 12.5% of its habitable sites is now subject to control in 1.3% of sites. Similar reductions are applied to other levels of control – see Appendix D). The model results under the adjusted levels of control are shown in Figure 3.10 and 3.11.

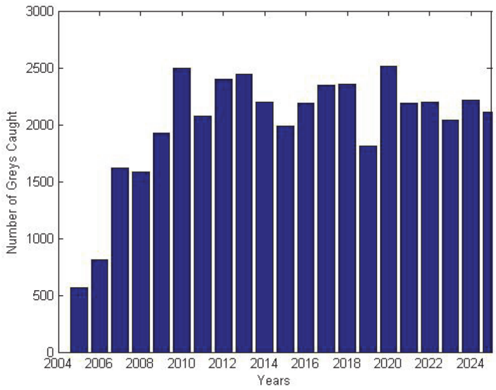

Figure 3.10. The total number of grey squirrels removed each year using the adjusted control procedure.

Figure 3.10 shows that the number of greys removed is now a better reflection of that taking place. This level of control has less of an impact on the spread of squirrelpox (Figure 3.11) and outbreaks can occur in central Scotland. There is however evidence that the control measures have reduced the spread of squirrelpox. The model predicts that:

1. The likelihood of spread from Southern Scotland to Central Scotland is reduced from 50% to 30% as a consequence of control.

2. There is evidence that the spread into western areas of Dumfries and Galloway and the northern and eastern Scottish Borders has been delayed. This suggests that the level of control currently applied is reducing the spread of squirrelpox, but will not prevent it becoming endemic across much of Southern Scotland. (Note, even at higher levels of control (see Figure 3.7) squirrelpox can still expand over much of Southern Scotland, although here this spread is further delayed)

3. The model results also predict that squirrelpox can spread to populations in Central Scotland through the same dispersal routes highlighted in the baseline results (section 3.1), but that the risk of an outbreak in this region has been reduced as a result of control.

Since current (or higher) levels of control cannot prevent squirrelpox becoming endemic in much of Southern Scotland a future alternative control strategy may be to focus resources on preventing squirrelpox reaching grey populations in Central Scotland. A possible strategy to achieve this would be to target control at the dispersal routes that allow squirrelpox spread from Southern to Central Scotland. The model can be used to assess the likely success of such targeted control.

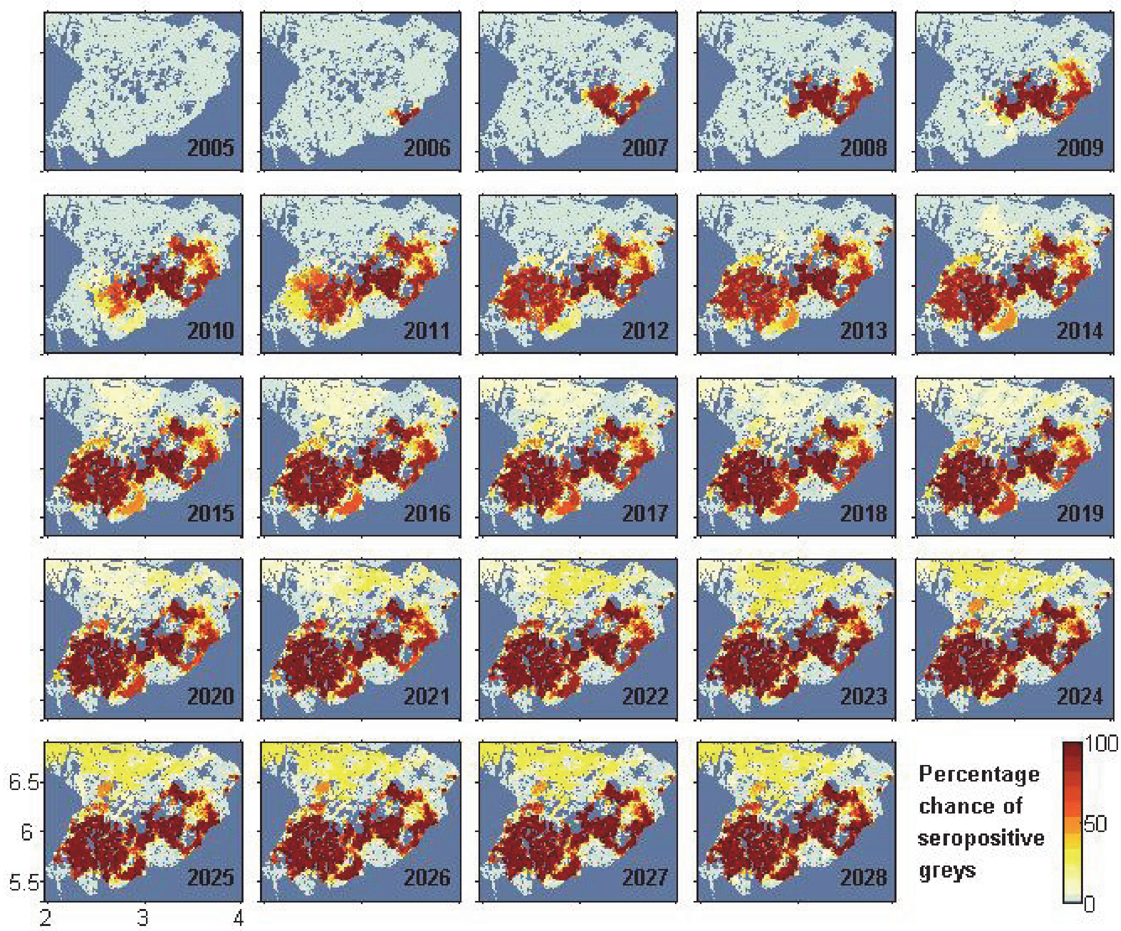

Figure 3.11. The percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2) and the adjusted control procedure is applied (see Appendix D). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

3.4 The spread of SQPV in Southern and Central Scotland under alternative control strategies

To assess whether the control effort could be allocated in a more effective manner to prevent further SQPV spread an alternative control strategy has been developed to limit spread along key disease dispersal routes. These dispersal routes are highlighted in Figures 3.3-3.5 where spread to Central Scotland occurred along forested routes in north-east Ayrshire, the Scottish Borders and East Lothian. A model control procedure was applied in targeted areas (pinch points in the woodland landscape) chosen in an effort to prevent SQPV spread to Central Scotland (Figure 3.12).

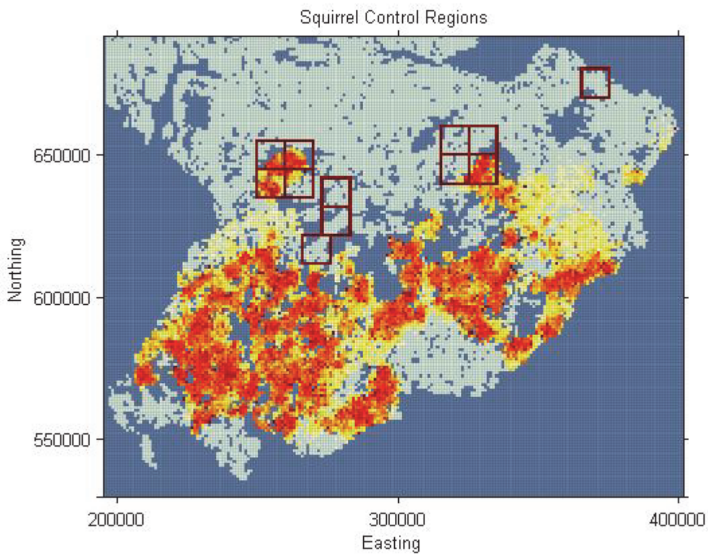

Figure 3.12: The highlighted regions indicate 10km x 10km grid squares in which the targeted control procedures were applied.

In each of the 10km grid squares highlighted in Figure 3.12 a variety of control procedures will be applied from 2013 onwards (no control is applied between 2005 and 2013). We examine the impact of applying control at an intensity level of either 20% or 40% of the habitable area in each 10km grid square in combination with either a 40% or 80% removal level of greys when control is applied to a 1km grid cell. The control procedure then follows that outlined in Appendix D. Figure 3.13 indicates the percentage occurrence of squirrelpox over time for an intensity level of 20 % and a removal level of 80%. Note that in 2 of the 10 simulations the disease spread beyond the control regions before control was applied and led to outbreaks and disease persistence in Central Scotland (Figure 3.13). In the remaining simulations this control strategy prevented the disease from spreading to Central Scotland. The control effort per year is shown in Figure 3.14 indicating that initially around 6000 greys must be controlled but that this number reduces (since squirrel abundance in the control regions reduces over time) to around 2000 per year by the fourth year of control. A control intensity level of 40% combined with an 80% removal rate produces similar findings in which disease spread to Central Scotland is prevented (unless it occurs prior to control). When the removal level of greys is 40% the disease can spread to Central Scotland after 2013 for both levels of intensity of control (in 2 out of the 10 simulations for both intensity levels).

The model results therefore suggest that a high removal rate is critical to prevent the disease spreading through the controlled regions since this reduces grey density to levels that restrict disease epidemics and therefore spread.

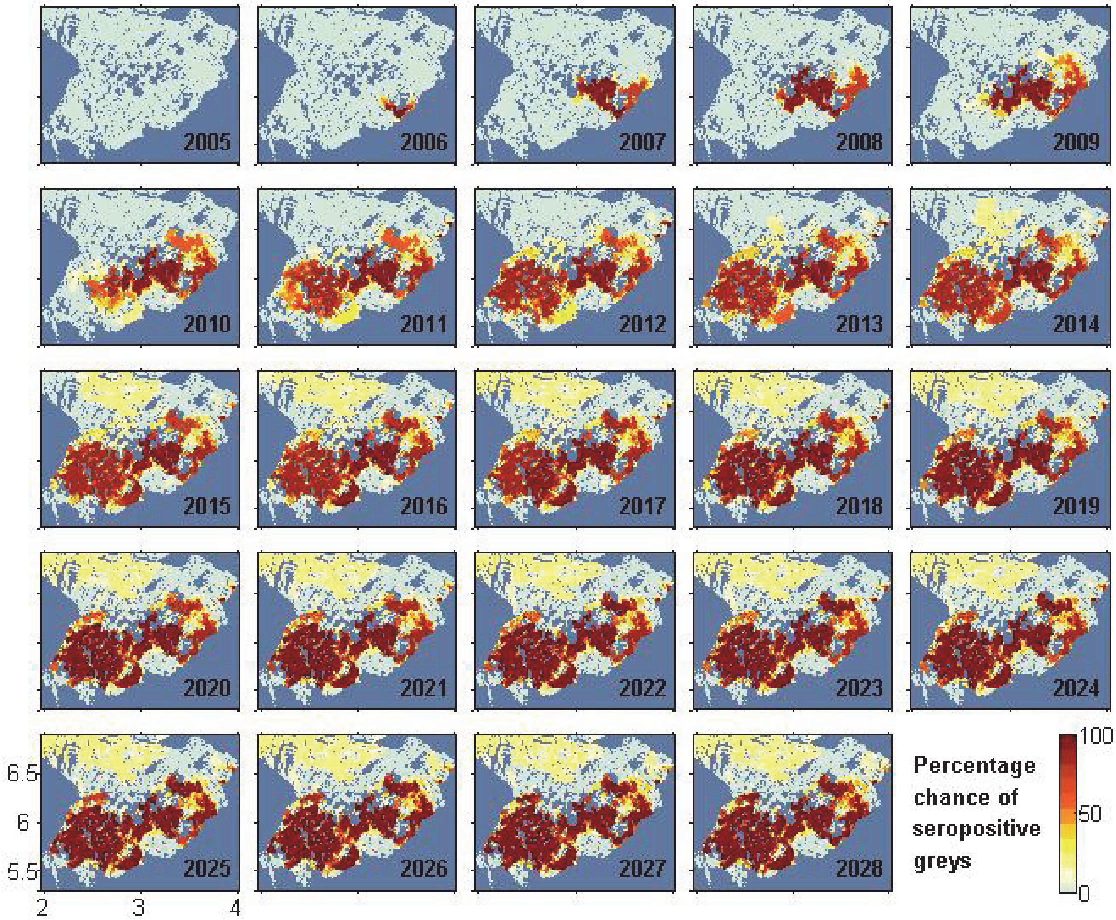

Figure 3.13. The percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2) and control is applied to the regions shown in Figure 3.13 with an intensity of 20% in each 10km grid square and a removal rate of 80% in 1km grid cells to which control is applied (see Appendix D for further details). Note, outbreaks in central Scotland occur in 2 out of 10 model simulations as the disease spreads beyond the control regions prior to control being applied (see year 2013). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

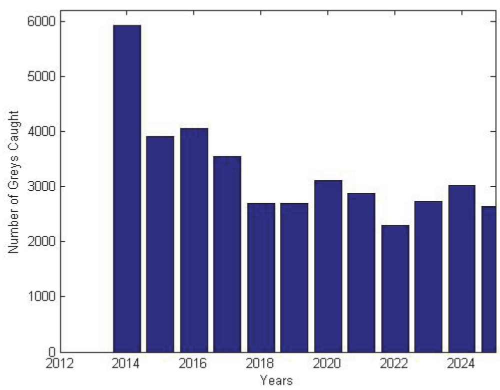

Figure 3.14. The total number of grey squirrels removed each year for the control levels in Figure 3.13.

3.5 Discussion

This report outlines the development and application of a mathematical model to assess the spread of squirrelpox through Southern and Central Scotland. The model was used to simulate the spread of squirrelpox in the absence of control measures to reduce grey squirrel abundance with these results forming a baseline from which the effectiveness of control can be compared.

<u>The key findings from the baseline analysis are:</u>

- In the absence of grey squirrel control squirrelpox is predicted to have spread and persist in most regions of southern Scotland by 2013. Spread to central Scotland occurs in 50% of the model simulations by 2028 (Figure 3.6).

- There is widespread geographical presence of squirrelpox in Southern Scotland and Central Scotland (following successful spread). However the link between southern and central populations tends to occur through distinct dispersal routes.

- Disease prevalence may be low or zero along these dispersal routes for many years but rare disease epidemics along these routes can lead to the establishment of new regions of high disease prevalence (figures 3.3-3.5). The disease can subsequently fade out along the dispersal routes leaving 'islands' of high seroprevalence surrounded by regions of low disease presence.

- The underlying abundance of squirrels in the model is based on estimates of squirrel density that may reflect 'good' habitat years. In reality the quality of the habitat will vary from year to year and no data are available for grey squirrels in Sitka spruce dominated conifer plantations where their presence may be very low, sporadic, or zero in the absence of other high quality, seed bearing tree species. With lower estimates of squirrel abundance, the model predicted a much reduced spread of squirrelpox or failure of the disease to establish (Appendix C). Variation in habitat quality between good and poor levels would therefore impact on the spread of squirrelpox. The disease could spread in good years but its spatial distribution may remain fixed (or contract) in poor years. The results in this report assume that the habitat quality is sufficiently good (level 1 values, Table 3.2) that the disease can establish and spread.

The model system was also used to assess the impact of current levels of grey squirrel control on the spread of squirrelpox. Assessment of the annual intensity of control in 10km grid were combined with estimates of the level of removal derived from trapping data. This method resulted in an approximately 10 fold overestimate in the annual total number of grey squirrels removed compared to recorded estimates from trapping data. This level of control did reduce the rate of spread of squirrelpox through Southern Scotland and prevented the disease spreading to Central Scotland (Figure 3.7). When the intensity of control was reduced to better reflect the observed annual total of greys removed the impact of control on disease spread was reduced. <u>The key findings when applying current levels of controls on grey abundance are:</u>

- Current levels of control reduce the rate of spread of squirrelpox in model simulations but do not prevent the disease from expanding to occupy most regions of Southern Scotland. The likelihood of spread from Southern to Central Scotland by 2028 is reduced from 50% to 30% as a consequence of control.

- Model simulations (both with and without control) indicate that there are bottlenecks in disease spread due to regions of low squirrel density that offer poor connectivity between regions of high abundance where the disease can persist over the long-term.

The model results indicate that the spread of squirrelpox from Southern to Central Scotland occurs along key forested dispersal routes and therefore a possible strategy to prevent spread into Central Scotland may be to apply control measures along these dispersal routes. The main results when applying control along dispersal routes between Southern and Central Scotland are:

- Applying control with a sufficiently high level of grey removal along key disease dispersal routes can prevent the spread of squirrelpox to Central Scotland. Here, the high grey removal rates reduce the grey density to levels that restrict disease epidemics and therefore spread.
- In some model simulations squirrelpox can spread beyond the control regions before the control strategy is applied. Observed squirrelpox outbreaks indicate that the current distribution of the disease has reached the northern extent of Southern Scotland and is therefore close to the dispersal corridors predicted by the model that connect Southern populations to those in Central Scotland. This suggests that there may be a pressing need to consider these control strategies in the field (or that it may be too late to apply these strategies). A further compounding factor is that the model only considers habitat as defined by the forestry inventory data set and so does not consider small (less that 0.5 ha) woodlands or urban habitat. This additional habitat may enhance dispersal and lead to difficulties in isolating dispersal routes in the field.

The model system has provided useful information in determining the likely spread of squirrelpox and the impact that control measures may have in reducing this spread. The current strategy is to control grey populations with the aim of preventing spread of squirrelpox through Southern Scotland and into Central Scotland. Should squirrelpox reach Central Scotland, the SSRS contingency plan indicates that control resources will be switched to intensify grey control and the squirrelpox containment effort to the north of Glasgow-Edinburgh.

3.6 Further Simulations based on feedback from the SSRS Steering Committee

The results for South Scotland were discussed at the SSRS steering committee in May 2013. The steering committee suggested three main areas where they felt further testing of the model could be undertaken. The suggestions were to:

i) attempt to account for poor conifer habitats (Sitka spruce plantations). Parts of Southern Scotland are dominated by Sitka spruce and would lead to lower squirrel densities that those reported for level 1 or 2 parameters (see Table 3.2).
ii) include urban areas. Urban areas could provide good habitat for squirrels and this could impact on SQPV spread and the potential to control SQPV along corridors/pinchpoints.
iii) include poor seed years. There is likely to be year to year variation in population density whereas the model assumes fixed density (at either level 1 or level 2 densities).

In response we undertook the following model simulations. (These simulations were undertaken in July (after much of the work on Central Scotland had been completed) but are presented along with the South Scotland results for clarity.)

3.6.1 Sitka dominated forests and Urban Areas (with control)

We combined points (i) and (ii) above to generate amended squirrel density maps that included a representation of Sitka dominated forests in Galloway and Eskdalemuir and to include urban habitat. The amended maps reduced the potential squirrel density for coniferous forest in Galloway and Eskdalemuir to 0.2 per hectare for red squirrels and 0.05 per hectare for grey squirrels (in both level 1 and level 2 scenarios). (The Galloway forest is represented (approximately) as the region from Girvan → Loch Doon ↓ Clatteringshaws Loch → New Galloway ↓ Kirkcudbright. Eskdalemuir is represented as an 8km x 15km rectangular region positioned over the Eskdalemuir forest). This reflects the poor quality habitat offered by Sitka spruce that form a substantial proportion of the coniferous habitat in these areas. We also extracted all urban habitat from the LandcoverMap 2007 (licensed to SNH by CEH) (this was not available when the initial simulations were undertaken). The potential density per hectare of red and grey squirrels in urban areas was set as - level 1: red 0.83, grey 0.9; level 2: red 0.33, grey 0.7. There is very little information about squirrel densities in urban habitat and it is likely to be highly variable. In some regions - parks/gardens - densities may approach those used for broadleaf habitat but the patchy nature of the habitat will reduce average density. Therefore we chose values equivalent to the (original) densities for coniferous forests as this offers a good habitat at values lower than those for continuous broadleaf forest. The amended densities are shown in Figure 3.15 (compare with Figure 3.1) and show a reduction in potential density in Galloway and Eskdalemuir and an increase in large urban areas (particularly across the central belt).

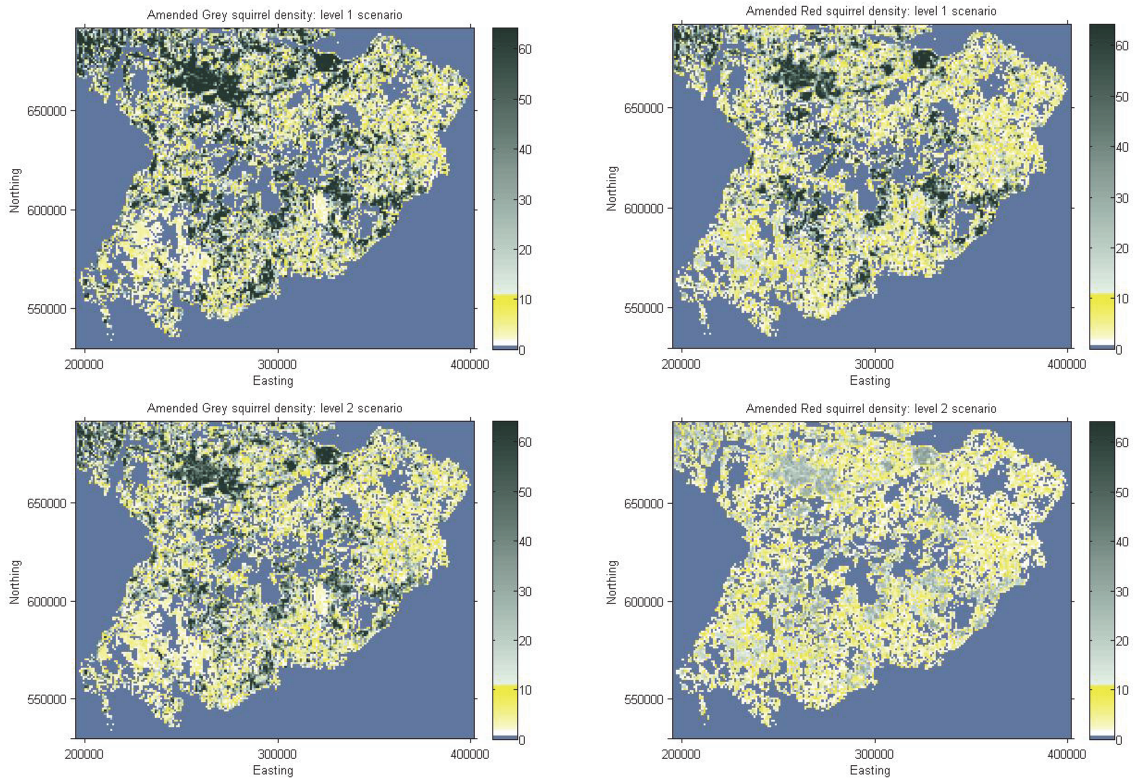

Figure 3.15. Estimates of densities in 1km x 1km grid squares used in the model assessments with the amendments described in section 3.6 to represent Sitka dominated forest in the Galloway and Eskdalemuir and to include urban habitat.

Model simulations were undertaken with the amended level 1 densities (and with realistic levels of control - see Figure 3.10 and 3.11) with the results for the percentage occurrence of squirrelpox over time shown in Figure 3.16 (compare with Figure 3.11). It can be seen that SQPV no longer spreads into Dumfries and Galloway and is absent in Eskdalemuir as the reduced densities in these regions cannot support the disease. However, disease spread does occur adjacent to these regions and the inclusion of urban habitat (with associated increases in squirrel density) leads to a higher chance of SQPV reaching central populations (compare Figure 3.16 with 3.11 noting that there is a 50% chance of SQPV reaching the central population when urban habitat is included rather that a 30% chance in its absence). The corridors along which the disease spreads that connect the southern and central populations are the same as those reported in section 3.2 (north-east Ayrshire, the Scottish Borders and East Lothian) but there is an additional corridor along the Ayrshire coast which is responsible for SQPV reaching the Central population in 40% of the simulations (Figure 3.17 which show a single model run). This corridor is a result of including urban habitat.

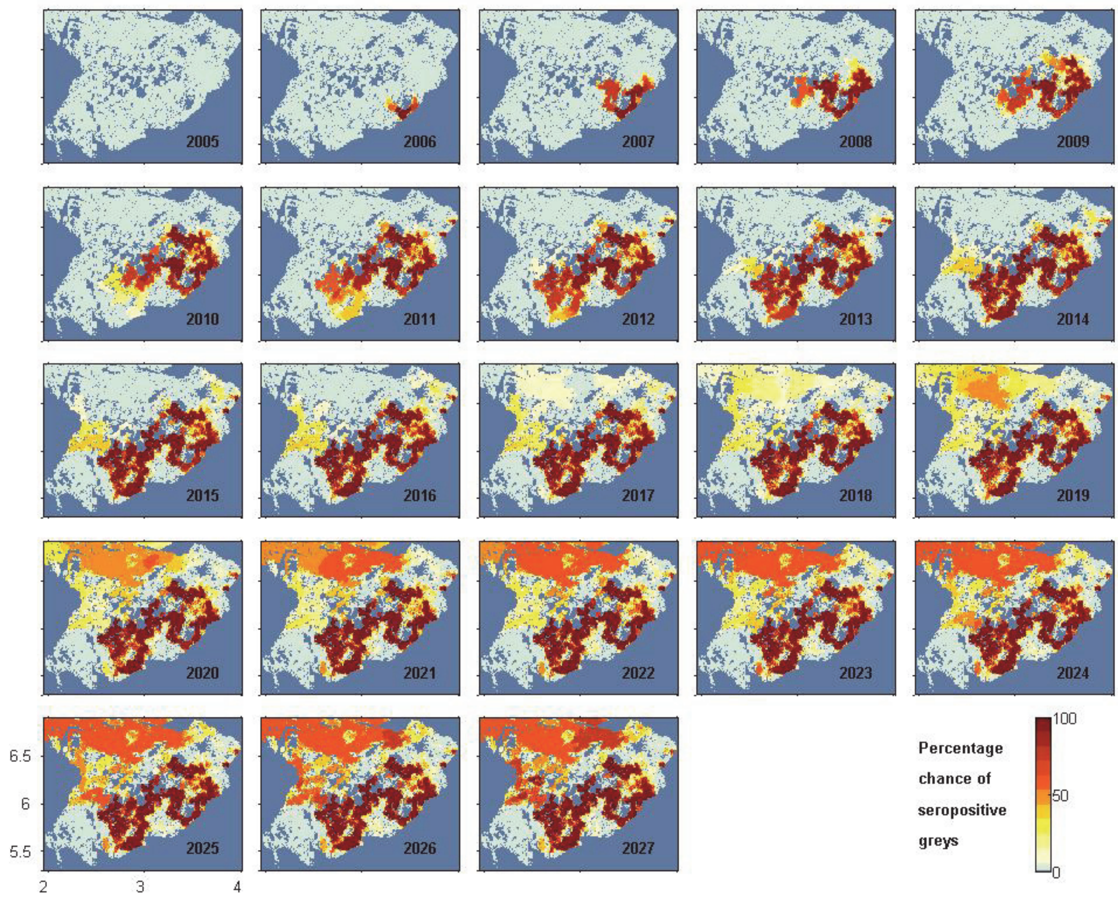

Figure 3.16. The percentage occurrence (in 10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here amended level 1 densities are used to define squirrel carrying capacities (see Section 3.6) and the adjusted control procedure is applied (see Appendix D). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

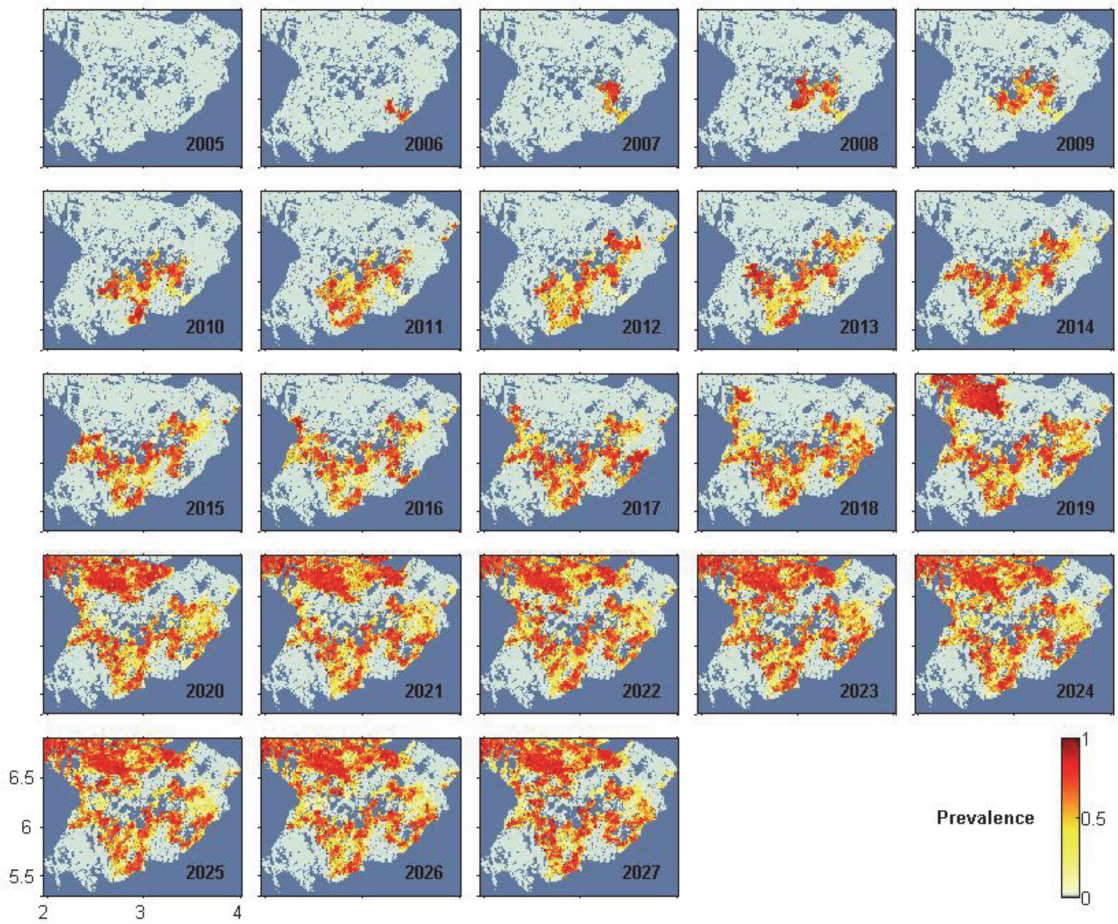

Figure 3.17. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). The disease expands into Central Scotland through a route along the Ayrshire coast which can be seen as the expansion in the region of seropositive greys between 2016 and 2018. Here amended level 1 densities are used to define squirrel carrying capacities (Section 3.6) and the adjusted control procedure is applied (see Appendix D). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

3.6.2 Yearly Variation, Sitka dominated forests and Urban Areas (with control)

We include yearly variation to allow the squirrel density to vary between the level 1 and level 2 values over time. Figure 3.18 indicates how this variation operates and shows that level 1 and level 2 densities are never fully realised but are approached every 6 years. This yearly variation is included in the amended model simulations with the results for the percentage occurrence of squirrelpox over time shown in Figure 3.19 (which should be compared with Figure 3.16 to understand the effect of yearly variation in density). The effect of including yearly variation is to slow down the spread of squirrelpox (compare the chance of SQPV reaching central populations by 2027 in Figure 3.16 and 3.19). The results in Figure 3.19 are shown for a longer time period to highlight that SQPV does eventually reach central population. The delay in spread is due to the imposed yearly variation which act to change population density to levels in which spread is limited (the lower level 2 densities) and those in which spread is extensive (the higher level 1 densities). SQPV reaches central population by spreading along the same distinct routes as those outlined for the amended results presented above without yearly variation (see section 3.6.1) (with the exception that SQPV spread through East Lothian to Central populations was not observed in any of the 10 simulations that included yearly variation).

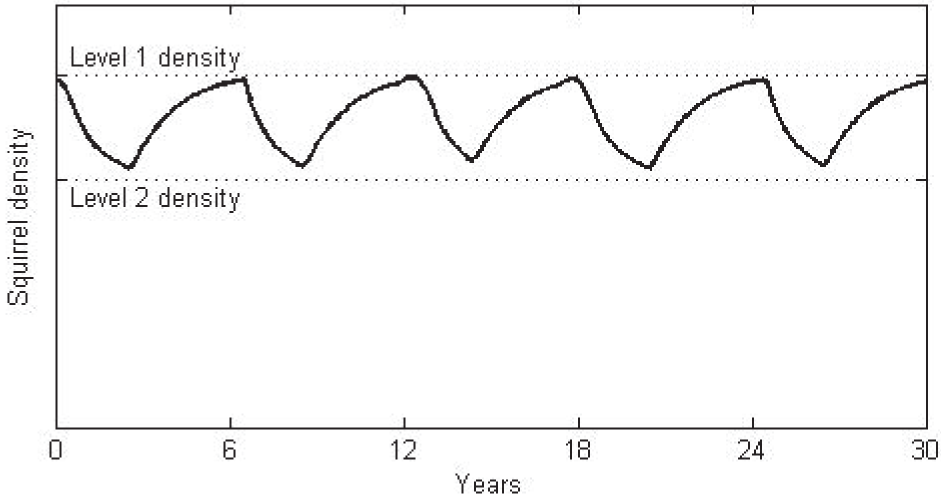

Figure 3.18. Squirrel population density over time indicating how a seasonal forcing component affects density allowing it to oscillate between level 1 and level 2 densities.

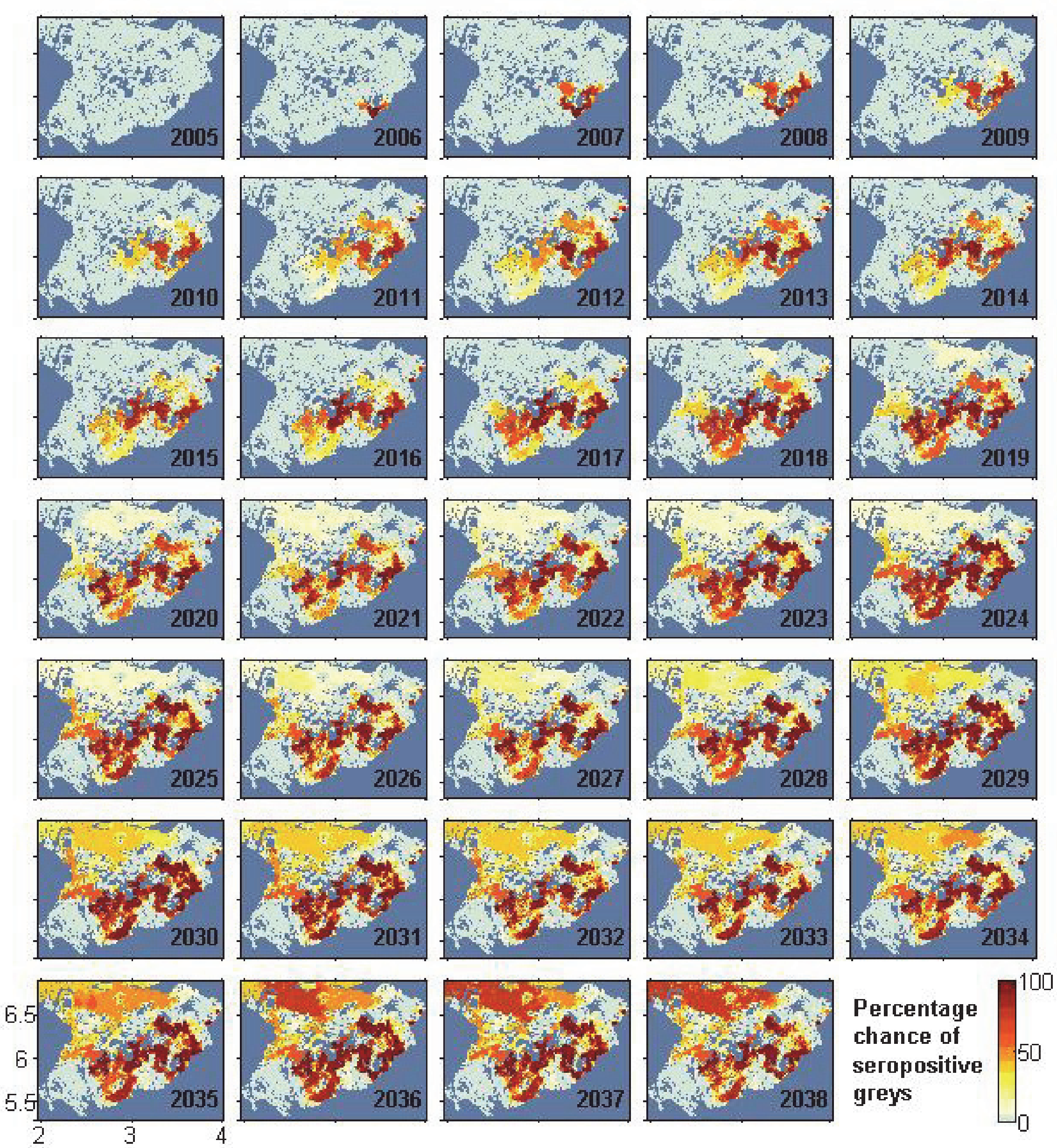

Figure 3.19. The percentage occurrence (in 10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here amended level 1 densities are used to define squirrel carrying capacities (see Section 3.6) and yearly variation is included such that the carrying capacity in each patch oscillates between level 1 and level 2 densities. The adjusted control procedure is applied (see Appendix D). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

3.6.3 Key Findings from the Further Model Simulations

In response to suggestions from the SSRS steering group further model simulations were undertaken to assess how poor habitat, urban habitat and variation in habitat quality would affect the spread of SQPV. The key results are as follows:

- Low density habitat prevents the spread of SQPV. When the coniferous habitat in Galloway and Eskdalemuir are assumed to be composed of Sitka spruce only, it reduces the potential squirrel densities in these regions to levels that cannot support SQPV spread. This highlights the potential importance of using more detailed habitat information to determine potential squirrel density distributions. In reality the coniferous forest composition throughout Scotland will contain a variety of tree species but accurate information about forest species composition is only readily available for the National Forest Estate.

- SQPV can spread around and beyond low density habitat regions. Although SQPV does not spread and establish in Galloway and Eskdalemuir, the model simulations indicate that SQPV can spread around and beyond these regions leading to outbreaks in Central regions. Therefore regions of poor habitat have an impact on the persistence of SQPV locally but may not have an impact on the large scale spread of SQPV as the low density regions can be circumnavigated.

- Urban areas promote the spread of SQPV. Urban areas provide additional, good quality habitat through which SQPV can spread and establish. The model simulations indicated that urban habitat has the potential to provide a corridor along which SQPV can spread that connects populations in the South and Central Scotland (such a corridor is evident in model runs along the Ayrshire coast, Figure 3.17).

- Poor habitat years slow the spread of SQPV. Variation in habitat quality in which density oscillates between level 1 and level 2 values slows the overall spread of SQPV through southern Scotland and therefore also delays the spread to Central Scotland. The SQPV distribution remains relatively fixed in low density years but expands in high density years.

- The amendments to the model do not change the key result that SQPV spread is rapid through high density grey populations, and that control measures may slow down the spread of SQPV but may not prevent it from spreading throughout suitable habitat in Southern Scotland. Spread from Southern to Central Scotland still occurs through distinct dispersal routes and urban areas may also act as dispersal corridors that connect regions of good quality habitat.

- The model shows that current control strategies in Southern Scotland may not prevent disease spread due to the contiguous nature of good forest habitat in these regions. However, it is important to note that whilst control may not prevent disease spread it would have contributed to local red survival and recovery post disease outbreak (and this is borne out by information from SSRS regarding red population recovery in areas that are subject to grey control).

4. CENTRAL AND NORTHERN SCOTLAND

In the next phase of modelling we assess the potential spread of squirrelpox through Central and Northern Scotland and we examine the potential for a containment line to inform the best control strategies. Should control be insufficient to prevent further squirrelpox spread (or the cost and level of control required be prohibitive) it will be important to understand the impact of the spread of squirrelpox through current disease-free grey populations into the remaining continuous red populations in the Highlands of Scotland. Hence the disease dynamics at the interface is also examined. The model framework is as described in section 2.

4.1 Habitat Composition and Initial Conditions

Following the methods outlined in sections 3.1 the Scottish Natural Heritage land classification maps for 2007 and Forestry Commission Scotland forest inventory maps for 2011 were used to determine the proportion of each 1km x 1km grid square that was occupied by coniferous forest, broadleaved forest, shrub or that was non-squirrel habitat (e.g. water bodies). The gridded habitat data was combined with the level 1 estimates of squirrel density (Table 3.2) to produce carrying capacities at the 1km x 1km grid square level (Figure 4.1a,b). This information was combined with predictions of red and grey squirrel occupancy (provided by SSRS from 10km x 10km squirrel occupancy records from 2008-present) to determine initial densities for red and grey squirrels (Figure 4.1c,d)

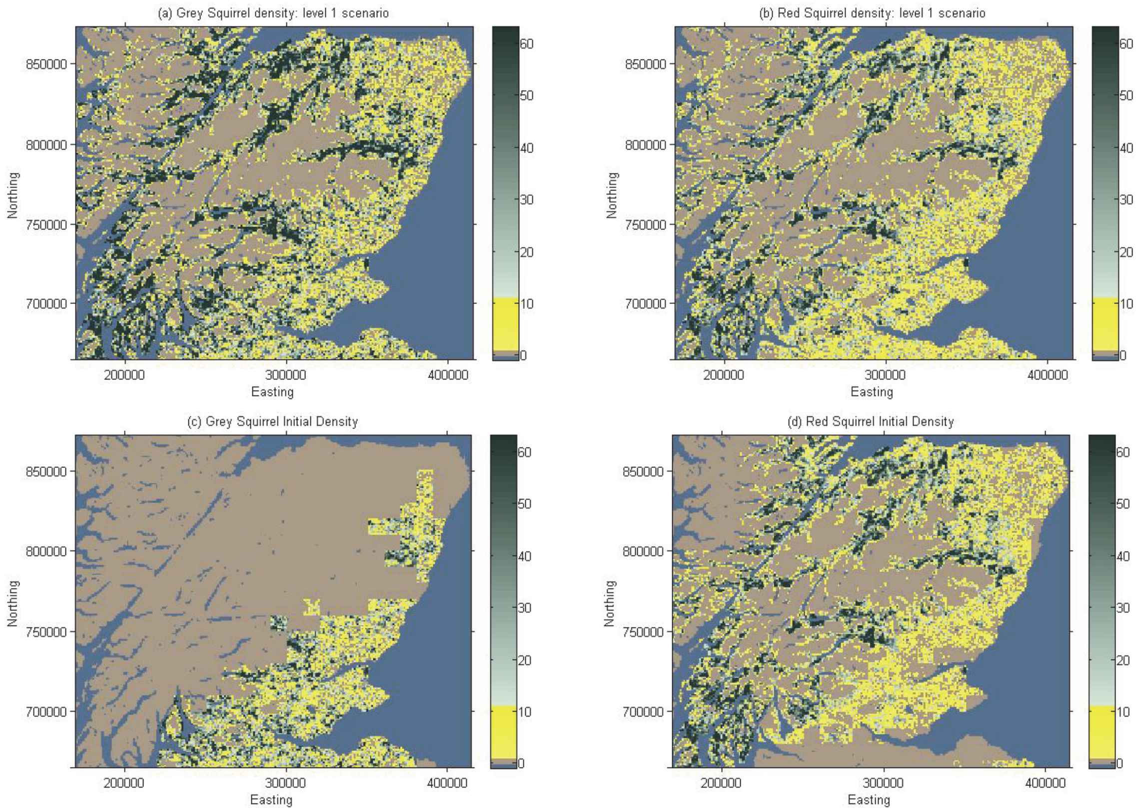

Figure 4.1 Estimates of densities in 1km x 1km grid squares used in the model assessments showing the carrying capacity for (a) grey and (b) red squirrels and the initial densities for (c) grey and (d) red squirrels.

4.2 The spread of SQPV in Central and Northern Scotland without control

Model simulations were undertaken to determine the rate and extent of squirrelpox spread in the absence of any control measures. These simulations provide baseline results to which the impact of control measures can be compared.

In order to determine the likelihood of squirrelpox spread, we combined the results from 10 individual model simulations to present a map of the percentage occurrence of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% (e.g. one in five grey squirrels have antibodies to squirrelpox) in a 1km grid square. Figure 4.2 shows the spread and establishment of squirrelpox across Central and Northern Scotland assuming that it was initially introduced in two areas in Central Scotland (to represent its spread from populations in which the disease persists in Southern Scotland).

The spread through central regions is rapid and occurs by year 4. Disease spreads through a narrow corridor (situated approximately between Alloa and Muckhart) between year 4 and 5 (approximately) and then expands to occupy most habitable regions of southern Perth and Kinross over the next 10 years, with further population linkage that connects to Central populations at approximately Kincardine and Dunblane. It is likely that these routes could also act as corridors for SQPV spread but their effectiveness is masked by the efficiency of spread along the Alloa-Muckhart corridor. The timing of individual simulations differs and depends on successful spread through the initial Alloa-Muckhart pinchpoint. This suggests that targeted control of grey numbers to reduce density along and at either end of these corridors may act to prevent or significantly slow the spread of squirrelpox into Southern Perth and Kinross and then beyond. In 3 of the 10 simulations the disease can spread and establish in Angus (through a corridor near Blairgowrie, see year 14 onwards) and in one simulation this also expands to Aberdeenshire (through a corridor north of Laurencekirk, see year 23 onwards). It is worth noting that the results in Figure 4.2 show seroprevalence and therefore can only highlight the spread of SQPV in grey populations (since SQPV is fatal to red squirrels they do not recover, become immune and show antibodies to the infection). To highlight whether SQPV can spread through red populations in Figure 4.3 we plot the occurrence of infection in reds and greys.

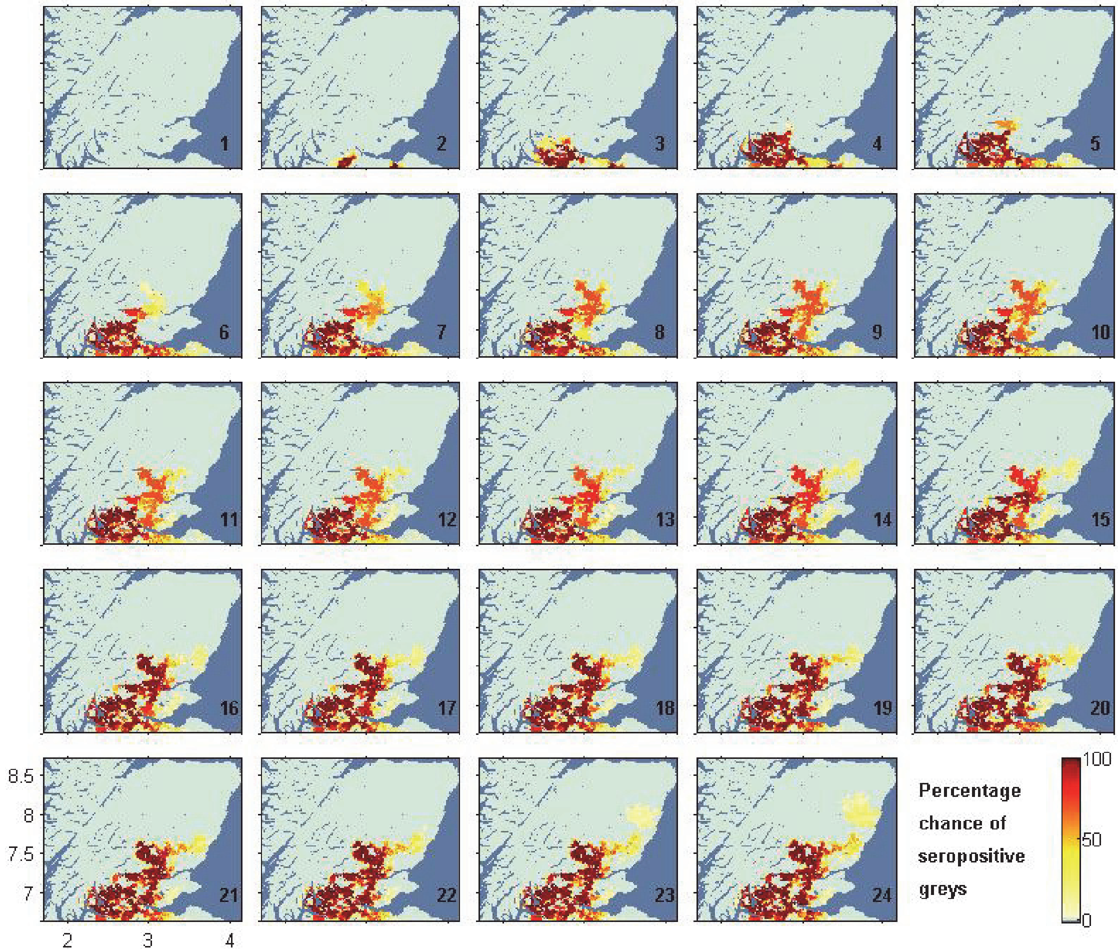

Figure 4.2 The percentage occurrence (in 10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2). Easting and Northing values (/ 10^5) are shown on the bottom left panel.

Figure 4.3 shows the occurrence of SQPV infection in red and grey squirrels (it shows where disease outbreaks occurred in any of the 10 simulations). It indicates that much of the infectious spread is through grey populations and when the population density of greys is sufficiently high the spread is rapid. There are outbreaks of disease in established high density red squirrel populations but these are constrained to regions that are adjacent to disease outbreaks in greys. Outbreaks can extend into regions which contain red squirrels only but the disease fades-out (the number of infective individuals tends to zero) and does not spread and establish over extensive areas in the same manner as it does in grey populations. The occurrence of SQPV outbreaks in a single model simulation is shown in Appendix F and confirms that outbreaks in red only populations are infrequent and local to adjacent outbreaks in grey populations. In summary, in the absence of control the disease rapidly spreads through established grey populations. Spread is reduced along corridors of poor quality habitat (low grey density) and this delays the arrival of SQPV in North East Scotland regions where greys are already established. Therefore over time the distribution of SQPV matches the distribution of grey squirrels (compare Figure 4.1c with 4.2 in year 24). Outbreaks of SQPV infection can occur in red squirrel dominated regions adjacent to established grey populations but the disease fades-out and does not extensively spread through established red squirrel only populations. This explains the absence of SQPV along western and northern regions (see Figure 4.3).

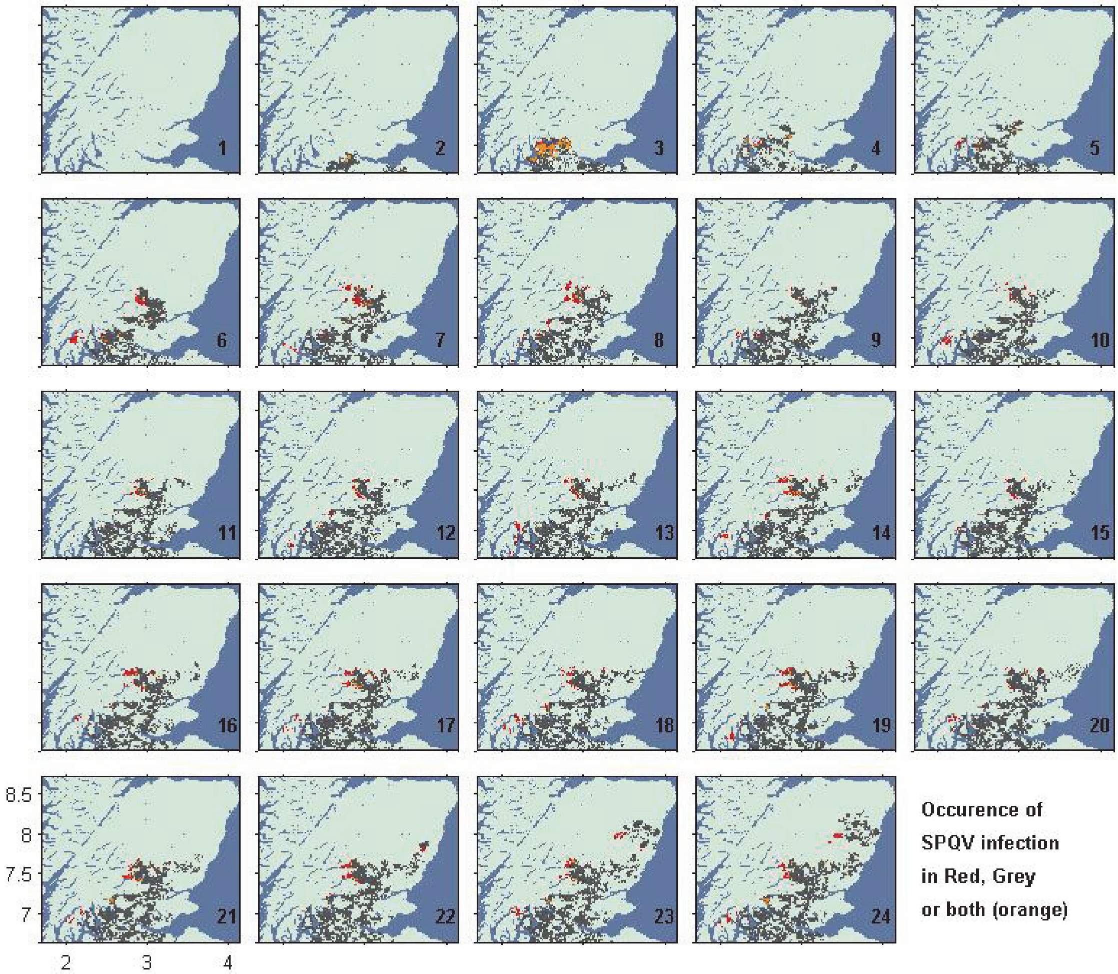

Figure 4.3. The occurrence of SQPV infected individuals in any of the 10 simulations over time. The red cells indicate the presence of infected red squirrels, grey cells infected grey squirrels and orange cells infected red and grey squirrels.

4.3 The spread of SQPV in Central and Northern Scotland with control

We incorporated control in a similar manner to that outlined in section 3.3. Data from SNH for 2009-2012 was provided on a 10km squared basis for SRDP contracts and the procedure to represent this data in the model is explained in Appendix D. Data from SSRS for 2007-2012 that included control from Grey Squirrel Control Officers, Volunteers, Forestry Commission Scotland and Traploan Schemes was provided on a 1km squared basis and provided information on the number of greys caught. This information can be input directly into the model. For years after 2012 the level of control was assumed to be the same as the 2012 level. Figure 4.4 shows the predicted number of greys caught in one realisation of the model. The total number caught rises from approximately 600 in 2007 (year 1); to around 2000 in 2012 (year 6) and thereafter decreases slightly. (In the model the same proportion of greys are removed from 2012 onwards but as the number of greys in a gridpatch is reduced due to removal in previous years the total number caught decreases from 2012 onwards.)

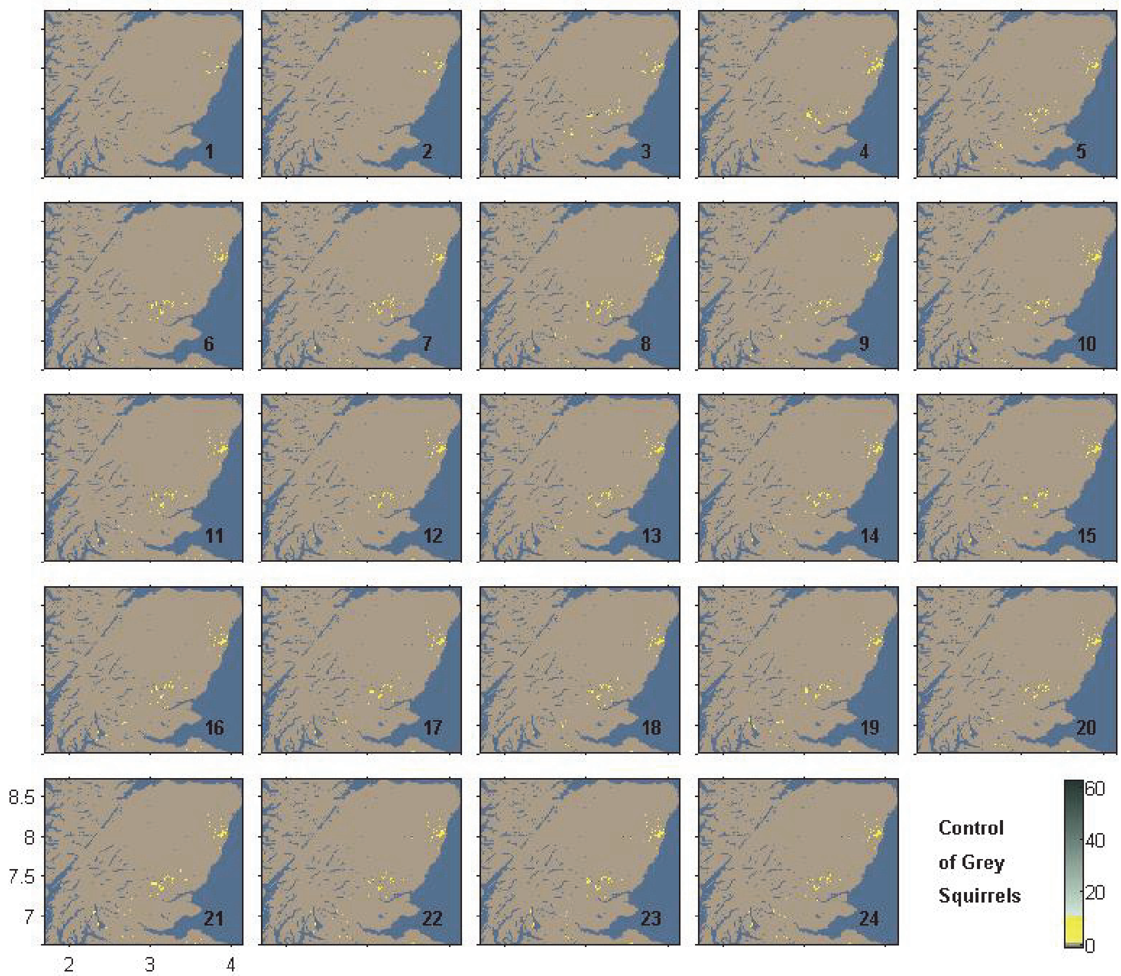

Figure 4.4: The spatial distribution of number of grey squirrels removed each year. Year 1 corresponds to 2007, which is the first year in which control data was available.

The model results for the spread of SQPV are shown in Figure 4.5. The control procedures have not had a marked effect on reducing SQPV spread. The lack of large scale impact of control is due to the localised nature of control (see Figure 4.4) and so SQPV is able to spread around and beyond the controlled areas. This result is to be expected as the current control strategies applied in Central and Northern Scotland were not introduced to prevent disease spread and are intended to prevent grey squirrel spread along key dispersal corridors and to protect local populations of reds. Although control does not prevent extensive spread of SQPV there is some reduction in the level of SQPV outbreaks locally. This can be seen in Figure 4.6 which indicates where infectious outbreaks occur in the model simulations. Comparing Figure 4.6 with 4.3 shows there are less pronounced outbreaks in red populations and grey populations in regions were control is applied (around Aberdeen and Dunkeld).

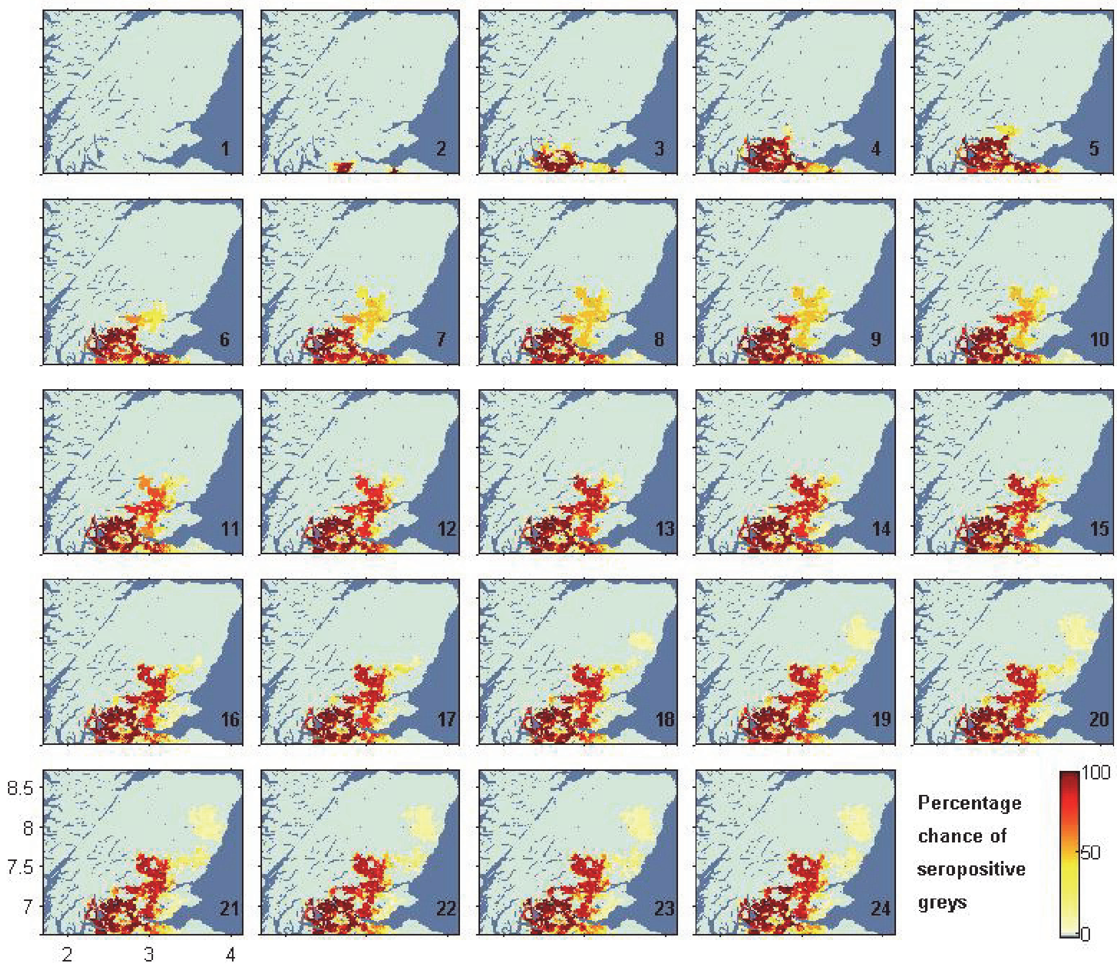

Figure 4.5 The percentage occurrence in (10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Here level 1 densities are used to define squirrel carrying capacities (Table 3.2) and control is applied as outlined in section 4.3. Easting and Northing values (/ 10^5) are shown on the bottom left panel.

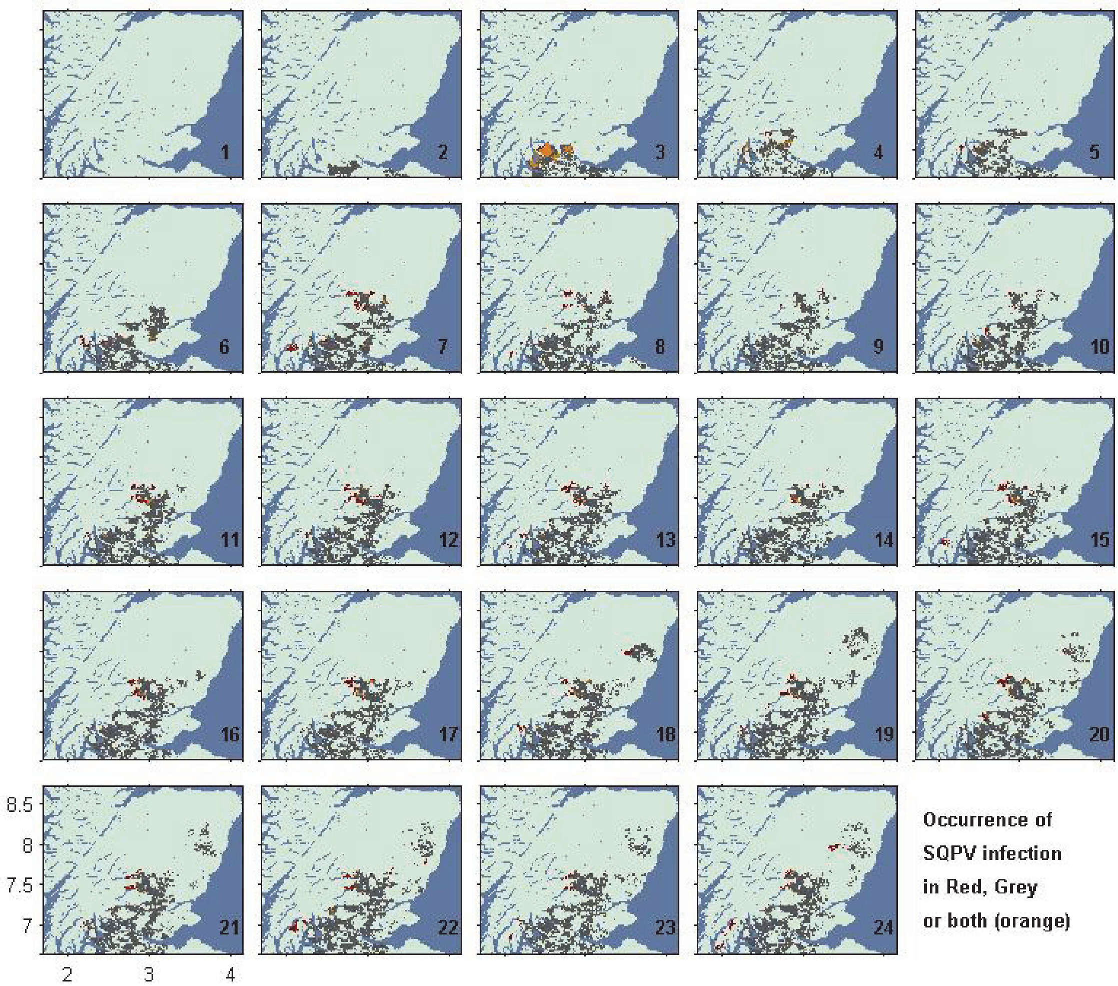

Figure 4.6. The occurrence of SQPV infected individuals in any of the 10 simulations over time with control. The red cells indicate the presence of infected red squirrels, grey cells infected grey squirrels and orange cells infected red and grey squirrels.

4.4 Discussion

In section 4 the mathematical model is used to assess the spread of squirrelpox through Central and Northern Scotland under the assumption that squirrelpox has spread through Southern Scotland. The model was used to simulate the spread of squirrelpox in the absence of control measures to reduce grey squirrel abundance and these results form a baseline from which the effectiveness of control can be compared. The key findings from the baseline analysis are:

- The spread of SQPV through the high density grey populations in Central Scotland is rapid and most areas in Central Scotland are predicted to support SQPV at endemic levels in greys within 5 years of initial (local) outbreaks.
- SQPV spread into established grey population beyond Central regions occurs through distinct corridors. The model outlines corridors between Alloa and Muckhart connecting Central populations with those in Perth and Kinross and a further corridor near Blairgowrie leading to SQPV spread in to Angus and potentially Aberdeenshire. Control

measures targeted at these corridors may act to prevent the spread of SQPV (as shown when the targeted control regime was employed in section 3.4 in South Scotland).

- The spread of SQPV is largely contained within the current distribution of grey squirrel populations. Outbreaks of SQPV in red squirrel only populations can occur in regions adjacent to outbreaks in grey populations. However, these outbreaks in red populations are predicted to be localised with squirrelpox infection fading-out and becoming extinct typically within a year of the initial outbreak. Therefore SQPV is not observed to spread through connected regions containing red squirrels in the same (extensive) manner that it does through grey populations. Importantly, the model suggests that SQPV will not continue to spread through the established populations of red squirrels in Western, Northern and Highland Scotland (where grey squirrels are absent).

The model was adapted to include a representation of the current levels of grey squirrel control under SSRS. The key findings when applying current levels of controls on grey abundance are:

- Current levels of control do not prevent the extensive spread of SQPV through established grey populations in Central and Northern Scotland. Control does reduce the level of SQPV seroprevalence and reduces infectious outbreaks locally but SQPV can spread around and beyond control regions. This result was expected, as the aim of control in these areas up to now was to contain grey squirrel spread and not the prevention of SQPV spread over a large area.
- There is some evidence that SQPV outbreaks in red populations that are adjacent to grey populations are reduced as a result of control. Here, by reducing grey density it reduces the chance of SQPV establishment and infectious outbreaks in grey populations and this affords some protection from SQPV for neighbouring red populations.
- The model used to assess the spread of SQPV in Central and Northern Scotland does not include either urban habitat or yearly variation in squirrel densities (these simulations were undertaken prior to the amended South Scotland model runs). Urban habitat will promote SQPV spread and may offer new corridors along which infection can spread, especially along the coast (see Figure 4.7). Yearly variation in squirrel densities will slow down the spread of SQPV and may prevent spread to Angus and Aberdeenshire (as this was a rare occurrence in current model simulations).

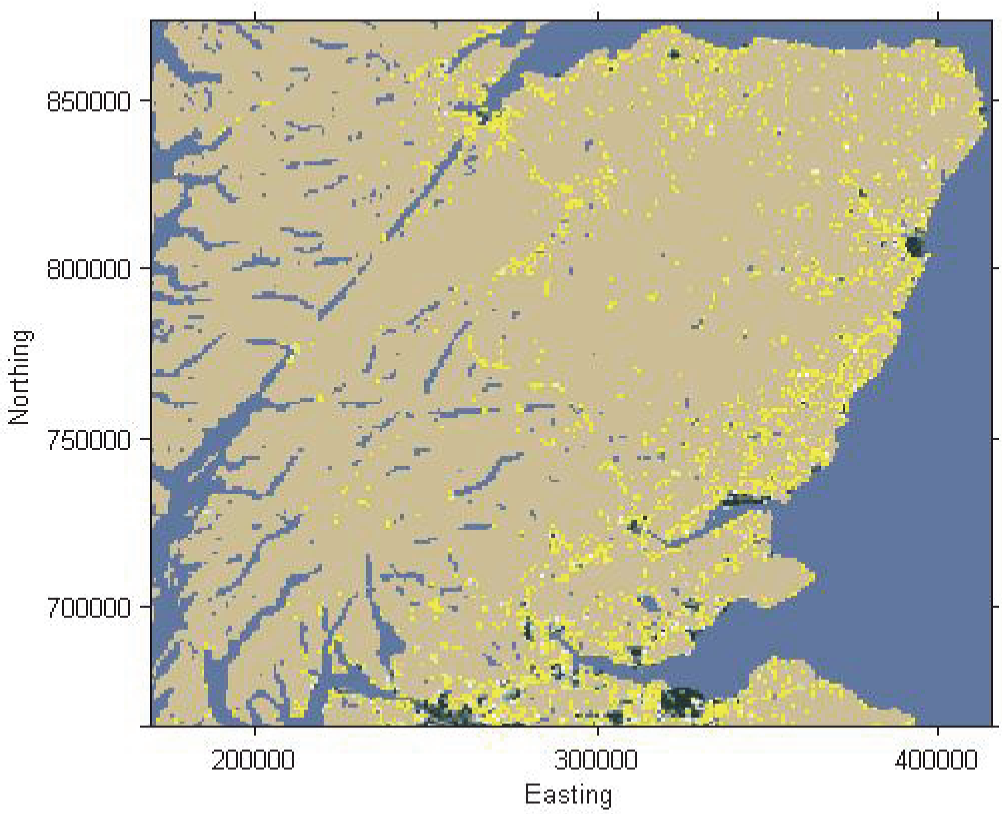

Figure 4.7. The intensity of urban habitat. This would offer additional habitat for squirrels and may provide additional routes along which SQPV can spread.

5. FLEET BASIN STRONGHOLD

The last scenario explored using the model is the control effort needed to maintain red squirrel populations in stronghold forests where grey squirrels and SQPV are present in the surrounding landscape. The Fleet Basin region in Dumfries and Galloway is used as an example and the model framework is as described in section 2.

5.1 Habitat Composition and Initial Conditions

The Fleet Basin red squirrel stronghold is contained within the National Forest Estate and therefore additional species level information can be extracted for the habitat composition. We used the Forestry Commission Scotland National Forest Estate Sub-compartment Database (SCDB) to extract species level information (at the 25m x 25m scale) and combined this with species specific potential densities derived from live-trapping studies in similar habitats for red and grey squirrels (see Appendix G) to determine approximate carrying capacities within FCS managed areas (Figure 5.1 top panels). To provide carrying capacity estimates in non-FCS managed regions we used the Forestry Commission Scotland forest inventory maps for 2011 which classifies species as coniferous, broadleaf or shrub in combination with the level 1 estimates assumed throughout this report (Table 3.2). As in section 4 we also assumed urban regions (extracted from LandcoverMap 2007 - licensed to SNH by CEH) can provide suitable habitat (setting potential density per hectare of red and grey squirrels in urban areas as red-0.83 and grey-0.9 per hectare). The carrying capacities used in the Fleet Basin stronghold assessment are shown in the bottom panels of Figure 5.1 (note the Fleet Basin stronghold can be identified as the inner rectangle, with model simulations being undertaken for the region within the outer rectangle). Initial conditions were broadly based on current red and grey squirrel distribution data from SSRS. Hence we assumed red and grey squirrels are at 50% of their respective carrying capacities for regions north and east of the Fleet Basin stronghold. Within the stronghold and to the south and west of the stronghold we assume reds are at 95% and greys at 5% of their carrying capacity. This assumption allows an investigation of the potential replacement of reds by greys. The disease is introduced into two areas (to the North East of New Galloway and near Kirkcudbright) at the beginning of each year to represent the threat of SQPV infection from populations outwith, but near the stronghold (and to approximate regions where seropositive Greys have been reported - see Appendix A).

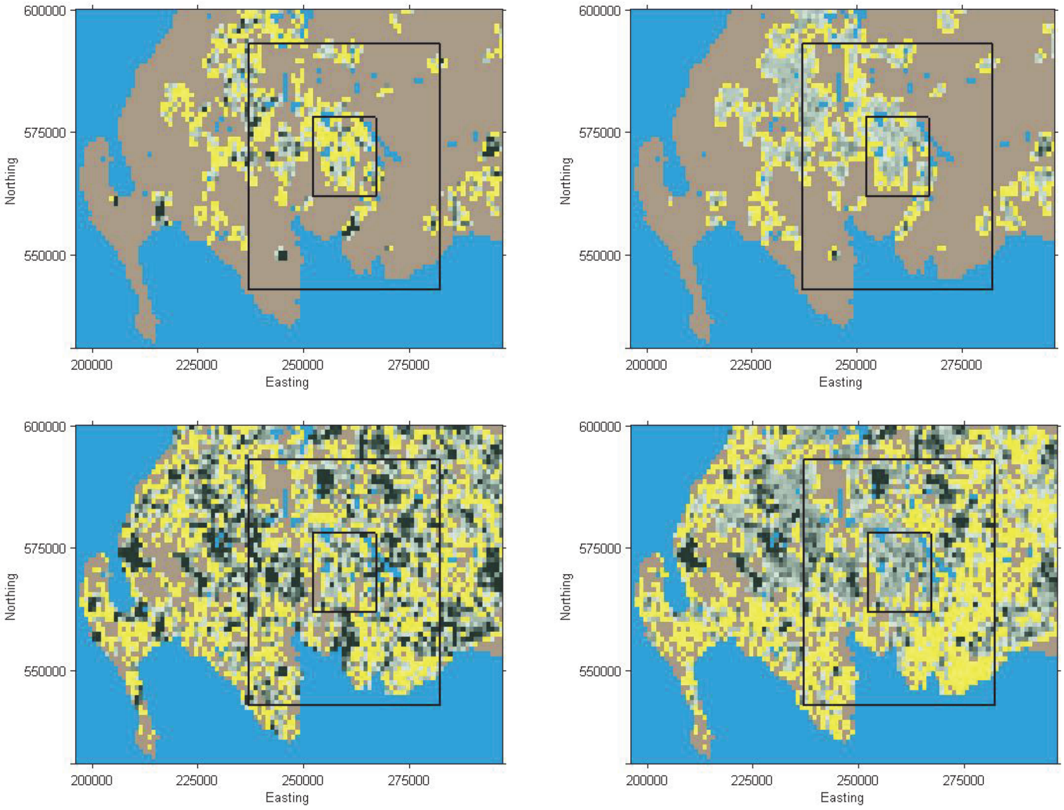

Figure 5.1. Estimates of densities for grey squirrels (left) an reds (right) in 1km x 1km grid squares used in the model assessments. The top graphs show estimates in FCS managed regions only and the bottom graphs combine estimates from FCS regions with the forest inventory and urban habitat data (see main text for a description). The inner rectangle (15km x 16km) represents the Fleet Basin stronghold and the outer (45km x 50km) rectangle is the region over which model simulations are undertaken.

5.2 The population and disease dynamics in the Fleet Stronghold without control

Ten replicate simulations with the initial conditions as described in section 5.1 were undertaken. The results for a single realisation showing how the density of red squirrels decreases and greys increases in most of the study region are shown in Figure 5.2 and 5.3. The occupancy of red and grey squirrels in 1km grid squares is shown in Figure 5.4. The single realisation is representative of the other simulations (which show a similar pattern). It is clear that greys can increase and replace reds in much of the region. This occurs as parameter values necessitate that greys outcompete reds in most habitats except regions predominantly dominated by Sitka spruce. Note, however that in model simulations greys were initialised with low density within and to the south and west of the Fleet stronghold. In reality greys may not currently be present in some of these regions and would therefore need to disperse into these regions before replacement could occur (and so the model results highlight the potential for red replacement). Reds are not replaced in the parts of the Fleet Stronghold and to the North West of this region where the habitat is Sitka dominated. This emphasises how red squirrel densities can be sustained in habitats in which red squirrels have a competitive advantage over greys and calls for a better understanding of the potential densities and competitive ability of reds and greys across conifer dominated forest and their species mixtures in the field.

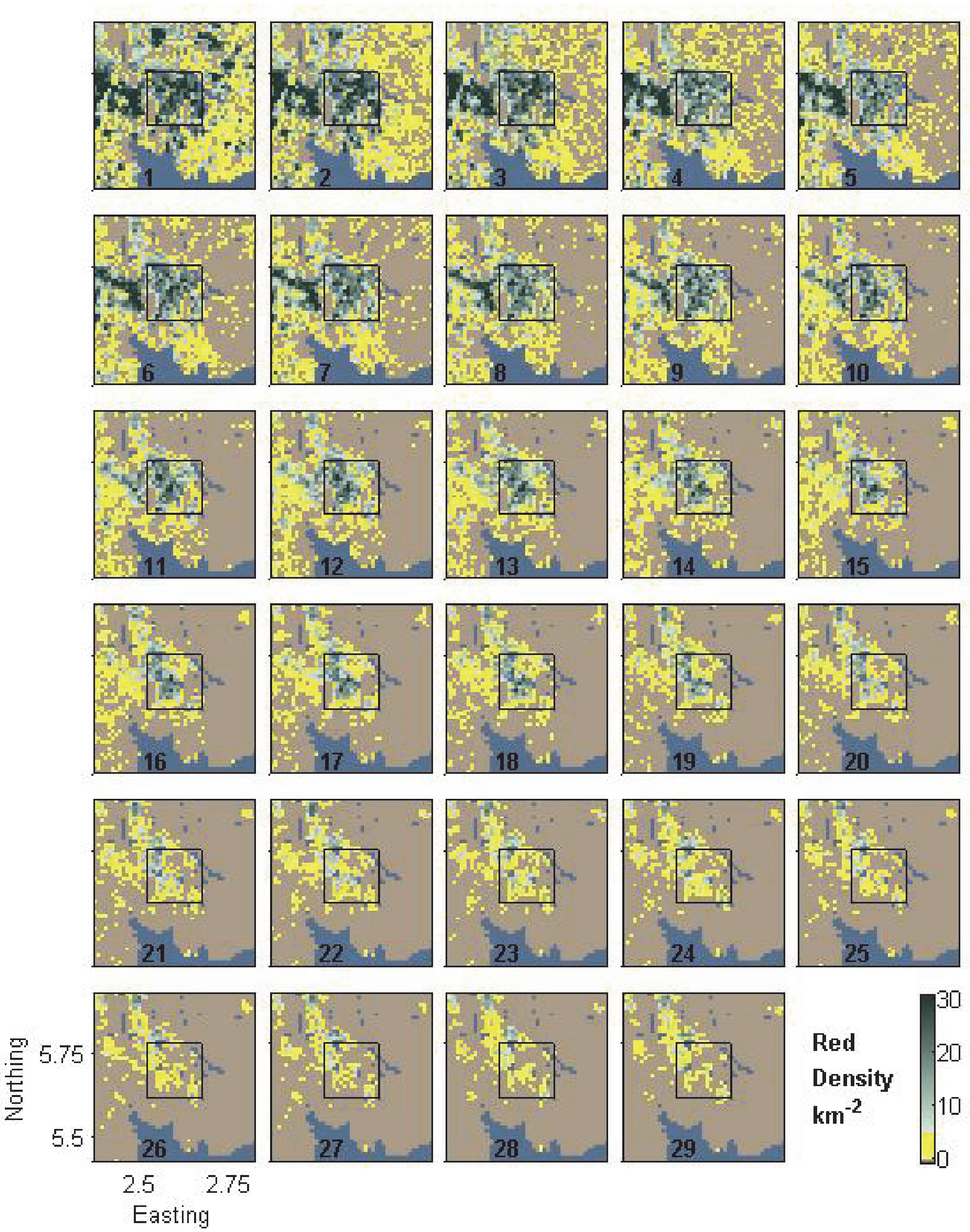

Figure 5.2. The density of red squirrels over one model realisation with initial conditions as described in section 5.1 and with no control of greys in the Fleet Stronghold (which is indicated by the central rectangle).

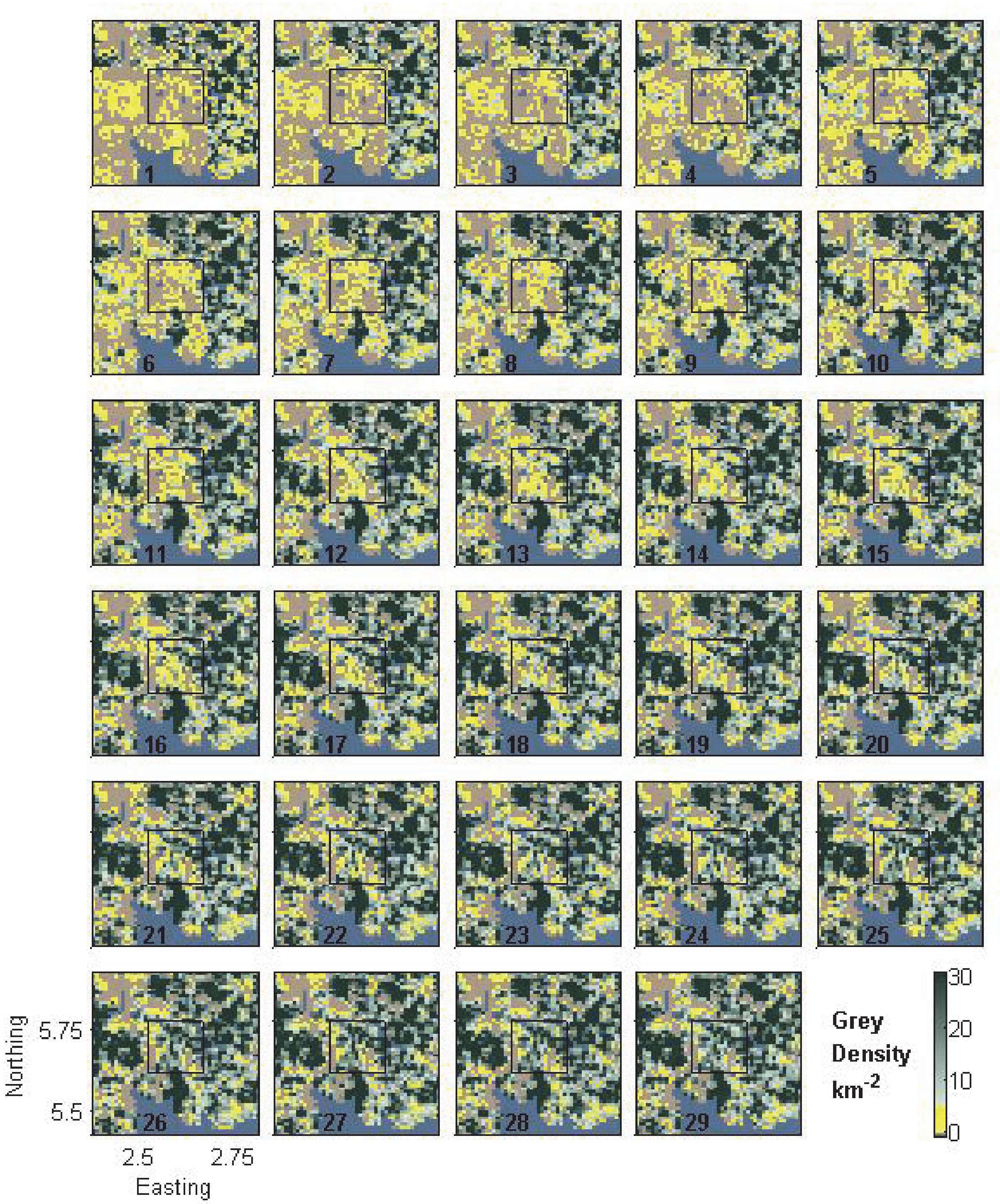

Figure 5.3. The density of grey squirrels over one model realisation with initial conditions as described in section 5.1 and with no control of greys in the Fleet Stronghold (which is indicated by the central rectangle).

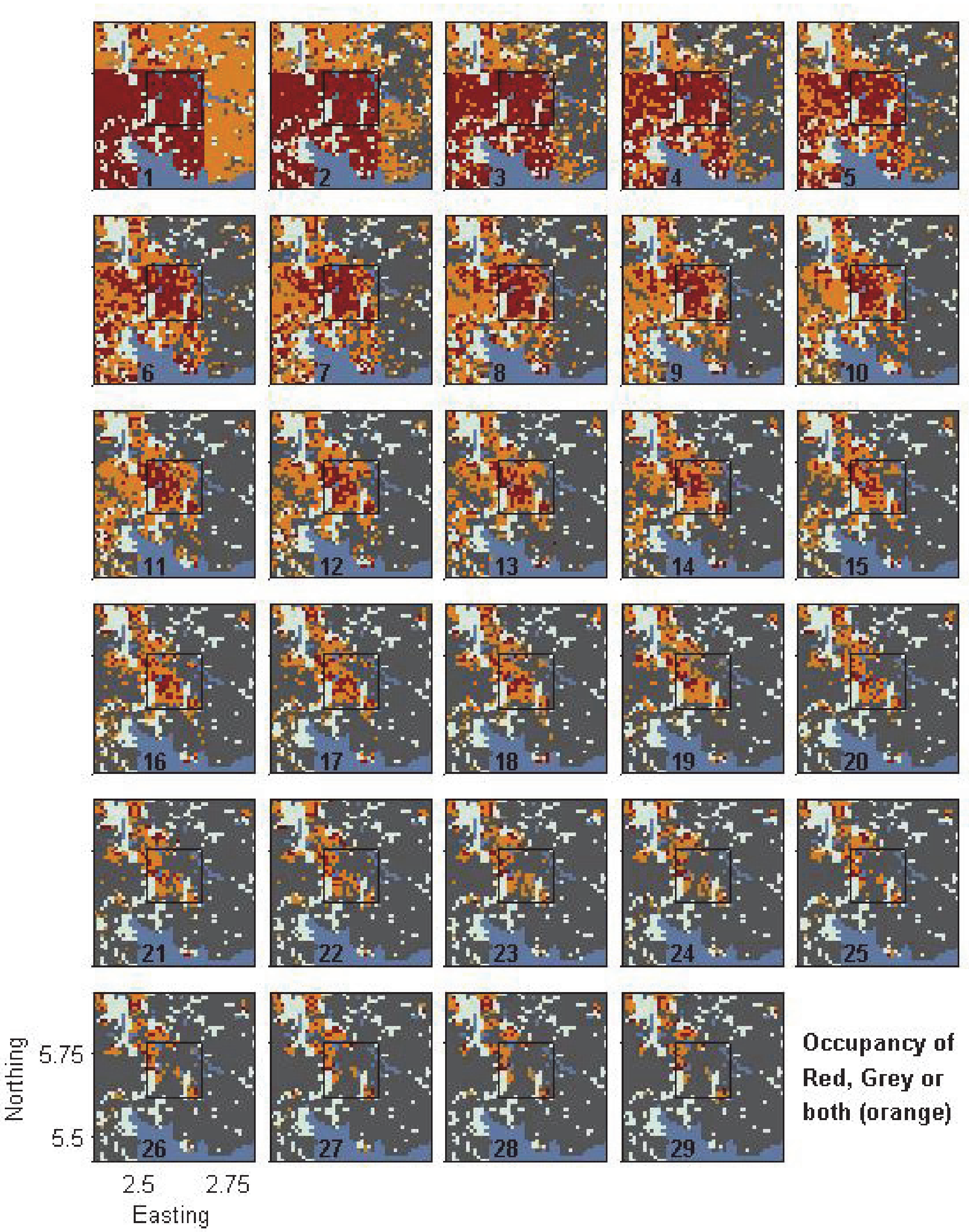

Figure 5.4. The occupancy of red or grey squirrels, or both in 1km gridsquares for one model realisation with initial conditions as described in section 5.1 and with no control of greys in the Fleet Stronghold (which is indicated by the central rectangle). Occupancy is defined as the density being above 20% of the carrying capacity for each squirrel type.

The disease dynamics indicating the occurrence of infection each year in reds and greys in a single model realisation is shown in Figure 5.5 and the percentage occurrence of seropositive greys over all 10 model realisations is shown in Figure 5.6. The disease spreads rapidly through populations where grey squirrels are at a sufficiently high density and results in infection in both reds and greys (indicated by the orange regions in Figure 5.5 to the north and east of the Fleet stronghold). This results in population crashes in red populations and their rapid replacement by greys (see Figure 5.4). This is followed by epidemic outbreaks in red populations in the Fleet stronghold, which occur periodically and will result in population crashes in red squirrel density. Red squirrels can recover from these epidemics as there are areas where red squirrels persist for the duration of the simulation.

The disease spreads rapidly through well connected grey populations that are at a sufficiently high density (i.e. across much of the study region in which greys were initialised at 50% of their carrying capacity - to the north and east of the Fleet Stronghold). Here the widespread occurrence of seropositive greys is predicted within 5 years given currently assumed model start up conditions (Figure 5.6). After this initial spread the progress of the disease mirrors the pattern of the replacement of reds by greys (see Figure 5.4). Here as greys exclude reds and the grey density increases to a sufficient level the disease can be supported. The exception to this is the west of the study region (Figure 5.6). Here greys squirrels increase in density and replace reds but the disease rarely spreads to this regions (seropositive greys occur in only 1 out of the 10 simulations with SQPV spread occurring through the Fleet Stronghold) as there is a corridor of poor habitat (poor connectivity) to the west of the Fleet Stronghold (see Figure 5.1).

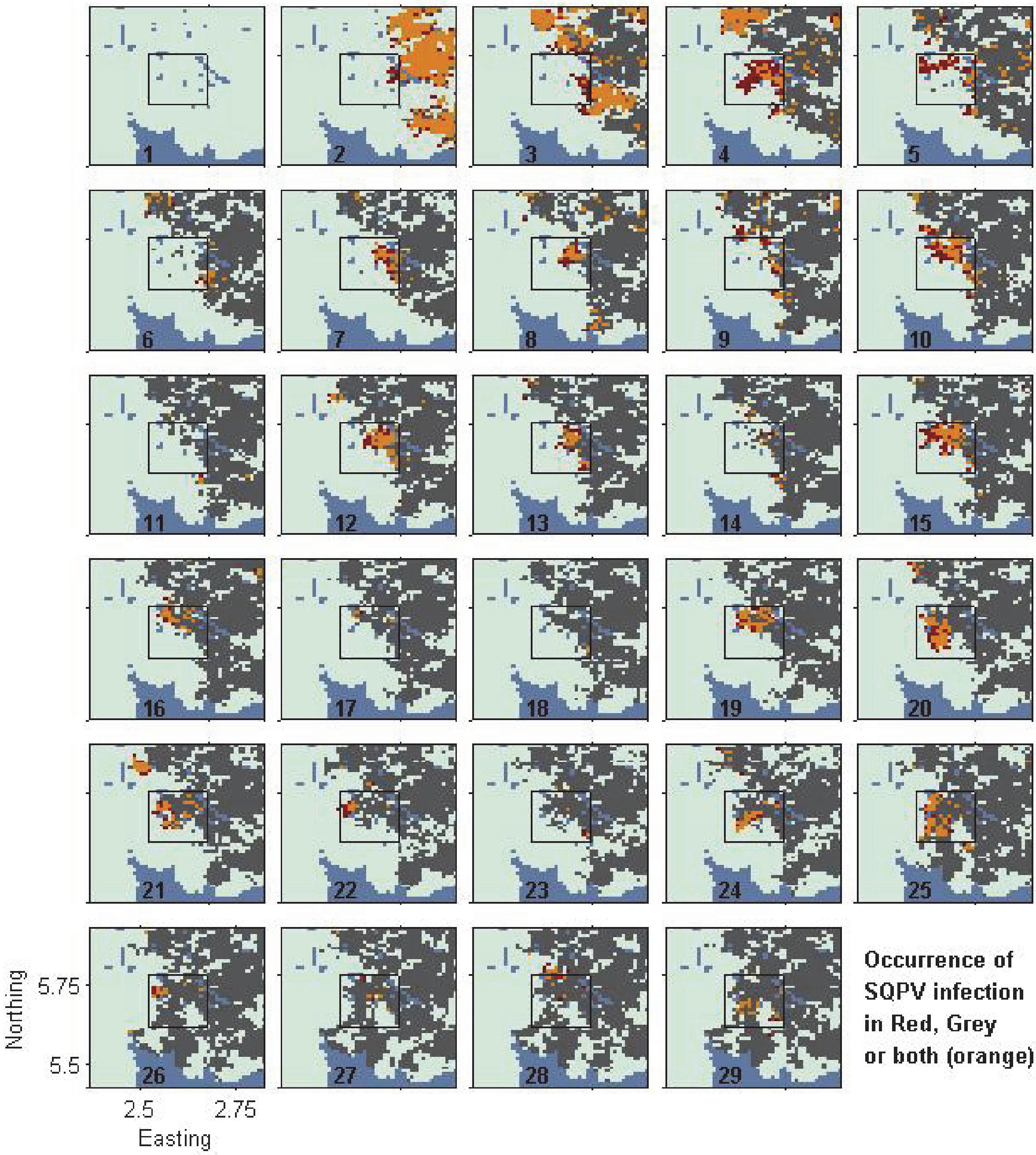

Figure 5.5. The occurrence of infection in red or grey squirrels, or both, in 1km grid squares for one model realisation with initial conditions as described in section 5.1 and with no control of greys in the Fleet Stronghold (which is indicated by the central rectangle).

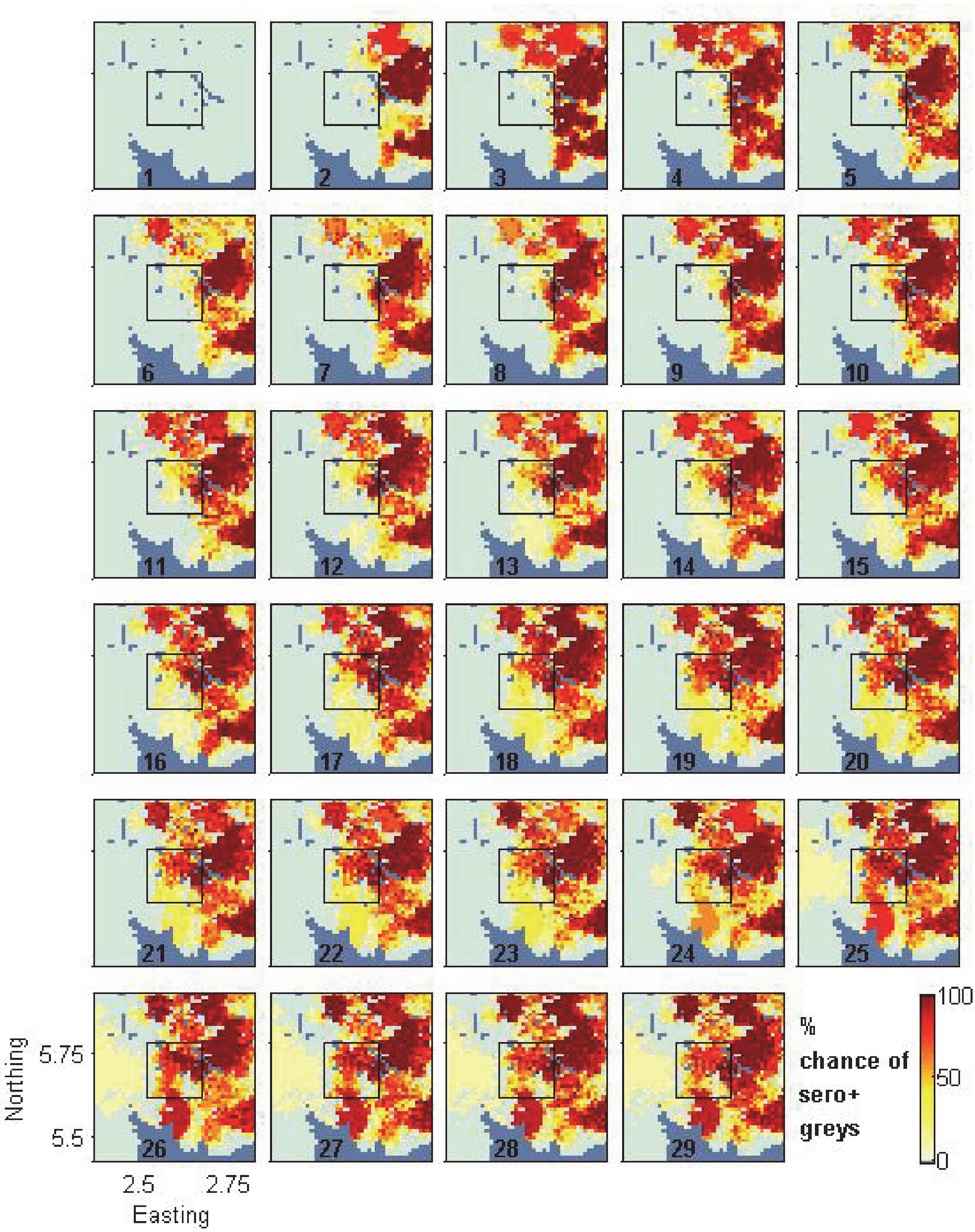

Figure 5.6. The percentage occurrence (in 10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Initial conditions are as described in section 5.1 and there is no control of greys in the Fleet Stronghold (which is indicated by the central rectangle).

5.3 The population and disease dynamics in the Fleet Stronghold with control

In the model, control is applied by removing all grey squirrels that occur in the Fleet Stronghold; an area of 15km x 16km = 240 km^2. In the field the Stronghold and neighbouring areas are monitored and trapping and removal is applied in areas where grey squirrels are observed. In the model grey squirrel numbers within the Fleet stronghold region are set to zero every 3 months. The effort required in the model to exclude greys from the Fleet stronghold is the removal of approximately 100 squirrels per year (Figure 5.7).

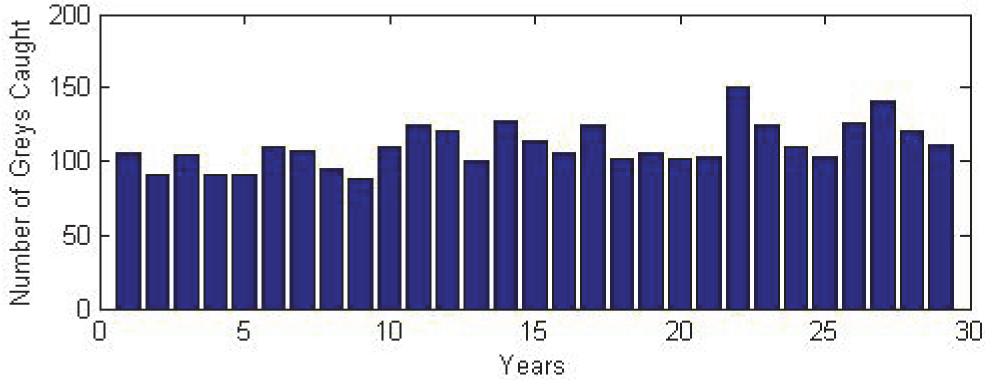

Figure 5.7. The number of greys removed each year to maintain the Fleet Stronghold as a grey-free zone. Initial conditions as described in section 5.1 and the results are shown for a single model realisation (but results are similar for other model runs).

The results for a single realisation showing the density of red and grey squirrels are shown in Figure 5.8 and 5.9. The occupancy of red and grey squirrels in 1km grid squares is shown in Figure 5.10. The control of greys allows red squirrels to persist in suitable habitat in the Fleet Stronghold (Figure 5.8). The control of greys does not appear to enhance red density or survival beyond the stronghold (the change in density and occupancy of reds and greys are similar with or without control in regions outside the Fleet Stronghold). These results highlight that grey control is an effective local measure to protect red populations in strongholds. The level of control required will depend on the density of grey squirrels in neighbouring habitats and the connectedness of these habitats to the stronghold. The more isolated the stronghold the less control is required.

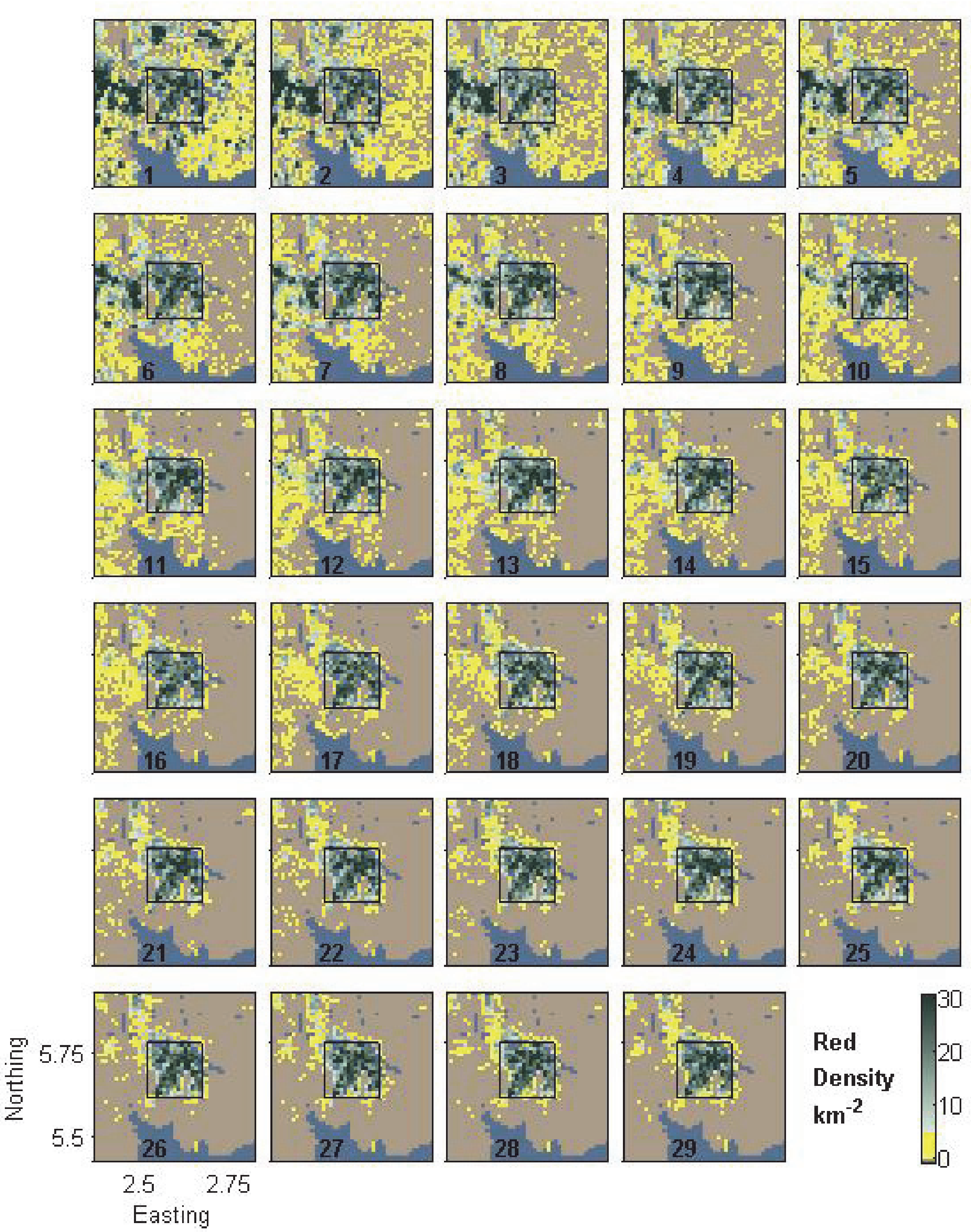

Figure 5.8. The density of red squirrels over one model realisation with initial conditions as described in section 5.1 and with control that excludes grey squirrels from the Fleet Stronghold (which is indicated by the central rectangle).

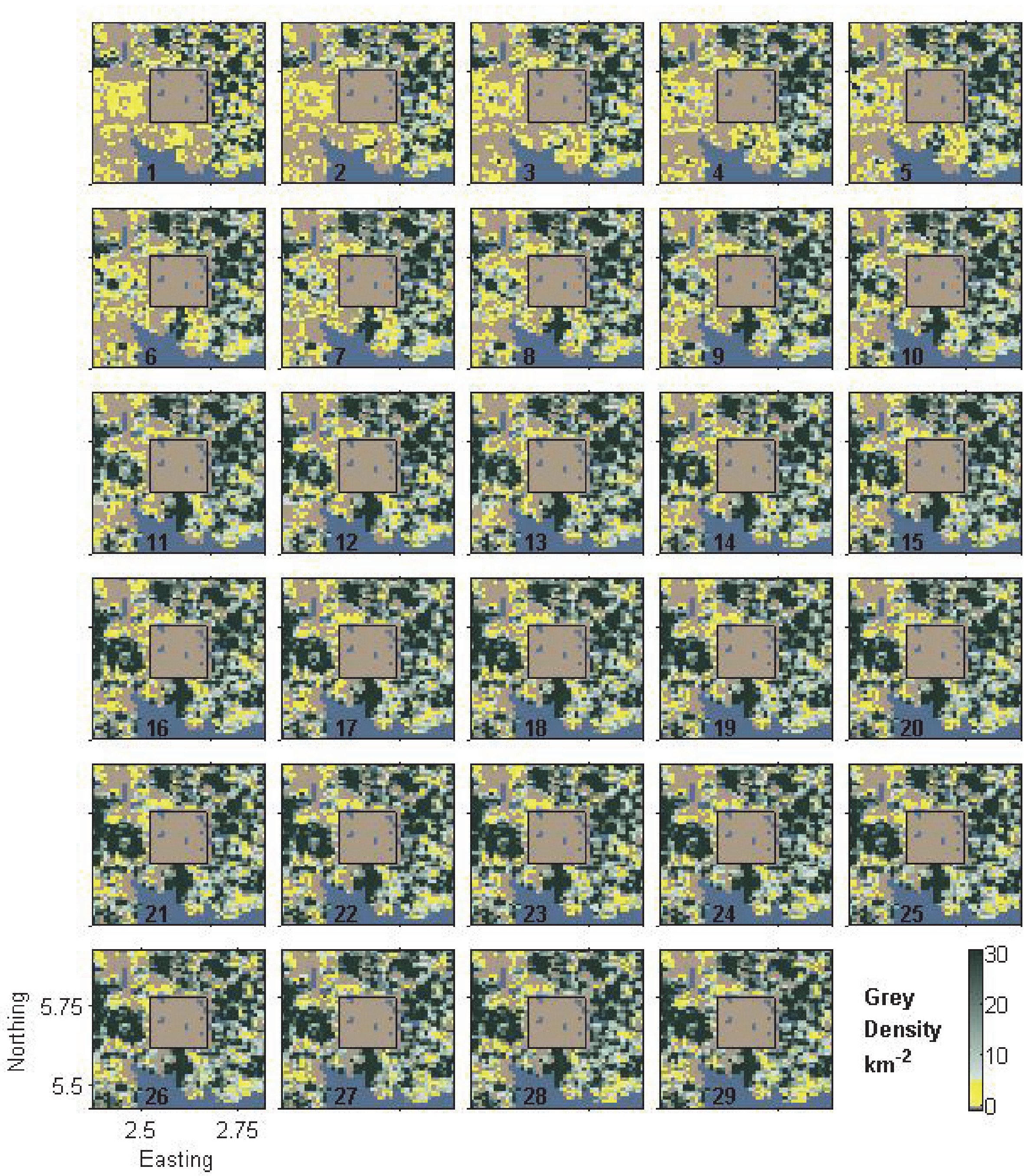

Figure 5.9. The density of grey squirrels over one model realisation with initial conditions as described in section 5.1 and with control that excludes grey squirrels from the Fleet Stronghold (which is indicated by the central rectangle).

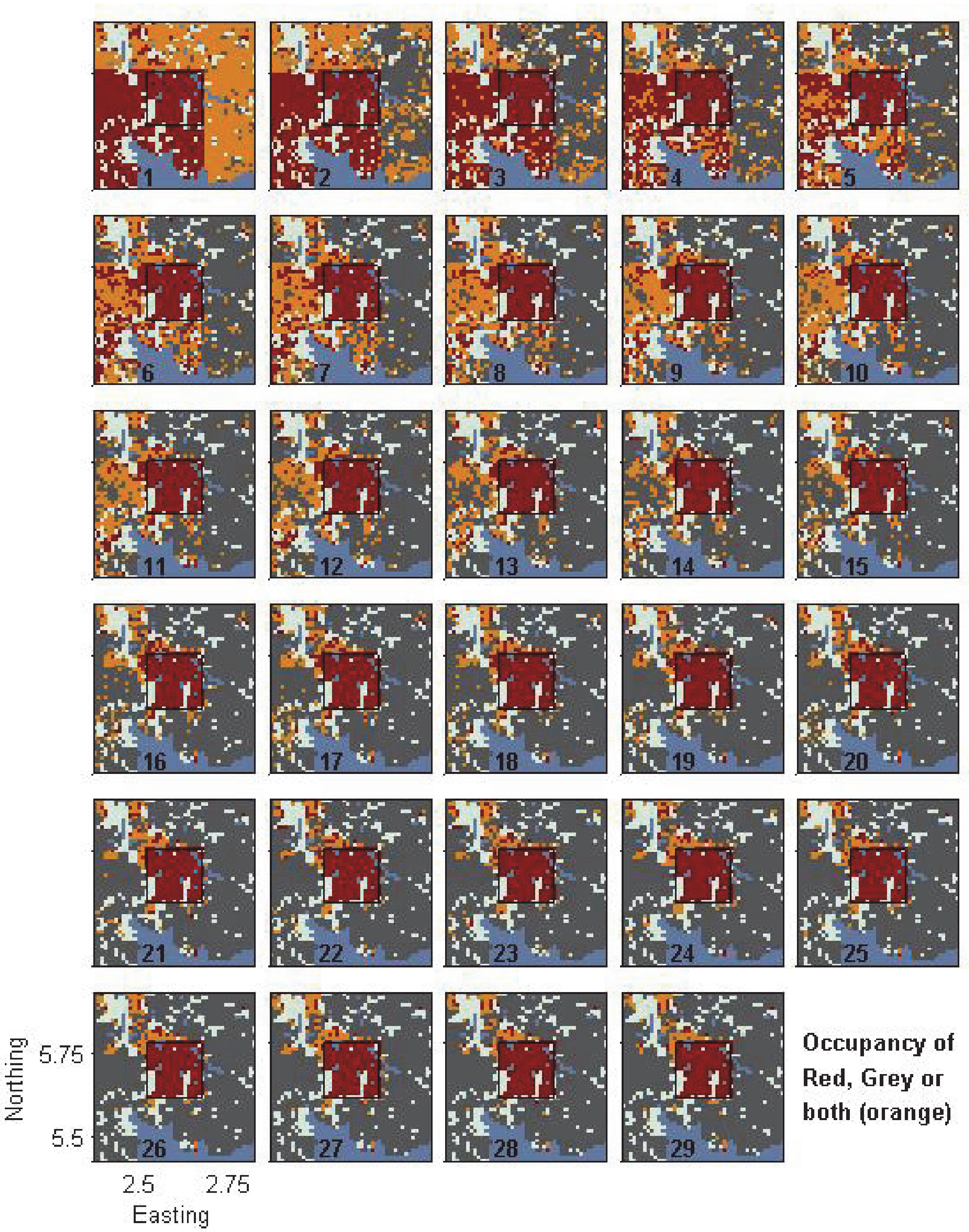

Figure 5.10. The occupancy of red or grey squirrels, or both in 1km gridsquares for one model realisation with initial conditions as described in section 5.1 and with control that excludes greys in the Fleet Stronghold (which is indicated by the central rectangle). Occupancy is defined as density being above 20% of the carrying capacity for each squirrel type.

The disease dynamics indicating the occurrence of infection each year in reds and greys in a single model realisation with control is shown in Figure 5.11 and the percentage occurrence of seropositive greys over all 10 model realisations (with control) is shown in Figure 5.12. The exclusion of greys from the Fleet Stronghold reduces the occurrence of SQPV outbreaks in the stronghold. Disease still spreads rapidly through grey populations to the north and east of the stronghold and connections between these populations and the stronghold leads to periodic outbreaks of infection in red populations within the stronghold. The outbreaks are often localised to the boundary of the Fleet Stronghold. However more wide spread outbreaks can occur in the stronghold, which can cause population crashes in red populations (see years 14-16 in Figure 5.11 and 5.8). In figure 5.13 we show the red squirrel density in a 1km x 1km gridsquare in which there is an SQPV outbreak over time. It can be seen that the red squirrel density drop rapidly to around 40% of its potential density due to the outbreak between years 14 and 16. This is followed by recovery to pre-infection levels. A key message therefore is that while control can protect red squirrel populations from exclusion in strongholds it cannot prevent periodic outbreaks of disease within the stronghold (which is transmitted through red (only) populations). The outbreak of infection in strongholds should therefore not be considered a failure in the conservation strategy (and it is difficult to prevent). The model also predicts that red squirrel numbers will recover following the epidemic outbreak (provided control measures are continued).

Control of greys in the stronghold has little effect on preventing spread of SQPV through predominantly grey populations beyond the stronghold (compare Figure 5.12 and 5.9). The exception is that control of greys prevents the spread of SQPV through the stronghold into populations to the west of the stronghold (which occurred in 1 of the 10 simulations without control).

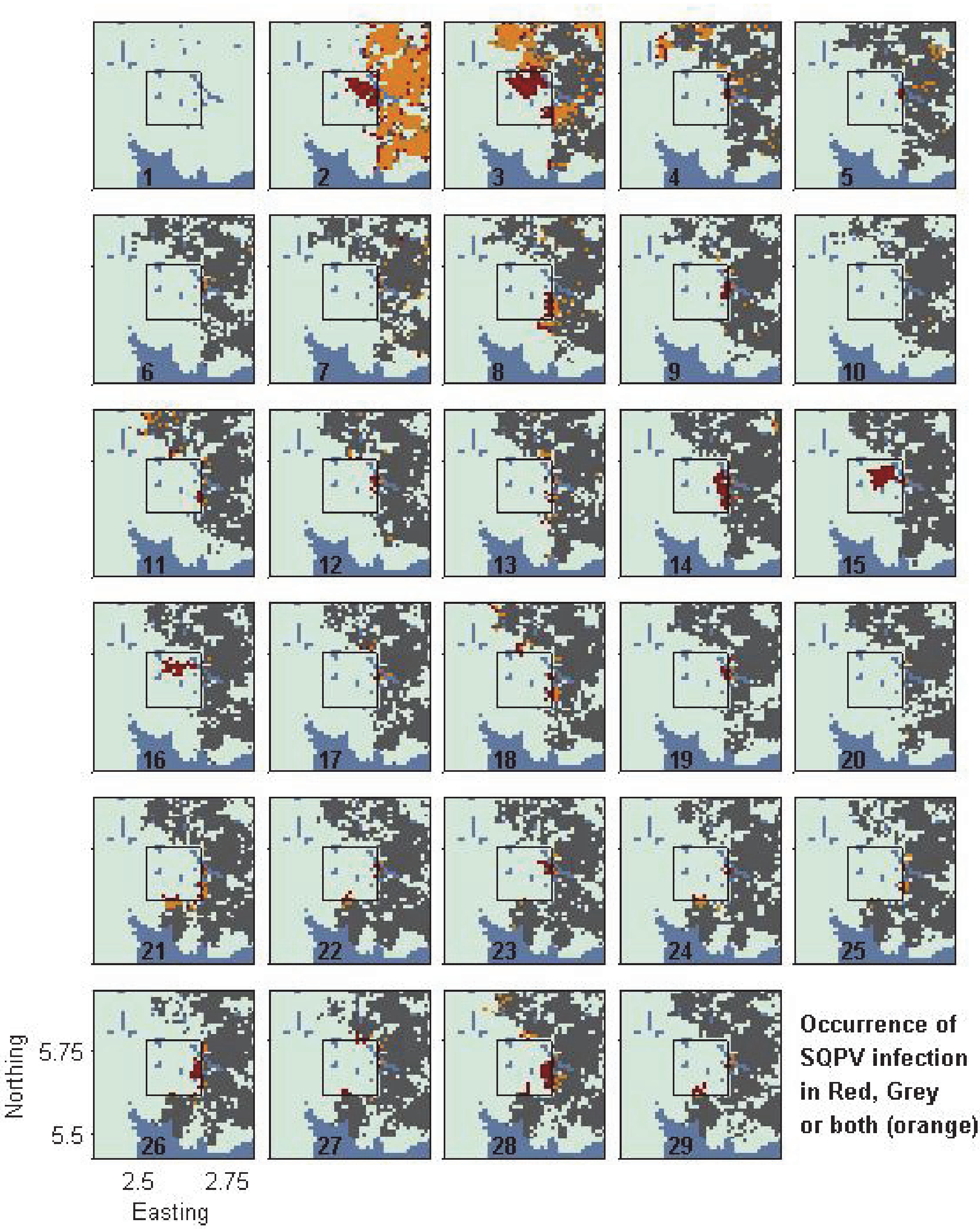

Figure 5.11. The occurrence of infection in red or grey squirrels, or both in 1km gridsquares for one model realisation with initial conditions as described in section 5.1 and with control to exclude grey squirrels from the Fleet Stronghold (which is indicated by the central rectangle).

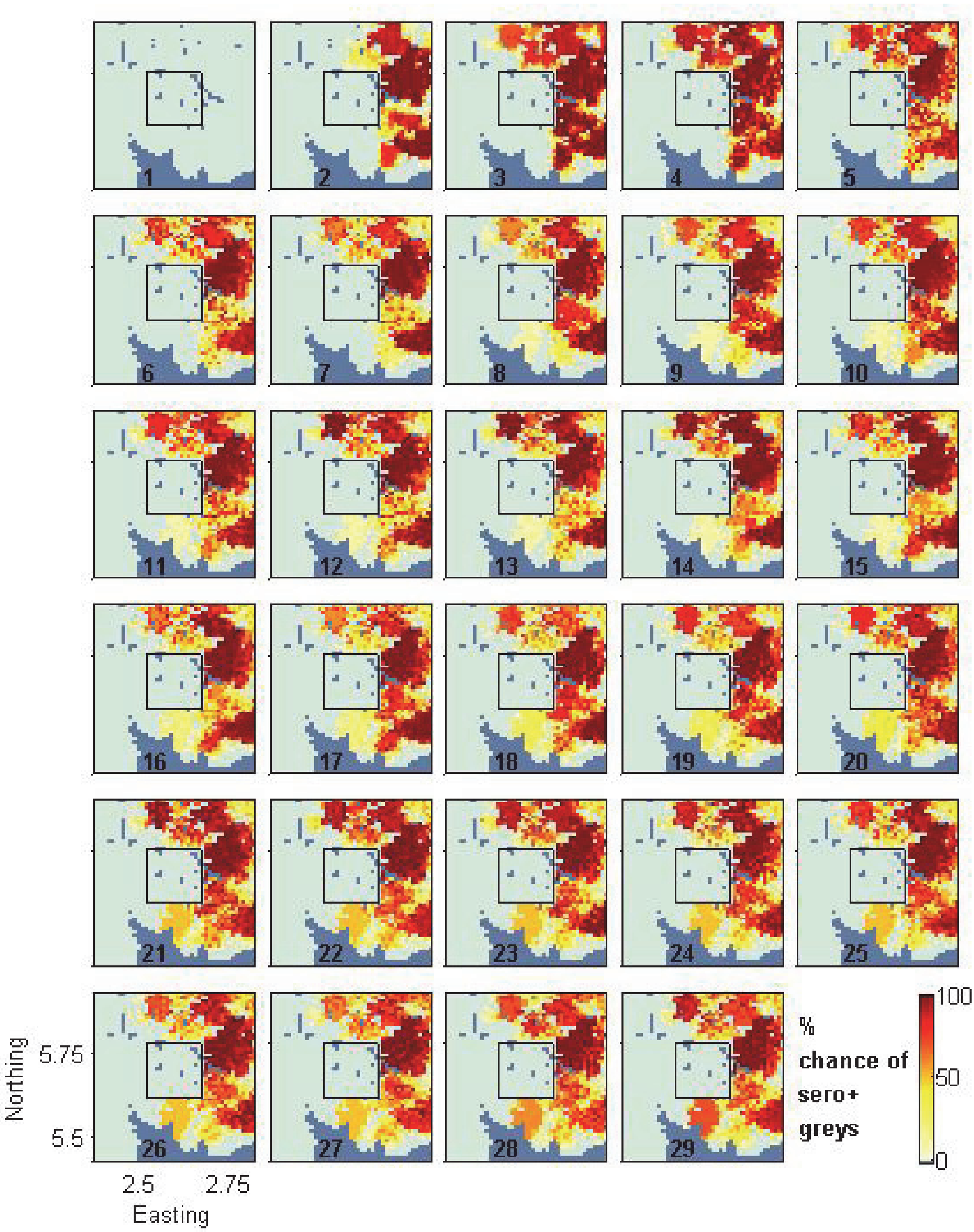

Figure 5.12. The percentage occurrence (in 10 model realisations) of squirrelpox over time. Squirrelpox is defined as occurring if seroprevalence is greater than 20% in a 1km grid square. Initial conditions as described in section 5.1 and with control to exclude greys from the Fleet Stronghold (which is indicated by the central rectangle).

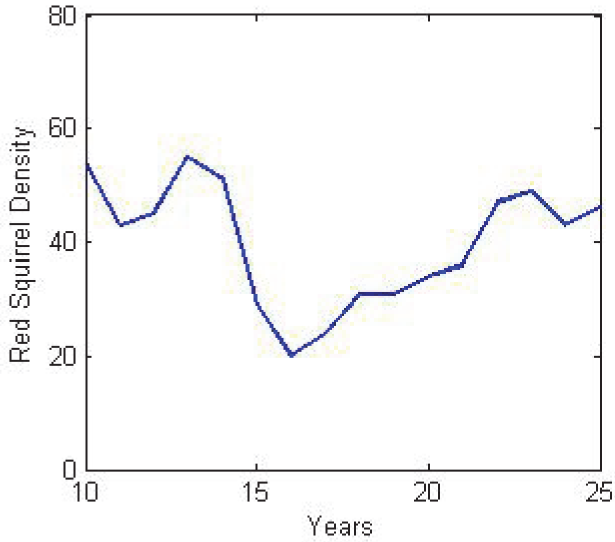

Figure 5.13. The density of red squirrels in a sample 1km x 1km gridpatch in the stronghold over time. The gridpatch is located in the region in which a squirrelpox outbreak occurs in years 14-16 in Figure 5.11.

5.4 Discussion

In section 5 the mathematical model is used to assess the population dynamics and spread of squirrelpox through a region in Dumfries and Galloway that contains the Fleet basin red squirrel stronghold. The key findings in the absence of grey squirrel control in the Fleet Stronghold are:

- Red squirrel populations survive in habitat regions in which they have a sufficient competitive advantage only (Sitka Spruce dominated forests). This emphases the need for a better understanding of red and grey squirrel potential densities and competitive interactions in specific conifer tree species mixtures.
- Grey squirrels replace reds throughout much of the region (including a large proportion of the Fleet Stronghold).
- Squirrelpox spreads rapidly through well-connected grey populations once grey populations are established and at sufficiently high density.

The mathematical model is adapted and control is applied to exclude grey squirrels from the Fleet Stronghold. <u>The key findings when grey squirrel control is applied are:</u>

- Grey squirrel control is an effective measure to protect red populations in strongholds. The level of control required will depend on the density of grey squirrels in neighbouring habitats and the connectedness of these habitats to the stronghold. In the model simulations with trapping and removal of greys at 3 monthly intervals (with a total annual removal of approximately 100 greys) was sufficient to maintain a viable red population(as defined by model persistence) in the stronghold.
- Outbreaks of SQPV occur periodically within the stronghold and result in populations crashes. The extent of SQPV epidemics within the stronghold is variable and often confined to localised areas at the boundary of the stronghold. A key message therefore is that while control can protect red squirrel populations from exclusion in strongholds it cannot prevent periodic outbreaks of disease within the stronghold

(although this should not be seen as a failure in the conservation strategy as reds are predicted to recover if control is maintained).

- Control of greys in the stronghold has little effect on red population survival or the spread of SQPV in regions beyond the stronghold.

Further possible development of the model are discussed in Appendix E

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APPENDIX A: SQUIRRELPOX DISTRIBUTION IN THE SOUTH OF SCOTLAND 2005-2012

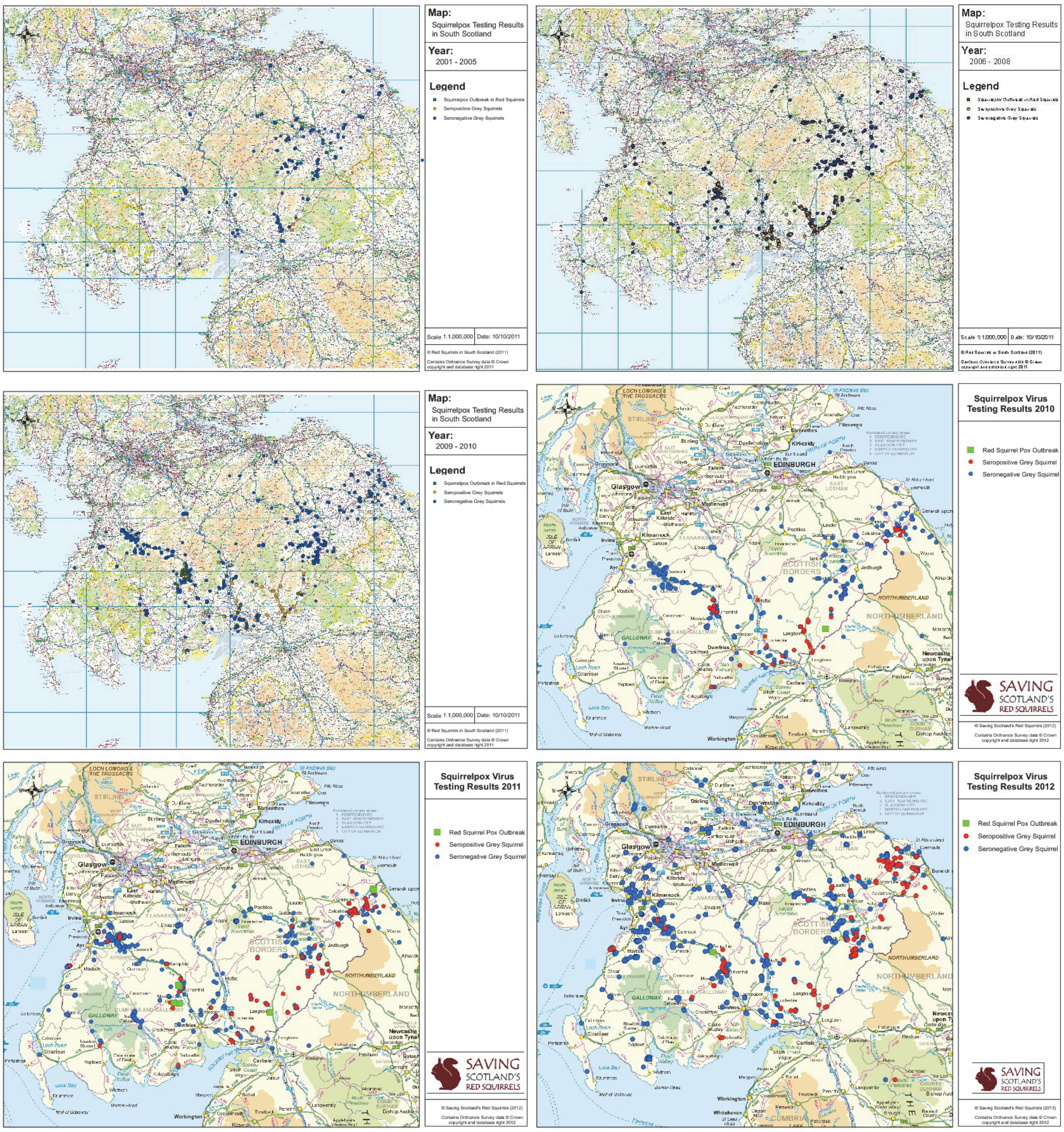


Figure A.1. The recorded incidence of squirrelpox in the south of Scotland between 2005 and 2012. Data provided by SNH and SSRS.

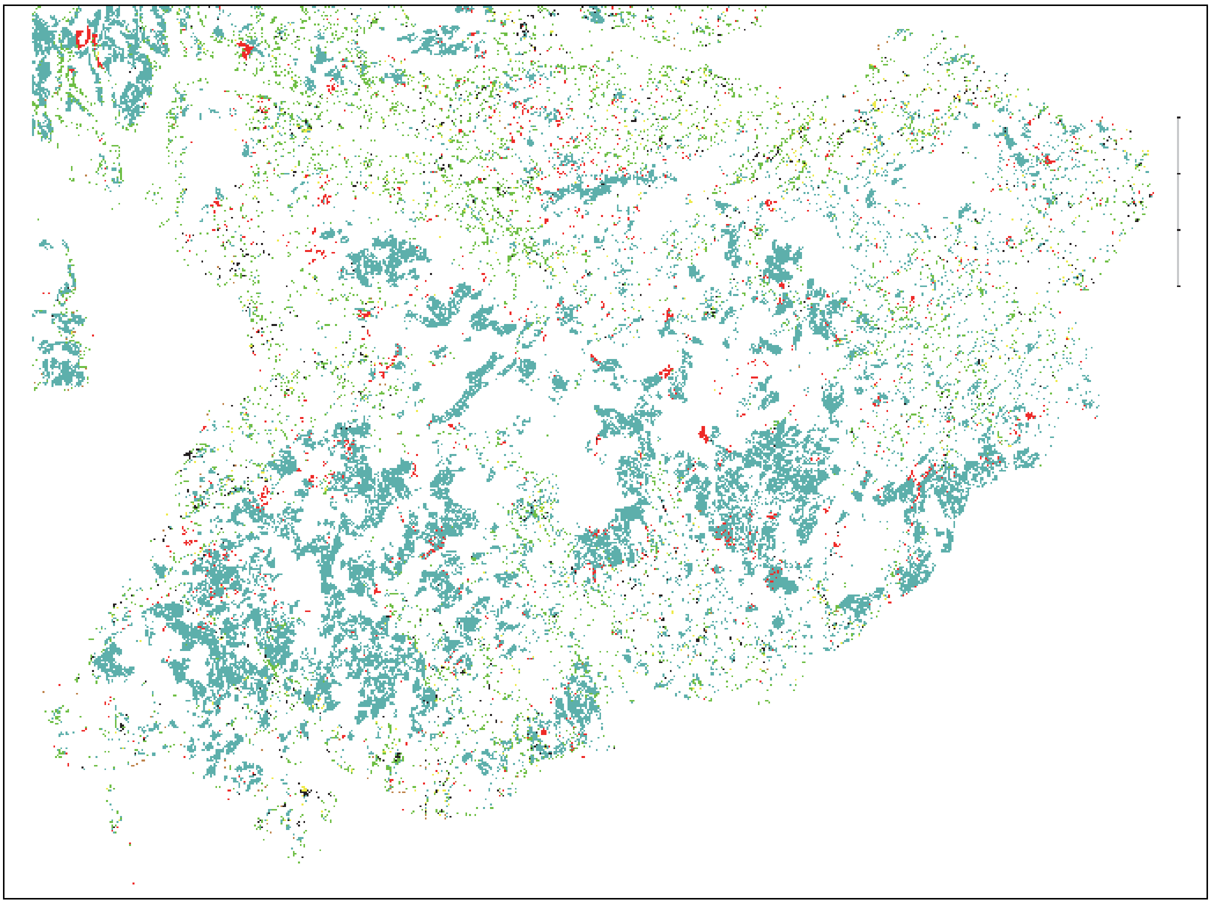


Figure A.2. Woodland cover map taken from the forest inventory records 2011 (http://www.forestry.gov.uk/datadownload). The data represents a total woodland cover of 360685 ha divided into the following categories: conifer – 74.6% (dark green), broadleaf – 16.1% (light green), mixed conifer – 1.6% (yellow), mixed broadleaf – 2.2% (black), shrub – 0.4% (brown), assumed woodland – 5.0% (red). In this project we combine conifer, mixed conifer and assumed woodland to form the conifer class, broadleaf and mixed broadleaf to form the broadleaf class (see Table 3.2). Data includes woodlands >0.5ha.

APPENDIX B: MATHEMATICAL MODEL

Since initial invasions/infection levels occur at low density it is essential to represent the stochastic nature of the dynamics as this can account for disease fade-out or unsuccessful invasion attempts which better reflect the population behaviour of natural systems. Therefore, at the forest patch level (1km x 1km grid square) we propose to adapt the deterministic framework of Tompkins *et al.* (2003) to develop a stochastic model of competition and shared disease to examine the interaction between red and grey squirrels. The Tompkins *et al.* (2003) model system is a suitable framework as this system highlighted how squirrelpox was a key driver of the rapid replacement of red squirrels by greys and compared well to observed spatial data.

The deterministic model of Tompkins et al (2003) where the dynamics of susceptible and infected red (S_R and I_R) and grey (S_G and I_G) squirrels and recovered (immune) greys (R_G) are represented by the following equations.

$$\begin{aligned}
\frac{dS_G}{dt} &= (a_G - q_G(H_G + c_R H_R))H_G - bS_G - \beta S_G(I_G + I_R) \\
\frac{dI_G}{dt} &= \beta S_G(I_G + I_R) - bI_G - \gamma I_G \\
\frac{dR_G}{dt} &= \gamma I_G - bR_G \\
\frac{dS_R}{dt} &= (a_R - q_R(H_R + c_G H_G))S_R - bS_R - \beta S_R(I_G + I_R) \\
\frac{dI_R}{dt} &= \beta S_R(I_G + I_R) - bI_R - \alpha I
\end{aligned} \qquad (1)$$

Here, H_G=S_G+I_G+R_G and H_R=S_R+I_R representing the total squirrel populations. In Tompkins et al (2003) the two species have the same rate of adult mortality (*b*) but different rates of maximum reproduction (a_R, a_G) and different carrying capacities (K_R, K_G) leading to susceptibilities to crowding (q_R, q_G) (since q = (a-b) / K). The competitive effect of grey squirrels on red squirrels is denoted by c_G, whilst that of red squirrels on grey squirrels is denoted by c_R. Squirrelpox virus is transmitted at the rate β both within and between each squirrel species with infected reds dying due to the disease at rate α and infected greys recovering at rate γ. To generate the stochastic model the rates in the deterministic model are converted to probabilities of events that account for changes in individual patch level abundance (Renshaw 1991). The probabilities are determined

Birth of Grey to S_G	$P(S_G \to S_G + 1)$	$:[(a_G - q_G(H_G + c_R H_R))H_G]/R$
Natural Death of S_G	$P(S_G \to S_G - 1)$	$:[bS_G]/R$
Infection of Grey	$P(S_G \to S_G - 1, I_G \to I_G + 1)$	$:[\beta S_G(I_G + I_R)]/R$
Natural Death of I_G	$P(I_G \to I_G - 1)$	$:[bI_G]/R$
Recovery of Grey	$P(I_G \to I_G - 1, R_G \to R_G + 1)$	$:[\gamma I_G]/R$
Natural Death of R_G	$P(R_G \to R_G - 1)$	$:[bR_G]/R$
Birth of Red to S_R	$P(S_R \to S_R + 1)$	$:[(a_R - q_R(H_R + c_G H_G))S_R]/R$
Natural Death of S_R	$P(S_G \to S_G - 1)$	$:[bS_R]/R$
Infection of Red	$P(S_R \to S_R - 1, I_R \to I_R + 1)$	$:[\beta S_R(I_G + I_R)]/R$
Natural/Diseased Death of I_R	$P(I_R \to I_R - 1)$	$:[(b + \alpha)I_G]/R$

(2)

In addition there are probabilities of individuals of each class moving to neighbouring patches. The probability of leaving the current patch for class S_G is

$$P(S_G \to S_G - 1) \quad : \left[mS_G \exp\left(-\left(K_G - \left(H_G + c_R H_R\right)\right)\right)\right] / R \tag{3}$$

here *m* is the long distance dispersal rate and the exponential function reflects the situation in which squirrels are less likely to disperse when the absolute density in the grid patch is below the carrying capacity and more likely to disperse when above it. (Similar terms are used to represent dispersal in other classes.) When an individual leaves a patch it enters a neighbouring habitable patch and therefore the density of the focal patch reduces by 1 and in the neighbouring patch is increased by 1 (the neighbouring patch is chosen at random from the 8 nearest neighbours , with appropriate weighting given to the four adjacent neighbours compared to the four corner neighbours).

As well a (rare) long distance dispersal squirrel movement occurs on a regular basis within their core range. This process will not lead to the permanent relocation of a squirrel to a new patch but could lead to transmission of infection by a susceptible entering an infected patch or an infected from a neighbouring patch entering the focal patch. This can occur along the boundary edge of a cell and leads to additional probabilities of infection (for say Greys) as follows

$$P(S_G \to S_G - 1, I_G \to I_G + 1) \quad : \left[\beta S_G \left(0.15 \sum_{Adjacent} \left(I_G + I_R\right) + 0.0375 \sum_{Corner} \left(I_G + I_R\right) \right) \right] / R \tag{4}$$

The scaling for the adjacent grid patches (0.15) and corner grid patches (0.0375) are determined by comparing the relative area of the patch with the overlapping areas at the grid boundary when the core range has a radius of 150m (leading to a core range of approximately 7ha (Smith 1999)).The same formulation is used for red squirrels.

In equations (2-4) $R = \sum \left[rates \right]$ (the sum of the terms in square brackets) and therefore transforms the rates to probabilities. The time between events can be determined as $T_{event} = -\ln(\sigma) / R$ where σ is a random number drawn from a uniform distribution between 0 and 1. The events are incremented at random with the associated probabilities updated due to changes in population density after each event. Individual simulations can be undertaken using a Gillespie algorithm and provide information of the behaviour in a single realisation. Monte Carlo methods can be used to generate multiple simulations to assess the average behaviour and variability across realisations.

<u>Grid Patch Size:</u>
The grid patch was chosen to be 1km x 1km as a size that contains the core range of grey and red squirrels and that reflects long distance movements of squirrels which can cross distances in the region of 1km through unsuitable habitat types with no or little cover when dispersing (e.g. see homing experiments of Goheen *et al.* 2003). Note that even at conservative distances of 1 km most of Southern Scotland becomes interlinked and there are no barriers for grey squirrels moving from south to north (see Figure B.1)

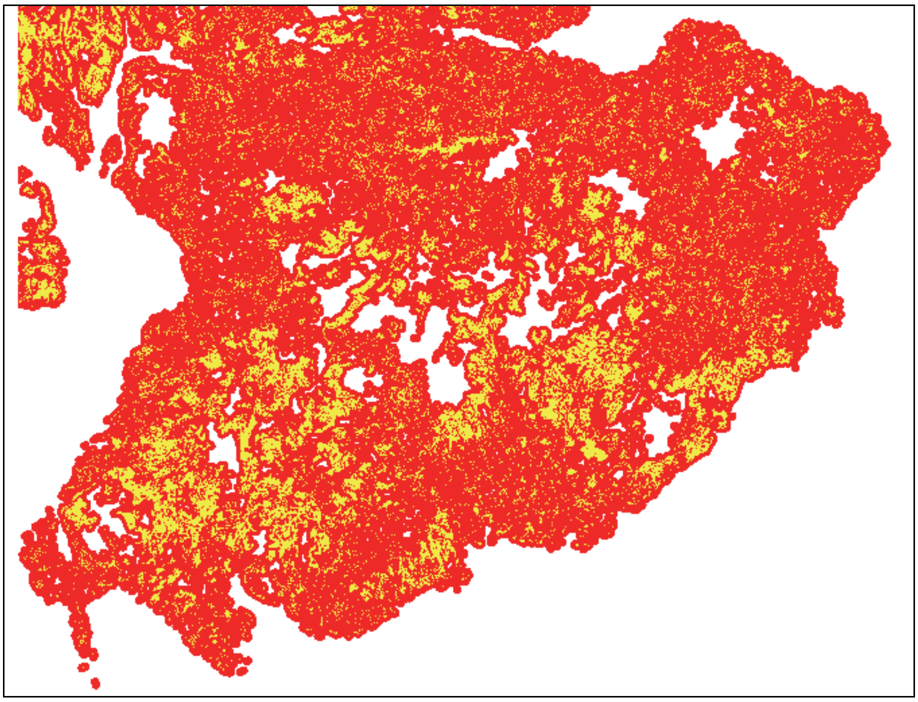


Figure B.1. The woodland of the South of Scotland (yellow) buffered by a 1km dispersal distance (red) illustrating that the majority of the South of Scotland is connected at this scale. Although there are regions where the woodland habitat is scarce the buffer map indicates that there are no barriers to spread from the South of Scotland to Central Scotland.

Parameter Estimates:

Parameter estimates were taken from Tompkins et al (2003) except those for disease transmission, *β*, and long distance dispersal, *m*, as these needs to be recalibrated for the grid size and habitat of the South of Scotland. Long distance dispersal, *m*, was set equal to the natural death rate, *b*, so that on average squirrels are predicted to disperse to a new home cell once in their lifetime. The disease transmission rate was set so that the seroprevalence of grey squirrels matched that observed from trapping data in Southern Scotland. Trapping data provided by SSRS recorded grey seroprevalence and trap locations. The trap location could be used in conjunction with the forest inventory records (assuming a core range radius of 150m) to determine the forest composition covered by the trapping regime. Following Tompkins et al (2003) the seroprevalence was then matched to the endemic equilibrium densities for grey squirrels of the deterministic model (equation 1) by assuming that

$$seroprevalence = R_G / H_G \quad \Rightarrow \quad \beta = \frac{\gamma(b+\gamma)}{K_G(\gamma - seroprevalence(b+\gamma))} \tag{5}$$

The relationship between seroprevalence and carrying capacity saturates as the carrying capacity increases (and therefore similar levels of seroprevalence correspond to very different squirrel densities when seroprevalence is high). For this reason we restricted the trapping data to sites which gave accurate trap positions and in which seroprevalence was below 75% (note, this does not restrict the seroprevalence in model). Results are shown in Table A.1 and disease transmission was chosen as β=0.55 as being in the predicted range.

Table A.1. Trapping data for sites in Southern Scotland provide records of seroprevalence and trap location. This can be used to estimate carrying capacity and disease transmission (using equation 5).

Location	Carrying Capacity, K_G	Seroprevalence, %	Estimate of β
Wauchope 1	49	47	0.54
Wauchope 2	60	63	0.63
Arton Castle	60	60	0.58

Initial Conditions:

The model was initialled to be reflective of the abundance of red and grey squirrels at the start of 2005 (based on observed data for the presence of red and grey squirrels in 2005; National Biodiversity Network's Gateway, http://data.nbn.org.uk/). In regions where only one squirrel species was predicted the model was initialised to be at the respective carrying capacity. 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. The only caveat is that in Dumfries and Galloway the 2005 observations predicted much of the region to be absent of greys but by 2007 to be occupied by reds and greys. For greys to spread over such an extent it was necessary to assume they were present at a low level in 2005 (5% of their carrying capacity) in these regions (see Figure B.2). In addition infection was assumed to be instigated from infected squirrels south of the Scottish border and so the model is initialled by assuming two infected greys are present in two grid cells (easting 341000-342000, northing 578000) to represent the first recorded squirrelpox outbreaks near Canonbie in Dumfries and Galloway in 2005. Outbreaks are also initialised near Coldstream and Eyemouth in the Scottish Borders from 2010 to reflect observed outbreaks in these regions.

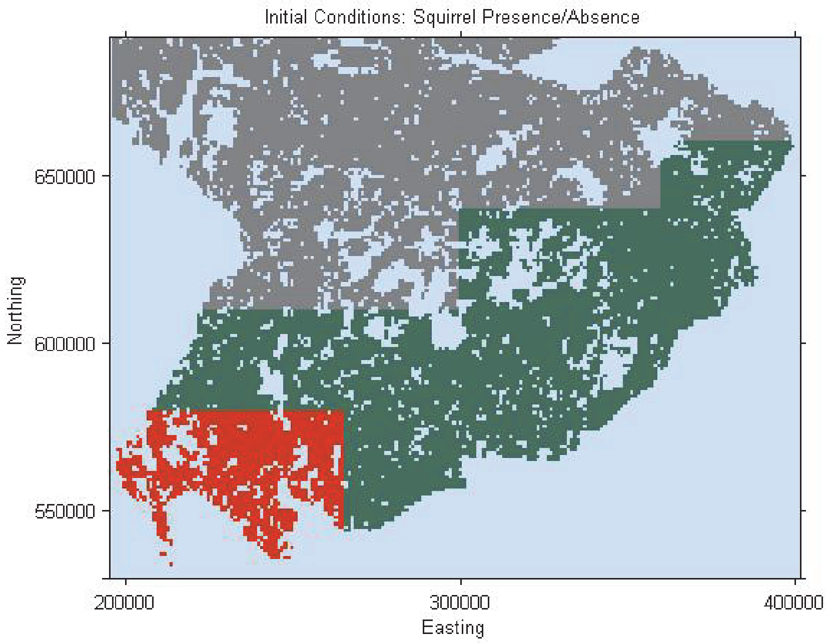


Figure B.2. Initial condition for all model scenarios. In grey shaded grid cells grey squirrels were initialised at their carrying capacity. In green shaded grid cell red and grey squirrels were assumed to have access to half the habitable area and densities were adjusted accordingly. In red shaded grid cells greys were assumed to be a 5% of their carrying capacity with the remainder of the region occupied by reds.

APPENDIX C: SIMULATION RESULTS FOR LEVEL 2 SQUIRREL DENSITIES

In 8 out of the 10 simulations that use level 2 densities (see Table 3.2) the disease fails to persist in the long-term. When the disease does persist there is only limited spread (Figure C.1).

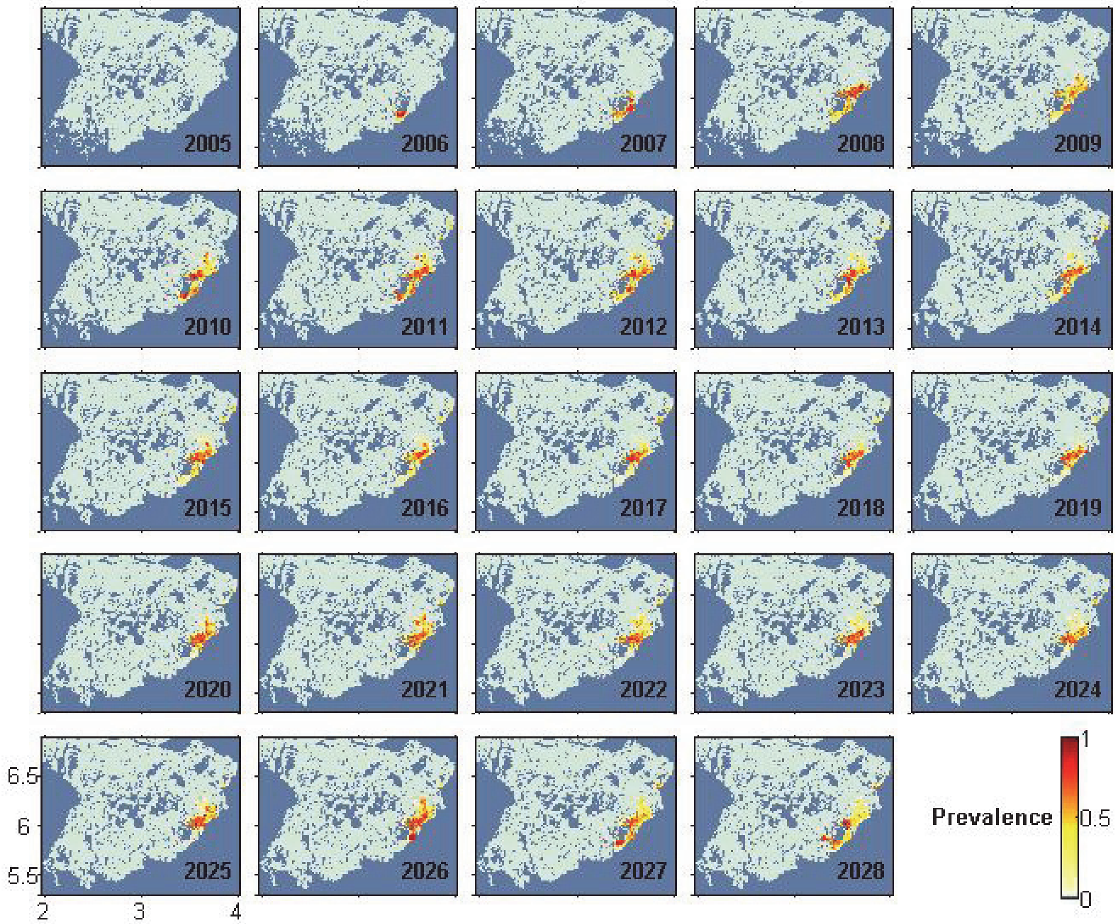


Figure C.1. The spread of squirrelpox from its initial introduction at low density in 2005 in a single model simulation. The presence of the disease is shown in terms of disease prevalence (defined as the proportion of immune grey squirrels). Here level 2 densities are used to define squirrel carrying capacities (Table 3.2) and at these densities the disease shows only limited spread. Easting and Northing values (/ 10^5) are shown on the bottom left panel.

APPENDIX D: HISTORICAL AND CURRENT CONTROL STRATEGIES

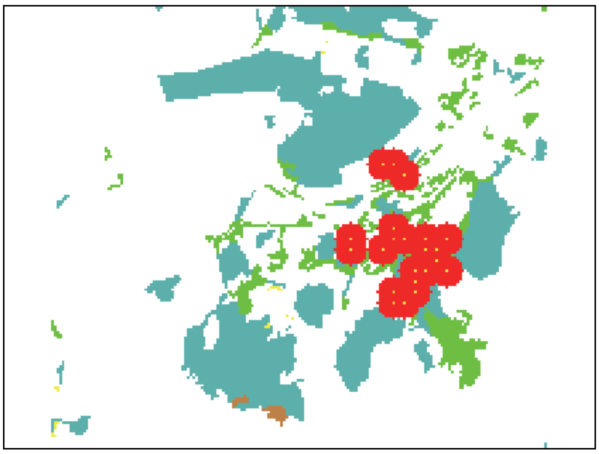
SNH and SSRS provided a variety of data regarding grey control strategies. This included records of trapping regimes, locations and number of animals caught to general overviews of the fraction of large scale regions that were trapped each year. The historical and current trapping data is not in an easily usable or consistent form to generate accurate control strategies that can be used in the model. Therefore we developed a strategy that uses the available data where possible (i.e. where trap locations were GPS recorded and sufficient traps were employed etc.) and that is designed to reflect the distribution and level of control in Southern Scotland between 2005-2012. The trapping data most suitable for analysis are shown in Table D.1.

Table D.1. Predictions of population size and proportion of greys caught determined using the software CAPTURE (Jacknife estimate) using trap data from GSCOs in selected sites for a range of trap days.

Site	N greys trapped (trap days, traps)	Mean pop. estimate	Pop. estimate range	Proportion greys caught (%)
Dawyck	45 (9, 26)	106	79-166	42 (27-59)
Culzean	24 (5, 24)	38	29-68	63 (35-83)
Duns	11 (32, 11)	19	12-122	58 (9-92)
Douglas	28 (5, 26)	47	36-79	60 (35-78)
The Glen	47 (9, 16)	135	104-184	35 (26-45)

*Note that the estimate for the proportion of greys caught was calculated using the mean with the lower and higher population estimate used to provide the range.

As a check on the population estimate derived from CAPTURE (Otis *et al.* 1991), the results were compared to those derived from literature estimates for population abundance at Dawyck and Douglas (as here the location of individual traps was recorded). The locations for the 26 traps employed at Dawyck were mapped using GRASS GIS and buffered by 150 m (to simulate an average home range, see Figure D.1). The trap plus buffer area covered a total of 82.5 ha of which 48.6 (15.86 ha conifer, 32.69 ha broadleaf) were forested. Using the level 1 estimates of grey squirrel density (Table 3.2), this would represent a total population of 114 grey squirrels for the area (compare to mean of 106 (79-166) in table above). Using the same method the location the 26 traps employed at Douglas covered a habitable area of 35 ha (19.25 ha conifer, 15.75 broadleaf) giving an estimate of density as 66 grey squirrels (compared to a simulated mean of 47 (36-79). These results are within the population estimate range produced using CAPTURE and provide confidence that literature based estimates used in the modelling procedure (Tables 3.1 and 3.2) are appropriate.



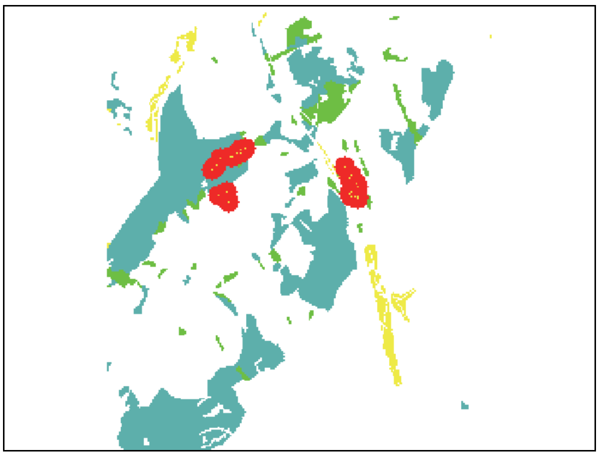


Figure D.1: Screenshots from GRASS GIS for Dawyck (left) and Douglas (right) indicating the trap locations buffered by a radius of 150m (red circles). The blue shading represents the location of conifer and green broadleaf habitat.

SNH provided data for SRDP contracts from 2009 in the form of number of traps to be used, the area over which control was to be applied and the 10km x 10km grid square location. The majority of the trapping data however was less detailed giving the percentage of the habitable region in 10km grid squares that was trapped. To use this data therefore requires knowledge of the proportion caught per trapping event. In this study we use an average value for the proportion caught for all trapping events which is determined as follow. The results from Dawyck and Douglas are used to derive a factor that converts number of traps and area over which traps are applied into a proportion of squirrels caught. The factor is derived at

C = proportion caught x (trapping area / number of traps)

At Dawyck, C = 0.42x(48.4/26) = 0.78 and at Douglas, C = 0.6 x (35/26) = 0.8.

Therefore, setting C=0.79 the proportion caught can be estimated for the SRDP data as:

Proportion caught = C x (number of traps / trapping area)

For the 115 regions with SRDP records this provided an average for the proportion caught per trapping event of 0.4. This average is used for each trapping event.

SSRS provided yearly data on the proportion of the habitable area of 10km x 10km grid squares that was trapped as a result of a coordinated trapping regime (by Grey Squirrel Control Officers, Volunteers or Forestry Commission Scotland) or in which trap loans to individuals have occurred. Data was presented annually (2005-2012) in terms of the location of the 10km grid squares (Figure D.2), the form of type of trapping (coordinated or trap loan) and the level of trapping divided into 5 levels of intensity (no trapping,0-25%, 25-50%, 50-75%, 75-100% of the habitable area was trapped in a particular year). This was used to design the trapping procedure in the model.

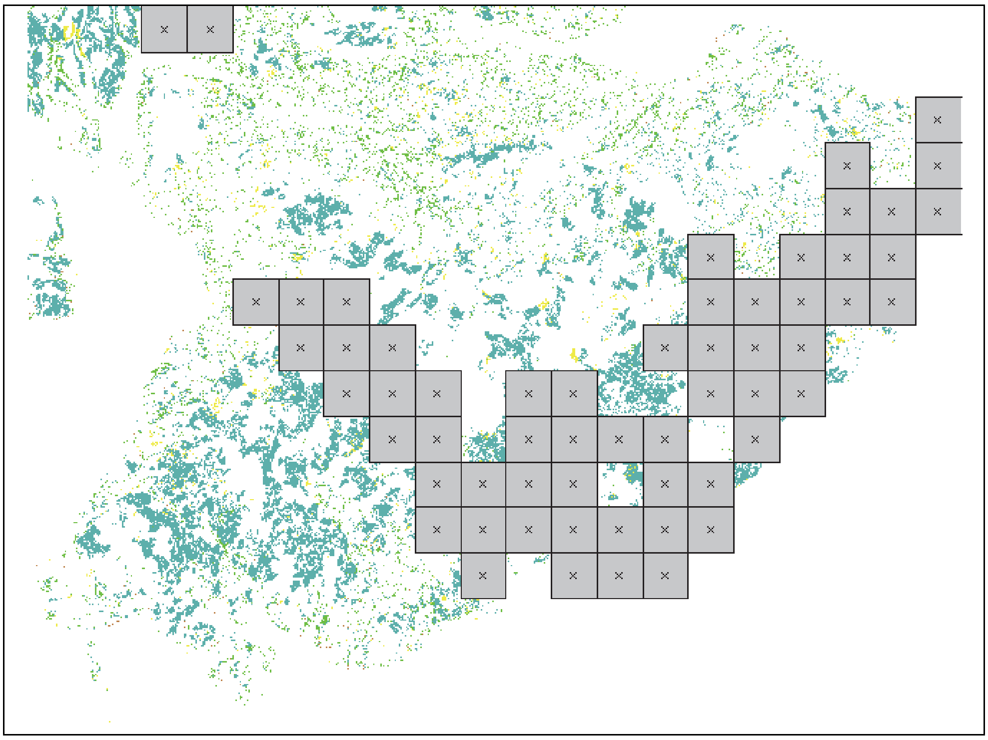


Figure D.2. The location of the 10km grid squares in which control is applied between 2005-2012. The coloured areas indicate woodland cover.

Original Control Procedure

For coordinated control regions the procedure is as follows. The mid points of the trapping intensity levels were used (i.e. 12.5% for 0-25% intensity) with these levels supplemented by the SNH (SRDP) data where relevant. Then for each year the assigned level of trapping was applied in each 10km grid square by locating the 1km grid cell with the highest seroprevalence (or highest density of greys if the disease is absent) and removing 40% of the grey squirrels in this grid cell. The model then systematically expands the control region to neighbouring 1km grid cells and removes 40% of greys in these grid cells until the desired percentage of the habitable region in the 10km grid square is controlled. This procedure is followed for all 10km grid squares in which there is coordinated control for each year. The SNH and SSRS data provided information on control between 2005-2012. The level and distribution of control used in 2012 is used in all subsequent years.

For control through the trap loan scheme, habitable 1km grid square sites are chosen at random within each 10km grid square until the desired percentage of the habitable region is covered. Since the levels of removal from the trap loan scheme is likely to be lower than that for coordinated removal events only 5% of the greys are removed in each 1km grid square due to trap loan control.

Adjusted Control Procedure (to better reflect actual numbers caught)

The amended control procedure retains the same level of grey removal (40%) when control occurs in a 1km grid cell but reduces the intensity of control (spatial extent to which control is applied) at the 10km grid square level. In the coordinated control strategy the intensity of control is converted to five levels of control (0, 1, 2, 3 and 4) and the percentage control for each level was set to give a better reflection of the reported number of grey squirrels caught. The level 1 control percentage is set at 1.3% of the habitable area (a ten fold reduction in the original value to reflect a ten fold overestimate of greys caught). Level 2 control is set at twice the level 1 value, etc. The percentage of the 10km grid square that was controlled through the trap loan scheme was reduced in a similar manner and a control event led to 2% of the greys are removed in each 1km grid cell.

APPENDIX E: MODEL DEVELOPMENTS

The short time-scale required to produce these results required that this study focussed on a best estimate set of parameters. The results from this study will be revisited as part of a PhD studentship at Heriot-Watt University over a longer time-scale (starting September 2013). This will allow the robustness and sensitivity of model parameters and results to be quantified. The following procedures could be undertaken.

- A test of the sensitivity of model results to changes in parameters. As shown in Appendix C when lower density estimates are used the disease spread is greatly reduced. Therefore, it is also important to assess the impact of changes to other model parameters, such as the disease transmission coefficient and the dispersal rate to which increases (decreases) in the parameter estimate are likely to increase (decrease) the rate of spread of squirrelpox.

- An assessment of whether other resources (in addition to the Forestry Commission inventory maps) could be used to improve estimates of the baseline habitat. At the moment general categories of broadleaf and conifer are used but at the local scale the species type may be of critical importance (as this will effect population densities). This may explain some of the discrepancies between the observed outbreaks of squirrelpox and the typical model findings (such as the lack of squirrelpox persistence in the eastern Scottish Borders and the possible increased spread into western Dumfries and Galloway). In addition, forestry inventory records categorise some regions (5% of the habitable area) as ‘assumed woodland’. In the model assessment these regions have been classified as conifer but further investigations could more accurately classify these regions (which may be significant as dispersal routes for disease).

- An assessment of the influence of temporal changes in the quality of habitat. Seasonal and annual changes in seed crops may produce marked impacts in local population densities.

- An increase in the number of simulations (from 10) for each scenario to improve the probability accuracies of different model outcomes.

- A reassessment of the way in which field based trapping efforts and control intensity are used to define the control procedure in the model (through further discussion with experts at SWT and SNH).

APPENDIX F: OCCURRENCE OF INFECTION IN A SINGLE MODEL REALISATION

Results for the occurrence of infection for a single model realisation in the absence of control. The patchy nature of infectious outbreaks is because the data is recorded at a single time point each year and so many infected individuals have either died due to the disease (reds) or recovered (greys) in between the recording period. The results highlight that outbreaks in red populations are local and adjacent to SQPV outbreaks in greys and that SQPV does not spread and establish over extensive regions in red only populations.

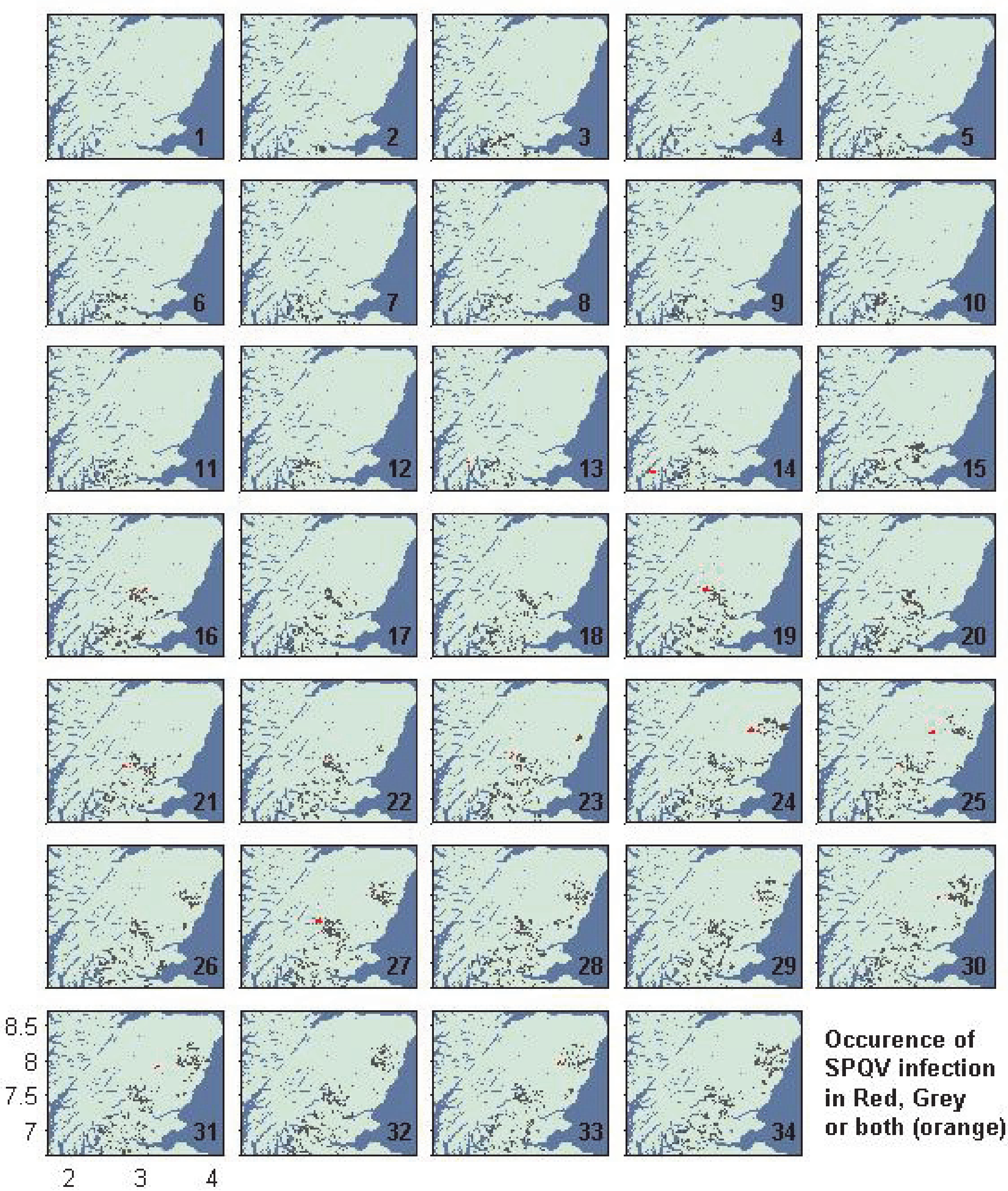


Figure F.1: The occurrence of SQPV infected individuals in a single model realisation over time. The red cells indicate the presence of infected red squirrels, grey cells infected grey squirrels and orange cells infected red and grey squirrels.

APPENDIX G: SPECIES SPECIFIC DENSITIES FOR RED AND GREY SQUIRRELS

Species specific potential densities for red and grey squirrels.

Tree Species	Red density /ha	Grey Density /ha
beech	1.1	1.49
bishop pine	0.79	0
Corscian pine	1.1	2.44
douglas fir	0.83	0.9
European larch	0.38	0.38
hawthorn	0.2	0.2
hazel	1	3
hybrid larch	0.38	0.38
Japanese larch	0.38	0.38
lodgepole pine	0.21	0.21
mixed broadleaf	1	3
mixed conifer	0.83	0.9
Monterey pine	0.21	0
mountain pine	0.21	0.21
Norway spruce	0.58	0.79
oak	1	3.4
other broadleaf	1	3
other spruce	0.2	0
Scots pine	0.83	0.79
Serbia spruce	0.21	0
sessile oak	1	3.4
Sitka spruce	0.2	0
small leaved lime	0.2	0
Sycamore	0	1.49
Weymoth pine	0.21	0.21
wild cherry	0.2	0.2

Estimates taken from the literature (Andrén and Lemnell 1992; Cartmel, 2000; Gurnell, 1983; Holm, 1991; Kenward *et al.* 1998; Lurz *et al.* 1998; Magris, 1998; Moller, 1986; Tittensor, 1970; Tonkin, 1983;, and references for Table 3.1). Personal communication with Craig Shuttleworth was also used to help define densities in different pine species.

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