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

Hannah Jones[a,*], Andrew White[a], Peter Lurz[b], Craig Shuttleworth[c]

[a] Department of Mathematics and the Maxwell Institute for Mathematical Sciences, Heriot-Watt University, Edinburgh EH14 4AS, United Kingdom
[b] Lurzengasse 3, D-97236 Randersacker, Germany
[c] School of Environment, Natural Resources and Geography, Bangor University, Deiniol Road, Bangor, Gwynedd LL57 2UW, United Kingdom

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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

* Corresponding author.
E-mail address: hej1@hw.ac.uk (H. Jones).

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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