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Mathematical models for invasive species management: Grey squirrel control on Anglesey

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ABSTRACT

The control of invasive species and protection of threatened native species require well-developed policy and species management strategies. Mathematical models provide a key tool that can be used to test, develop and optimise strategies to manage invasive species. We use the native red squirrel and invasive grey squirrel system on the Island of Anglesey, UK, as a case study system in which to parameterise a mathematical model that includes the control of grey squirrels. We develop a stochastic, spatial model that represents the real habitat structure, distribution and linkage on Anglesey and the neighbouring mainland and includes the key population and epidemiological dynamics of the red-grey-squirrelpox system. The model also includes a representation of the trapping and removal of grey squirrels which is parameterised from field data on Anglesey in which grey squirrel were removed and red squirrels reintroduced between 1998–2013. The model is used to assess different management procedures to protect red squirrels from island re-invasion by grey squirrels, including the threat of squirrelpox spread posed by endemic mainland grey populations. The findings have important implications for the conservation of threatened red squirrels throughout the UK and in Europe. Moreover, the modelling framework is based on well-understood, classical models of competitive and epidemiological interactions and therefore the techniques can be adapted and applied more generally to manage the threat of invasive species in a wide range of natural systems.

1. Introduction

The accidental, deliberate and environmental change induced redistribution of organisms is causing an invasive threat to native species diversity at the global scale (Ehrenfeld, 2010; Kolar and Lodge, 2001; Mack et al., 2000; Manchester and Bullock, 2000; Martin-Albarracin et al., 2015; Simberloff, 2011). In many cases the impacts of invading species are not considered until the problem is severe and then extensive intervention is required to limit the impacts or eradicate the invader (Mack et al., 2000). Early intervention is the most cost effective and successful strategy to limit the impact of invasive species (Hulme, 2006; Manchester and Bullock, 2000), requiring well-developed contingency strategies that can be invoked at the onset of invasion (Manchester and Bullock, 2000).

The eradication of invasive species is often required to protect native species. For example, the muskrat (*Ondatra zibethicus*) was successfully eradicated from the UK in the 1930s. Here, the negative effects of muskrats on agriculture observed in continental Europe led to early intervention in the UK and population control was undertaken before the muskrat could spread extensively (Gosling and Baker, 1989; Manchester and Bullock, 2000). However, eradication attempts in the past have not always been successful, resulting in detrimental impacts to native biodiversity and to future eradication campaigns which depend on public support (Mack et al., 2000). For example, the eradication of the coypu (*Myocastor coypus*) from the UK initially failed. The invasive threat posed by coypus was initially underestimated and allowed populations to increase in density and spread (Gosling and Baker, 1989). Following the failure of the first eradication campaign (1962–1965), extensive preliminary investigation into coypus population biology was used to provide a detailed control strategy and an assessment of the likelihood of successful eradication (Gosling and Baker, 1989). Mathematical modelling was used to determine the optimal trapping procedure, with the procedure modified in response to data gathered from control on the ground (Gosling and Baker, 1989; Manchester and Bullock, 2000). The combination of preliminary

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planning, modelling and responsive adjustments to the control scheme led to the eradication of the coypu within 8 years (Gosling and Baker, 1989). This highlights how an assessment of the population biology combined with population modelling is important to ensure eradication is efficient and successful (Bonesi et al., 2007). In this study we use population modelling techniques to aid the management of invasive grey squirrel control in the UK.

The replacement of the native red squirrel (*Sciurus vulgaris*) by the North Amercian grey squirrel (*S. carolinensis*) in the UK is an example of disease-mediated ecological invasion. Grey squirrels are abundant throughout most of the UK having replaced red squirrels in the majority of England and Wales and in parts of southern Scotland and Ireland (Bryce, 1997; Gurnell et al., 2004; Halliwell et al., 2015; O'Teangana et al., 2000). The remaining widespread red squirrel populations are in northern Scotland, along with often fragmented populations, typically sympatric with grey squirrels, in southern and central Scotland, northern England and Wales (Halliwell et al., 2015). Preventing further grey squirrel population expansion and removing sympatric grey squirrels are major priorities in conserving the remaining red squirrel populations (DEFRA, 2007; FCS, 2012; Forum, 2009; Parrott et al., 2009; Schuchert et al., 2014). Grey squirrels outcompete red squirrels in many habitats and also carry squirrelpox – an asymptomatic infection harmless to grey squirrels that produces pathological disease in red squirrels (McInnes et al., 2006; Sainsbury et al., 2008).

Mathematical models have highlighted the potential of grey control to protect red populations and to prevent the spread of squirrelpox (White et al., 2014, 2015), but to date have not been able to provide detailed grey squirrel control strategies, instead focussing on hypothetical control (or reduced fecundity) scenarios (Rushton et al., 2002). However, one of the questions posed by red squirrel conservation organisations is where and how much control is required to protect remaining key red squirrel populations? While mathematical modelling can be used to inform on this question, up to now it has been limited by a lack of suitable data from which to parameterise the model (particularly in terms of the initial distribution and density of red and grey squirrels in regions where grey squirrel control has been undertaken). The 710km^2 Isle of Anglesey located off the coast of north-west Wales (see Fig. 1) provides a case study region in which a mathematical model of grey squirrel control can be parameterised and thereby provide a tool that can be used to develop red squirrel conservation strategies to protect red squirrels throughout the UK.

Until the 1960s, red squirrels were the only squirrel species that inhabited Anglesey (Walker, 1968). However, the grey squirrel was expanding its range across the UK and they were recorded moving west along the north Wales coast, reaching Flintshire and Denhighshire (1945–1952), before being recorded in Caernarvonshire (Gwynedd) in the late 1950s (Shorten, 1954). The first grey squirrels were reported on Anglesey in 1966 (Walker, 1968), though potentially grey squirrels dispersed to the island prior to this. Two bridges, the Britannia Bridge (1850/1972) and the Menai Bridge (1826) connect the island to the mainland with the former being thought to be the primary route squirrels use to enter and leave the island (Schuchert et al., 2014) (see Fig. 1). Suitable habitat for squirrels extends to the waterfront on either side of the Britannia Bridge with the lower level providing a clear dispersal corridor as it is used infrequently by trains. From c. 1966, grey squirrels established and spread on the island, reaching an abundance of 3000–4000 by 1998 (Halliwell et al., 2015) and almost completely replacing red squirrels (with approximately 40 red squirrels remaining on Anglesey by 1998, Shuttleworth, 2003). Grey squirrel control measures were implemented from 1998 and led to the eradication of grey squirrels from Anglesey by 2013 (Shuttleworth et al., 2015b). Moreover, in the period 2004–2013, red squirrels were reintroduced to many parts of the island with the result that it supports a population of approximately 700 red squirrels (in 2015) (Halliwell et al., 2015). The island of Anglesey therefore provides a unique case study system from which to parametrise key squirrel life history parameters and to model the control of grey squirrels. In particular, the key population data of red squirrels at their carrying capacity in 1966 (with no grey squirrels) and grey squirrels at their carrying capacity in 1998 (with few red squirrels) allows the dispersal and invasive replacement of reds by greys to be modelled. The well-documented removal of grey squirrels through trapping by 2013 (Schuchert et al., 2014) allows key grey squirrel control processes to be modelled.

Table 1
Estimates of squirrel densities per hectare for the different habitats recorded in the landcover data on Anglesey and neighbouring mainland, taken from the following sources (Bosch and Lurz, 2012; Gurnell, 1983, 1996).

Habitat	Red squirrels (/ha)	Grey squirrels (/ha)
Semi-natural broadleaved woodland	0.65	2.50
Planted broadleaved woodland	0.65	2.50
Semi-natural coniferous woodland	0.35	0.6
Planted coniferous woodland	0.35	0.6
Semi-natural mixed woodland	0.65	1.25
Planted mixed woodland	0.65	1.25
Dense scrub	0.25	0.65
Introduced scrub	0.25	0.65
Gardens	0.315	0.94
Caravan site	0.16	0.47

A key aim of this study is to develop a mathematical model that includes the control of grey squirrels on Anglesey. This model can then be used to assess different management procedures that will protect red squirrels from island re-invasion by grey squirrels; including the threat of squirrelpox spread posed by mainland grey populations. Anglesey contains fragmented woodlands that support low/medium densities of red squirrels, and is therefore similar habitat to that found within many of the remaining geographical red squirrel stronghold areas elsewhere in the UK. Consequently, the findings will have wider implications for the conservation of red squirrels throughout the UK (and elsewhere in Europe where grey squirrel invasion is also leading to the replacement of native red squirrels (Martinoli et al., 2010; Wauters et al., 2005)). Moreover, the modelling framework developed in this study is based on well-understood, classical models of competitive and epidemiological interactions (Tompkins et al., 2003). The techniques, therefore, can be adapted and applied more generally to manage the threat of invasive species in a wide range of natural systems.

2. Methods

The overall modelling framework represents the abundance of red and grey squirrels and squirrelpox infection status in 1 km by 1 km grid squares. Gridsquares are linked by dispersal and the potential squirrel density in each grid square is based on landcover data that approximates the real heterogeneous habitat of Anglesey.

2.1. A mathematical model of the Anglesey squirrel system

2.1.1. Calculating potential squirrel abundance

Using GRASS GIS software (Version 6.4, http://grass.osgeo.org/), we used digital landcover maps supplied by Natural Resources Wales to extract the dominant habitat type at a 25 m by 25 m scale for Anglesey and the adjacent mainland. This data was combined with estimates of squirrel densities in different habitat types (Table 1) and summed to obtain the potential density of red and grey squirrels at a 1 km × 1 km patch level (this scale has been used successfully to model the UK squirrel system in previous studies, Macpherson et al., 2016; White et al., 2014, 2015). When these estimates are combined with the model (see below) they predict

Fig. 1. A map of Anglesey (left: © OpenStreetMap), a photograph of the lower level of the Britannia Bridge which provides a dispersal corridor between the mainland and Anglesey (centre: © HannahJones) and a photograph of the habitat surrounding the bridge which enables squirrels to gain access to the bridge (right: with squirrel ecologists and modellers enjoying the sunshine, © Peter Lurz).

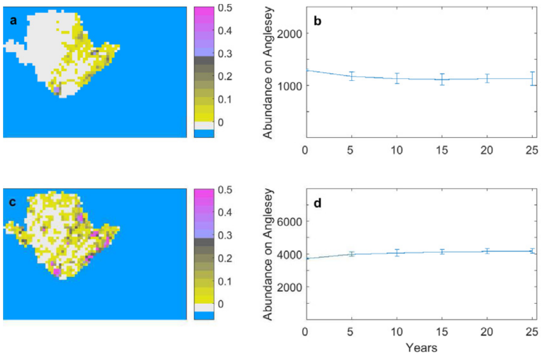

Fig. 2. Squirrel density approximations: A map of the density (/ha) of (a) red squirrels and (c) grey squirrels on Anglesey after 25 years for a single model realisation using the estimates of potential density shown in Table 1 (the colour bar indicates squirrel density per hectare which is determined by dividing the number of squirrels in each 1 km by 1 km cell by 100). The graphs in (b) and (d) show the change in average abundance for red and grey squirrels over a 25-year time period for 20 model realisations (with 95% confidence intervals). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

that Anglesey can support approximately 4000 grey squirrels and 1000 red squirrels (Fig. 2) which is in good agreement with field estimates (Halliwell et al., 2015; Schuchert et al., 2014).

2.1.2. The model framework

We base our model framework on previous mathematical models of the UK squirrel system in realistic landscapes which have adapted classical deterministic approaches (Tompkins et al., 2003) to consider a spatial, stochastic model of the red/grey/squirrelpox system (Macpherson et al., 2016; White and Lurz, 2014; White et al., 2014, 2016). Here, the deterministic underpinning allows the key population dynamical processes to be understood (Tompkins et al., 2003) and the stochastic adaptation provides essential realism when squirrel numbers become low and therefore the chance of extinction and the fade-out of infection is represented. The stochastic model is developed by modifying the deterministic system of Tompkins et al. (2003) which represents the population densities of susceptible and infected reds (S_R, I_R) and susceptible, infected and immune greys (S_G, I_G, R_G) at time t, in years, in each 1 km by 1 km grid cell. The underlying deterministic model is as follows:

$$\frac{dS_G}{dt} = A_G(t) - bS_G - \beta S_G(I_G + I_R) \tag{1}$$

$$\frac{dI_G}{dt} = \beta S_G(I_G + I_R) - bI_G - \gamma I_G \tag{2}$$

$$\frac{dR_G}{dt} = \gamma I_G - bR_G \tag{3}$$

$$\frac{dS_R}{dt} = A_R(t) - bS_R - \beta S_R(I_G + I_R) \tag{4}$$

$$\frac{dI_R}{dt} = \beta S_R(I_G + I_R) - bI_R - \alpha I_R \tag{5}$$

where $H_G = S_G + I_G + R_G$ and $H_R = S_R + I_R$ represent the total squirrel populations and

$$\text{where} \quad A_G(t) = \begin{cases} a_G\left(1 - q_G(H_G + c_R H_R)\right)H_G & t_n \le t < t_{n+1} + 0.5 \\ 0 & t_n + 0.5 \le t < t_{n+1} \end{cases}$$

represents the periodic birth rate of grey squirrels assuming births occur during six months of the year (March–September). This seasonality in reproduction causes the population density to exhibit annual oscillations around the potential density. Towards the end of the breeding season, the population density is above the potential density, triggering an increase in squirrel dispersal as is observed in the natural system (Jones et al., 2016; Macpherson, 2014). The term for $A_R(t)$ is equivalent to $A_G(t)$ with the subscripts for R and G interchanged. This term assumes a density dependent birth rate for both species which is modified due to the susceptibility to crowding (q_R, q_G) that depends on intraspecific and interspecific competition (c_R, c_G). The susceptiblities to crowding (q_R, q_G) are set to ensure that the average density over one year is equal to the potential density in each grid square and the competitive effect of grey squirrels on red squirrel is $c_G = 1.65$ and red squirrels on grey squirrels is $c_R = 0.61$ (Bryce et al., 2001). All other life-history and disease processes occur throughout the year. The species have the same rate of adult mortality, $b = 0.9$ (Barkalow et al., 1970), but different rates of maximum reproduction, $a_G = 3.4$ and $a_R = 3.0$ (Okubo et al., 1989). The model assumes that squirrelpox infection occurs due to density dependent contacts between susceptible and infected squirrels. The transmission rate of squirrelpox virus between and within each species is $\beta = 3.27$ obtained by matching the model to the seroprevalence on the mainland adjacent to Anglesey of 67% (Schuchert et al., 2014). The model assumes susceptible-infected-recovered (SIR) dynamics for grey squirrels with infected grey squirrels recovering at rate $\gamma = 13$ (Tompkins et al., 2002). The model assumes susceptible-infected (SI) dynamics for red squirrels as infection in generally fatal, with the rate of disease induced mortality $\alpha = 26$ (Tompkins et al., 2002). Further details of the parameter estimation can be found in the supplementary information, Table S1.

To generate the stochastic model, the rates in the deterministic model are converted to probabilities of events that account for changes in individual grid cell level abundance (Renshaw, 1991). The probabilities are given in Table 2.

The events in Table 2 are incremented at random and the associated probabilities are updated following population density changes after each event. The time between events is an exponentially distributed random variable, $T_{\text{event}} = -\ln(\sigma)/R$ where σ is a random number from the uniform distribution between 0 and 1 (Renshaw, 1991). The model is coded using Fortran 90 and individual simulations are undertaken using a Gillespie algorithm and provide information of the behaviour in a single realisation (Renshaw, 1991). Multiple realisations are generated to assess the

Table 2
The stochastic model within each 1 km by 1 km grid square indicating the probability of different events. Here $R = \sum[rates]$ (the sum of the rates in square brackets). Note, the birth terms shown in the table apply for the breeding season only (and are set to zero otherwise). Transmission can occur from infected squirrels within the focal grid square and also from the 8 neighbouring grid cells due to daily movement within a core range of radius, $\theta = 0.15$ km. The dispersal term is shown for the class S_G only but is similar for all other classes. The model assumes density dependent dispersal such that squirrel dispersal increases as density increases and the dispersal rate is $m = 2b$ when the patch density is equal to the potential density. Therefore, individuals undergo long distance dispersal on average twice in their lifetime and relocate to a different patch up to a distance of 2 km from the focal patch (with dispersal probability weighted appropriately for patches within the dispersal range). This mechanism also accounts for dispersal across the Britannia Bridge with the additional assumptions that the Bridge is 400 m in length and connects a specific gridcell on Anglesey with one on the mainland. The dispersal parameter values were set by comparing model results and field data for the expansion of grey squirrels and replacement of red squirrels on Anglesey between 1966 and 1998 (Jones et al., 2016).

Birth of grey to S_G	$P(S_G \to S_G + 1)$	$:[a_G(1 - q_G(H_G + c_R H_R))H_G]/R$
Natural death of S_G	$P(S_G \to S_G - 1)$	$:[bS_G]/R$
Infection of grey	$P(S_G \to S_G - 1, I_G \to I_G + 1)$	$:\left[\beta S_G \left((I_G + I_R)/R + \theta \sum_{Adjacent} (I_G + I_R) + \theta^2 \sum_{Corner} (I_G + I_R)\right)\right]/R$
Natural death of I_G	$P(I_G \to I_G - 1)$	$:[bI_G]/R$
Recovery of grey	$P(I_G \to I_G - 1, R_G \to R_G + 1)$	$:[\gamma_G I_G]/R$
Natural death of R_G	$P(R_G \to R_G - 1)$	$:[bR_G]/R$
Birth of red to S_R	$P(S_R \to S_R + 1)$	$:[(a_R - q_R(H_R + c_G H_G))H_R]/R$
Natural death of S_R	$P(S_R \to S_R - 1)$	$:[bS_R]/R$
Infection of red	$P(S_R \to S_R - 1, I_R \to I_R + 1)$	$:\left[\beta S_R \left((I_G + I_R) + \theta \sum_{Adjacent} (I_G + I_R) + \theta^2 \sum_{Corner} (I_G + I_R)\right)\right]/R$
Death of I_R	$P(I_R \to I_R - 1)$	$:[(b + \alpha)I_R]/R$
Dispersal of S_G	$P(S_G \to S_G - 1)$	$:[mS_G(H_G + c_R H_R)/K_G]$

average behaviour and variability (see Jones et al., 2016; White et al., 2014, 2016, for further details of the model set-up).

To simulate the replacement of red squirrels by greys on Anglesey the model was initialised with the red squirrel abundance and known distribution as shown in Fig. 2 (at the end of the 25 year period) representing the conditions in 1966. Grey squirrels were introduced at the Britannia Bridge and model dispersal parameters that led to the (near) replacement of red squirrels and the expansion and increase in abundance of grey squirrels were fitted so that the abundance of grey squirrel was between 3000–4000 by 1998 (after 33 years in the model). A sensitivity analysis of the maximum dispersal distance and dispersal rate was undertaken in Jones et al. (2016) which also determined the parameter values that gave the best fit to the observed range expansion of grey squirrels on Anglesey between 1966–1998. Here it was found that the maximum dispersal distance of 2 km and the dispersal parameter of $m = 2b$ (which represents that an individual squirrel makes on average two long distance relocations in its lifetime) was required to enable grey squirrels to expand across Anglesey and replace most red squirrel populations in 33 years, which closely matched field observations. In this study we wish to adapt the model to represent the control and eradication of grey squirrels and the reintroduction and expansion of red squirrels as reported on Anglesey between 1998–2013.

Table 3
The control effort and number of grey squirrels caught on Anglesey and the mainland (adjacent to the Britannia Bridge) for the grey squirrel eradication programme reported in Schuchert et al. (2014). In 2013, 1 grey squirrel was dispatched prior to being caught.

Year	Anglesey		Mainland	
	Trapdays	Greys caught	Trapdays	Greys caught
1998	16,923	1100	0	0
1999	14,000	700	0	0
2000	17,391	800	1380	0
2001	18,571	520	1380	0
2002	35,591	1128	1380	177
2003	30,959	421	1042	156
2004	27,546	419	668	38
2005	27,758	587	0	0
2006	35,039	165	0	0
2007	52,414	237	276	36
2008	38,300	146	2098	254
2009	33,698	105	2126	160
2010	23,392	49	4706	597
2011	6832	3	4550	425
2012	24,105	22	4735	506
2013	16,317	0 (1)	6305	508

2.1.3. *Grey squirrel control and the reintroduction of red squirrels on Anglesey*

In the 1990s, a conservation project was undertaken to conserve and increase the remaining red squirrel population on Anglesey (Forum, 2009; Shuttleworth, 2003). From 1998–2002, the primary aim was to increase the red squirrel population on Anglesey by removing grey squirrels, mostly in the south of the island (Ogden et al., 2005). Following initial successes, the grey squirrel control effort on Anglesey (and the mainland adjacent to the Britannia Bridge) was expanded and intensified and was coupled with a reintroduction program of red squirrels from 2004–2013. The regions in which control was applied and the locations for red squirrel reintroductions are shown in the supplementary information, Figs. S1 and S2 and data on the control effort and the number of grey squirrels caught is available in Schuchert et al. (2014) and shown in Table 3.

We consider two control strategies in an attempt to match the data of Schuchert et al. (2014). Control strategy 1 focusses control on suitable woodland sites (Shuttleworth, 2003), which we assume to be gridsquares with potential density $K_G > 3$ in the model, within the specified control regions (Fig. S3) for the entire control period 1998–2013. We divide total trapdays (Table 3) by the number of suitable gridcells to provide the trap effort per gridcell per year. For each year between 1998–2013 we convert this to the trap effort per gridcell per day, T_i (T_A for Anglesey, T_M for the mainland) by assuming trapping occurs for 6 months between April and September (183 days). The maximum trap effort per grid cell per day occurred on the mainland in 2013: $T_{\max} = 3.14$. Control strategy 2 uses the same method as strategy 1 on the mainland and on Anglesey between 1998–2005. Between 2005–2013 the strategy on Anglesey is changed to focus on gridcells where grey squirrels remain. Here, control was applied in gridcells where grey squirrels were present and in a 2 km buffer around these grid cells at either a level to reflect the trap effort per day per gridcell or at $T_{\max}$, whichever is smaller. Any remaining trapdays were distributed across cells in which $K_G > 3$ in the trappable region.

The inclusion of grey squirrel control introduces additional events (to those listed in Table 2). For example the probability of

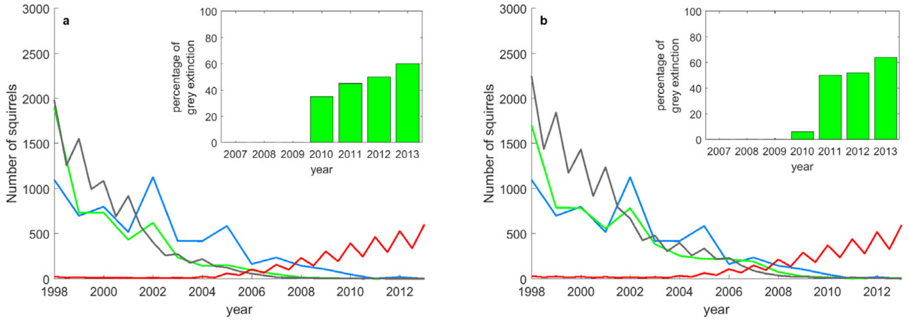

Fig. 3. Comparison of control strategies 1 and 2: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 3) and those caught in the model under (a) control strategy 1 with $c = 4.4$ and (b) control strategy 2 with $c = 3.5$. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. Here, both scenarios satisfy the criteria that 50% of realisations should show grey extinction between 2011–2013 (but not prior to this time) and the best fit statistic is $S = 6867$ for scenario 1 and $S = 2072$ for scenario 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

trapping and removing a susceptible grey squirrel is represented as follows:

$$\text{Control of} \quad S_G \, P(S_G \to S_G - 1) : [cT_i(S_G)]/R$$

where c reflects the rate of capture per trap effort per day. Similar terms are included for all squirrel classes but if a red squirrel is caught there is no change in density (to represent that it is released). To compare the model findings with the observed data we ran 20 realisations of model for 16 years (1998–2013) including trapping for different values of $c \in [2.0, 5.0]$ starting with initial conditions to reflect the grey squirrel density and distribution in 1998 (see Fig. S4). Red squirrel reintroductions were included at the sites documented during 2004–2013 (Fig. S2) (Lawton et al., 2015). Extinction of grey squirrels on Anglesey occurred by 2013 (Halliwell et al., 2015) and therefore we required that grey squirrel extinction in the model occurred on Anglesey in greater than 50% of the realisations between 2011–2013 (and that it did not occur in greater that 50% of the realisations before 2011). For model simulations that satisfy this requirement, we determine the value of c that gives the best fit to data in terms of minimising the following statistic:

$$S = \sum_{i=1998}^{2010} \frac{(E_i - O_i)^2}{E_i} \tag{6}$$

where E_i is the number of greys caught in the model in year i and O_i is the actual number caught. S is averaged over all realisations. The value of S for relevant model simulation is given in the figure legends and the scenario with the lowest value of S is deemed the best fit of the observed data for the eradication of grey squirrels on Anglesey.

In Fig. 3 we present the best fits to data for the two control scenarios (with further results shown in Figs. S5–S8). This indicates that strategy 2 provides the best fit to the observed data (and so provides a best estimate of $c = 3.5$). Here, all key woodland sites are initially targeted and later control is focussed where grey squirrels are still present. We now use the model to examine whether a more efficient control strategy could have been used to eradicate grey squirrels from Anglesey and to develop strategies to maintain and protect the established red squirrels on Anglesey from future invasion.

3. Results

3.1. Alternative eradication strategies

Using the same number of trapdays as in the 1998–2013 eradication campaign (Table 3) we used the model to test different control strategies to determine if the grey squirrels on Anglesey could have been eradicated more quickly. A common approach to eradicating invasive species is to 'knockdown' and 'mop up' (Veitch and Clout, 2002), preferentially targeting control in habitats containing the most abundant populations. Using this strategy, the general method that was tested was to apply grey squirrel control in the best habitat first and then increase the region over which control was applied in response to trapping data. Three specific approaches are outlined in Table 4. In particular in approach A, trapping occurs in the best 10% of habitat until the number of grey squirrels caught dropped below 25% of the initial trapping value. Then trapping is applied to the best 20% of habitat until the number caught drops below 25% and then trapping is applied in regions where greys are still present (and a buffer around these regions). Fig. 4 shows the results for the different approaches outlined in Table 4 and indicates that both trapping approaches B and C would lead to eradication of grey squirrels on Anglesey in at least 50% of realisations by 2010. (*Note*: we also tested these trapping approaches when the change between stages was triggered if the number of greys caught fell below 50% and 10% of the initial number caught (see Fig. S9.) The value of 25% shown in Fig. 4 gave the best results). These results suggest that grey squirrels could have been eradicated from Anglesey by 2010 using the same trap effort per year as in the actual eradication programme (in which eradication occurred by 2013).

3.2. Strategies to protect red squirrels on Anglesey

To highlight the importance of ongoing control of grey squirrels for the protection of red squirrels, we undertook model simulations in which grey squirrel control was stopped from 2014 onwards (Fig. 5). The model predicts that grey squirrels will disperse from the mainland to Anglesey and that the replacement of red squirrels by greys would occur within approximately 35 years (this is similar to the observed red replacement on Anglesey between 1966–1998). This highlights the importance of continued grey squirrel control to protect the red squirrel populations on Anglesey. The model was therefore used to develop resource efficient grey squirrel control strategies that could be included in current and future red squirrel conservation policy.

To estimate the trap effort required to maintain red squirrel populations on Anglesey we considered a range of strategies of control on the mainland, adjacent to the Britannia Bridge, and on Anglesey. We assume control on the mainland occurs for 6 months each year at a percentage of the maximum control effort (T_{max}). Furthermore, we assume control occurs on Anglesey in response to sightings of grey squirrels. In the model we approximate this with control occurring for one month in gridcells (and those in a 2 km

Table 4
The details of three alternative trapping approaches that could have been used to remove grey squirrels from Anglesey. Stage 1 traps in the most suitable habitat first – determined as the specified percentage of habitat with the highest potential density. When the number of grey squirrels trapped drops below 25% of the initial number caught, the trapping approach changes to stage 2 in which trapping is applied in the specified percentage of habitat with the highest potential density. When the number of grey squirrels caught in stage 2 drops below 25% of the initial number caught in this stage, the approach changes to stage 3. In stage 3 trapping is applied to all grid cells in which grey squirrels are present and habitable grids cells within a 2 km buffer around occupied grid cells. In all trapping approaches grey control is applied on the mainland in the cells indicated in Fig. S3 at the levels reported in Table 3.

Trapping approach	Stage 1 (% of habitat trapped)	Stage 2 (% of habitat trapped)	Stage 3
A	10	20	All $H_G > 0$ grid cells plus 2 km buffer
B	20	40	All $H_G > 0$ grid cells plus 2 km buffer
C	10	40	All $H_G > 0$ grid cells plus 2 km buffer

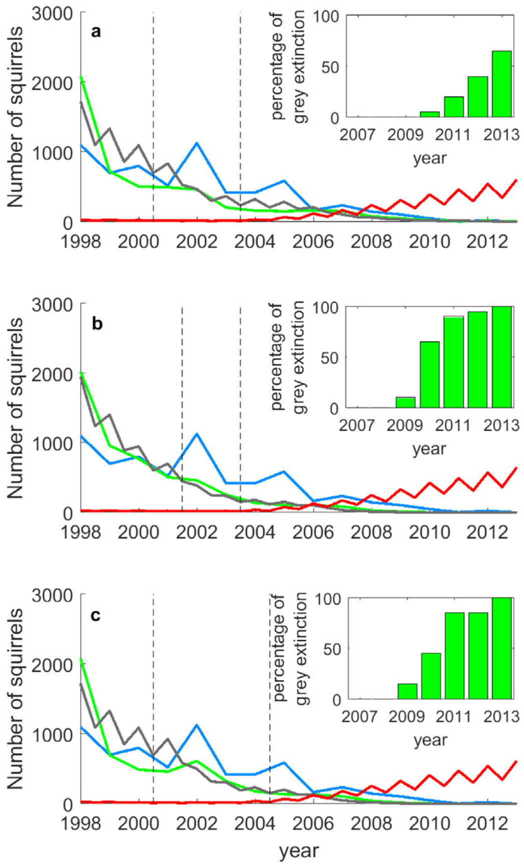

Fig. 4. Comparison of trapping approaches: A comparison of the actual number of grey squirrels caught on Anglesey (see Table 3) and those caught in the model under (a) trapping approach A, (b) trapping approach B and (c) trapping approach C (see Table 4). The blue line shows the actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

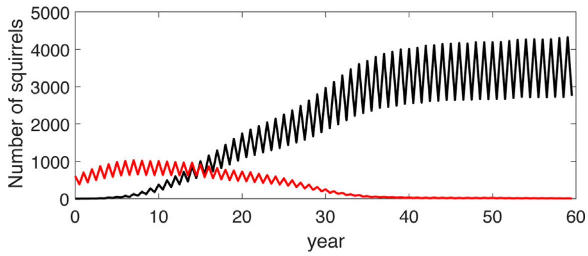

Fig. 5. Result of ceasing control: Average of 20 model realisations from 2014–2074 showing grey and red squirrel abundance on Anglesey if grey squirrel control is ceased on Anglesey and the mainland in 2014.

Table 5
Control strategies to protect the red squirrel stronghold on Anglesey after eradication of grey squirrels. The trap effort per grid cells per day as a percentage of T_{max} on Anglesey (T_A) is shown in column 2 and the trap effort per grid cell per day as a percentage of T_{max} on the mainland adjacent to the Britannia Bridge (T_M) is shown in column 3. If realisations have occurred in which >50 grey squirrels were present during the year on Anglesey, the control method is not adequate (column 4, marked with "Yes").

Continual control method	T_A (% of T_{max})	T_M (% of T_{max})	>50 greys on Anglesey	Average trapdays
1	100	0	Yes	2484
2	100	10	Yes	2224
3	100	50	No	3395
4	100	100	No	6420
5	50	50	Yes	4045
6	50	100	Yes	6549
7	10	50	Yes	4193
8	10	100	Yes	7102

buffer around them) in which grey squirrels are present (again with an effort that is a percentage of T_{max}). The different combinations are presented in Table 5 (with results for the different control level combinations shown in Figs. S10–S17). Control methods 1 and 2 which have no or limited control on the mainland, but high intensity control on Anglesey in response to grey detection do succeed in protecting red populations on Anglesey (Figs. S10 and S11). However, the dispersal of grey squirrels from the mainland means there is a continual presence of grey squirrels on Anglesey, and therefore a need for a high level of trapping in response to grey squirrel detection. Since grey squirrel detection on the ground will rely on reporting from the general public, a control method that limits the grey squirrel presence on Anglesey would be more desirable. Only two combinations prevent grey squirrels from establishing on Anglesey and of these the method with the lowest trapping effort suggests that the mainland should be trapped at 50% of T_{max} and the response to sighting of grey squirrel on Anglesey should be at T_{max}. The population and epidemiological dynamics and trap effort in the model for this scenario is shown in Fig. 6. Red squirrel densities on Anglesey are conserved and grey squirrels are detected on Anglesey at sporadic intervals and low levels. The number of trapdays per year to achieve this level of control required there to be a continual effort of 3153 trapdays per year on the mainland and then responsive control that ranges from zero to 3726 trapdays per year on Anglesey. Control scenarios in which trapping on Anglesey occurred at less than T_{max} failed to prevent grey squirrels from establishing on Anglesey and in some scenarios led to a significant decline in red squirrel abundance (Figs. S14–S17). As grey squirrels do disperse to Anglesey, there is a risk of squirrelpox being spread to red squirrels. The model suggests that squirrelpox outbreaks in red squirrels will only affect a small number of red squirrels (Fig. 6). The spread of squirrelpox throughout the established red squirrel population on Anglesey did not occur in model simulations.

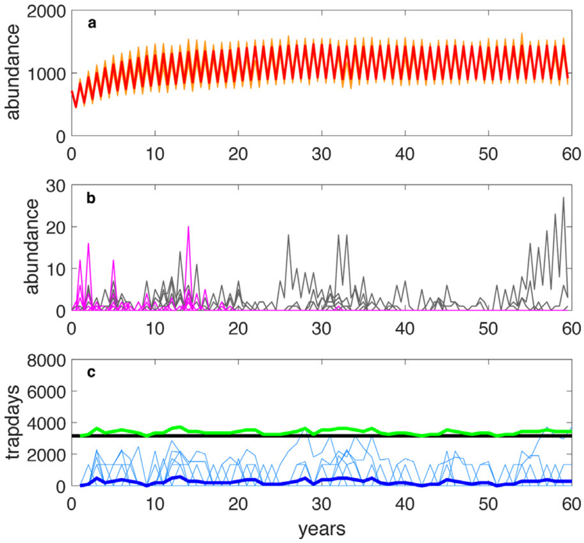

Fig. 6. Model results using control method 3 in Table 5. Results show the output for all 20 model realisations with in (a) red abundance, (b) grey abundance (black line) and infected red abundance (pink line) and (c) number of trapdays on Anglesey (blue line, average in bold blue), on the mainland (black line) and the average total trapdays (green line). Control on the mainland occurs for 6 months each year at 50% of T_{max} and control occurs for one month in gridcells (and those in a 2 km buffer around them) in which grey squirrels are present at T_{max} on Anglesey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

4. Discussion

We have developed a mathematical model encapsulating the red squirrel, grey squirrel and squirrelpox system that can represent the real-life trapping and removal of grey squirrels in landscapes that are the subject of ongoing management intervention. The model provided a good representation of the observed removal of grey squirrels from Anglesey between 1998–2013. The model also allowed alternative control strategies to be considered that may have better utilised the limited finances available to implement trapping effort on Anglesey. In particular, a control strategy that initially focussed on the best grey squirrel habitat, to reduce the impact of source populations, before switching to more widespread grey control was shown to eradicate grey squirrels from Anglesey by 2010, three years earlier than in the field. This highlights the potential of mathematical models in the design of eradication and control programmes.

The mathematical model was also used to determine the effort required to protect the red squirrel population on Anglesey from future grey squirrel invasion. The model provided quantitative predications that recommended a continual trapping effort in mainland sites adjacent to the Britannia Bridge to minimise grey dispersal to Anglesey, and high intensity trapping in response to observations of grey squirrels that do reach Anglesey. The model suggest that this strategy requires on average 3395 trap days per year, with a range of 3153–6878, dependent on whether trapping was required on Anglesey. This equates to the effort comfortably encompassed by one full time grey squirrel trapping operative. This predicted control effort was shown to maintain a stable population of approximately 1000 red squirrels on Anglesey. It is worth noting that if grey control was not continued then grey re-invasion and complete replacement of red squirrels would re-occur within 35 years. These projections can be used to support regional policy and funding decisions to efficiently protect red squirrels on Anglesey (Shuttleworth et al., 2015a).

It is important to recognise that the model framework used in this study is a simplification of the real system. In particular, it simplifies the life history and epidemiological processes, it assumes a fixed habitat structure and relies on estimates that link tree species distributions to squirrel abundance (and better regional information on the suitability of different tree species would certainly enhance the model predictions). Nevertheless the model provides key information that would be difficult to gain in field settings. Therefore, it is an invaluable tool to shape policy and design conservation strategies to protect red squirrels from the threat of grey squirrel invasion. For instance the current conservation strategy in the UK is to protect red squirrels by using grey squirrel control in and around designated red squirrel strongholds/priority regions (RSNE, 2016) and along a containment region that spans from east to west Scotland in the Scottish Highlands (Scottish Squirrel Group, 2015). By extracting habitat specific information from digital landcover data for these regions, the model could forecast the likelihood of grey squirrel establishment and determine the control effort (in terms of trapdays) required to protect red squirrel populations. In particular, the model framework highlights key dispersal corridors in which grey squirrel control can be focussed to prevent further range expansion or protect key priority regions. By providing estimates of where and how much grey control should be applied it allows red squirrel conservation organisations to better utilise current resources and to plan future resource requirements. The detailed model study presented here that focussed on grey squirrel control on Anglesey will enable the model framework to be modified to determine the distribution and level of control required to protect red squirrels in other regions. For instance work is currently being undertaken, in collaboration with Saving Scotlands Red Squirrels (Saving Scotland's Red Squirrels, 2016) to modify the model to determine the location and level of control required to prevent grey squirrel range expansion beyond the highland line (which extends from Loch Lomond in the west to Montrose in the east and which forms the interface between red and grey squirrels in highland Scotland) and to exclude grey squirrels from the Dumfries and Galloway forest park. Model extensions could further be used to shape conservation strategies to protect red squirrels beyond the UK, such as in northern Italy where red squirrels are also threatened by grey squirrels invasion (Bertolino et al., 2016).

The trapping effort reported to eradicate grey squirrels from Anglesey is a valuable long term and “real-world” data set that highlights the challenges of landscape control (see Parrott et al., 2009; Schuchert et al., 2014; Shuttleworth et al., 2015b for retrospective critical reviews). We note that other mammalian eradication studies have highlighted the potential for trappers to try to prolong a project by trapping at a lower rate than those reported (Gosling and Baker, 1989). Such issues may arise when there is a lack of incentives to complete the work, with a fear of unemployment if the species is eradicated (Gosling and Baker, 1989). To assess the importance of trapping efficiency, we ran the best fit model for Anglesey (Fig. 3b) using (a) 80% and (b) 120% of the reported trap effort of Table 3. Scenario (a) represents when trappers reported a greater number of hours than were actually worked and results indicate that grey squirrels would not be eradicated with this level of control (Fig. 7a). Scenario (b) represents when trappers reported the correct hours but were not working at full efficiency (Fig. 7b). Here, if the higher level of control had been applied, grey squirrel extinction could have occurred around 2009–2010. This highlights the need for correct incentification and close management of staff in conservation projects. Management oversight during eradication did indeed find isolated examples of a contractor failing to distribute traps thoroughly across a woodland (Shuttleworth, personal observation). Parallels can be drawn with the eradication of the coypu in the UK (Gosling and Baker, 1989). Here, a bonus scheme that incentified early eradication of coypus was employed and this is considered to have played a major role in the successful eradication (Gosling and Baker, 1989).

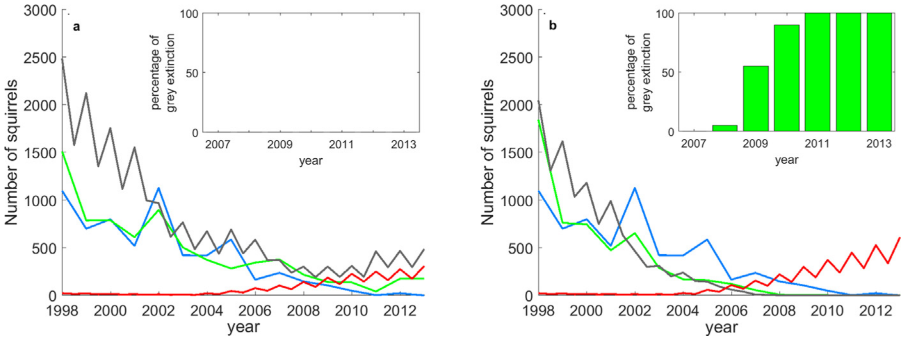

Fig. 7. Increased and decreased trapping competence with (a) 80% of trap effort and (b) 120% of trap effort. The blue line shows that actual number of grey squirrels caught. The other lines show averages over 20 model realisations for the number caught in the model (green line), the abundance of grey squirrels (grey line) and red squirrels (red line) on Anglesey. The inset panels show the percentage of runs in which greys squirrels have become extinct by the specified year. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

The model also allows for an assessment of the impact of squirrelpox on the effort to conserve red squirrels on Anglesey. While future grey control could limit the dispersal of grey squirrels to Anglesey, it could not prevent occasional incursions (as evidenced by three greys removed from the island in autumn 2015, Shuttleworth et al., 2016). The model predicts that the dispersal of infected grey squirrels could lead to squirrelpox transmission to red squirrels. However, within the established red squirrels, squirrelpox outbreaks are localised and the infection fades out and does not spread widely throughout the population. Squirrelpox, is therefore predicted to have a minor effect on the total red population abundance on Anglesey. This confirms previous model findings (Jones et al., 2016; Macpherson et al., 2016; White et al., 2015, 2016) and evidence from the field where squirrelpox outbreaks in red squirrel populations in protected stronghold regions are short-lived, with red squirrel abundance returning to pre-infection levels following disease fade-out (Chantrey et al., 2014; White and Lurz, 2014). The evidence therefore suggests that grey squirrel control in and around vulnerable red squirrel populations should be the primary strategy for red squirrel conservation, rather than focussing on preventing the spread of sqiurrelpox. Localised outbreaks of squirrelpox in protected red squirrel populations may occur as an unavoidable consequence of red populations beings adjacent to squirrelpox carrying greys. Provided greys are prevented from establishing in protected red squirrel strongholds then red density can, over time, return to pre-infection levels following an outbreak (White et al., 2014, 2015).

Well-developed conservation strategies are required to protect native species from the threat of invasion. In this study we have shown how mathematical modelling can play a key role in policy and planning to eradicate or manage invasive species. The model has been applied to the key case study system of the invasion of grey squirrels in the UK. The approach is based on combining well understood mathematical modelling frameworks with spatial information on habitat distribution, structure and actual levels of control. The approach could therefore be applied to a wide range of systems in which invasive species pose a threat to native species and ecosystems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at 10.1016/j.ecolmodel.2017.05.020.

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