Institution: The University of Edinburgh/Heriot-Watt University (Maxwell Institute)

Unit of Assessment: B10, Mathematical Sciences

Title of case study: Mathematical modelling drives conservation efforts and policy to prevent squirrelpox spread and the replacement of red squirrels by invasive greys in the UK

1. Summary of the impact

Mathematical modelling of squirrel populations published in 2003 by White (Maxwell Institute), Tompkins and Boots (Stirling) highlighted how squirrelpox virus transmitted by invasive grey squirrels to reds is a critical factor in the decline of UK red squirrels. As a consequence of this research the role of squirrelpox is now universally accepted. This has had an impact on policy and practice since 2006 with priority given to the control of grey squirrel numbers in order to prevent the spread of squirrelpox. The modelling framework developed at the Maxwell Institute was reported to the Saving Scotland's Red Squirrel steering group and has been used to design the conservation strategies currently applied throughout Scotland. The research has therefore had an impact on the environment, contributing to the mitigation of a problem that is estimated to cost £14M/year to the UK economy.

2. Underpinning research

Since its introduction into the UK, the grey squirrel has 'replaced' the native red squirrel 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 conservation priority. As such the UK red squirrel is a protected species (Nature Conservation Act 2004) and was one of the first species identified for conservation under the UK Biodiversity Action Plan (DEFRA 2007).

Mathematical model. The focal publication by White (Maxwell Institute), who led the mathematical model development and analysis, Tompkins and Boots [1] employs mathematical modelling techniques to provide evidence that squirrelpox infection was a key driver of the rapid replacement of red squirrels by greys in the UK. The modelling framework and mathematical analysis were developed by White as part of an EPSRC-NERC Environmental Mathematics and Statistics Fellowship (NER/T/S/2002/00162). The model consists of a system of five nonlinear ODEs that represent competition for resources and transmission of squirrelpox virus that is carried by, but avirulent to, the grey squirrels yet lethal to reds. The occurrence of squirrelpox virus was known prior to this paper but this study was the first to show that squirrelpox accelerates the process of replacement and therefore that disease was a causative factor in the decline of red squirrels in the UK. Moreover, the findings predicted that the instantaneous number of infections was low even though the effect on the population dynamics was marked, indicating that low visibility did not equate to low importance of the disease. This explained the difficulty in observing such infection in the field and why squirrelpox was previously overlooked as a key determinant of red replacement.

In addition to outlining the underlying mechanisms that drive the red/grey/squirrelpox interaction the publication [1] broadened our understanding of the processes underlying ecological invasions in general with the model framework becoming a textbook theoretical example from which to understand the importance of parasites introduced with invading competitive species (Keeling and Rohani, *Modelling infectious diseases in humans and animals*, 2008). The specific methods are applicable for studying the replacement of red squirrels by greys across Europe (greys pose a threat in Italy, France, Switzerland and Germany). Moreover, disease-mediated invasion is a global widespread phenomenon that effects a wide range of taxa (Strauss, A. *et al*., *Functional Ecology*,

26, 1249-1261, 2012) and mathematical techniques outlined in [1] can be applied to a wide range of other ecologically important systems in which disease carrying invaders threaten native species (e.g. in an analogous manner native crayfish populations are threatened at the global scale from the spread of crayfish plague carried by the introduced signal crayfish).

Attribution. A. R. White has been with the Maxwell Institute since 1999. D. M. Tompkins and M. Boots were at the University of Stirling during the period of the underpinning research.

3. References to the research

[1] Tompkins D.M., White A. R. and Boots, M., Ecological replacement of native red squirrels by invasive greys driven by disease. *Ecology Letters*. **6**, 189-196 (2003). http://dx.doi.org/10.1046/j.1461-0248.2003.00417.x

This mathematical study was published in Ecology Letters (the top journal in the field) to ensure it received maximum exposure to a biological audience and to conservation practitioners. (Cited by 156; Ecology Letters Impact Factor – 17.557, Ranked 1/131 in Ecology.)

Grant

EPSRC-NERC Environmental Mathematics and Statistics Fellowship (NER/T/S/2002/00162), 'Spatial modelling techniques applied to ecological and laboratory systems' (2003). Value £100K.

4. Details of the impact

The paper [1] received keen media interest leading to dissemination of results to the wider public [2-6] and to the now widely accepted view that squirrelpox is a key determinant in the replacement of red squirrels by greys. The work has greatly improved public understanding of this issue as evidenced by many subsequent media articles highlighting the disease threat to red squirrels (e.g. there are 74 news articles on the BBC website alone since 2008 discussing the threat from squirrelpox to red squirrels – search 'pox squirrel').

The publication has had an impact on environmental policy in Government and NGO sectors guiding specific management and planning decisions to bring about environmental benefits through the conservation of a key threatened native species. The economic impact of the research, though difficult to quantify, is not negligible: it is estimated that the invasion of grey squirrels have cost the British economy £14 million per annum [2]. Large-scale control of grey squirrels (trapping and removal of greys) has been implemented in an attempt to reduce grey abundance to a level that will not support disease persistence and therefore prevent its spread. These procedures which began in 2006 are ongoing and are implemented at large scale across the UK to protect remaining red squirrel populations. Evidence of these impacts is outlined below.

Scottish Natural Heritage (SNH) identified key sites where management to benefit red squirrels should be prioritised with the central aim 'to maintain viable self-sustaining populations of red squirrels in the future' [7]. The report states that 'Tompkins *et al*. (2003) [1] have demonstrated that, even at low levels of infection in grey squirrels, squirrelpox virus accelerates the process of replacement and has therefore been a crucial factor in the decline of red squirrels in the UK.' The impact of the Maxwell Institute's research [1] was therefore to highlight potential risks associated with the infection. Its findings were incorporated in the 'Scottish Red Squirrel Action Plan 2006-2011' [8], launched by SNH, **Forestry Commission Scotland** (FCS) and the **Scottish Government**, one of the aims of which is to halt the decline of red squirrel populations and slow down or contain the spread of deadly squirrelpox. Control strategies were implemented on the ground from 2008. In practice in regions where disease incidence is reported in greys they are trapped and removed with the aim of eradicating squirrelpox (locally).

This work is ongoing with the Government and NGO sectors coordinating their effort through **Saving Scotland's Red Squirrel** (SSRS) - http://www.scottishsquirrels.org.uk/). A further impact since 2008 was the initiation of targeted control of greys aimed at slowing and containing the spread of squirrelpox and the establishment of 18 red squirrel strongholds, totalling approximately 100,000 hectares, throughout Scotland, in which greys and squirrelpox can be excluded. The SSRS budget to implement squirrelpox control is approximately £400K per year (similar schemes run in England and Wales). Therefore as a result of [1] disease management is at the forefront of red squirrel conservation strategies [8-10] with red squirrel stronghold locations chosen to minimise infection risk.

In 2013 White entered a partnership agreement with SNH to provide 'A Modelling Assessment of Control Strategies to Prevent/Reduce Squirrelpox Spread'. The modelling assessment extended the framework of [1] and assessed current grey squirrel control efforts indicating that they had reduced the rate of spread of squirrelpox but would not prevent the disease from expanding to occupy most regions of Southern Scotland over the next 5-10 years. The work highlighted how the spread of disease to the currently disease-free high density populations of Central Scotland may be prevented by targeting grey control to specific dispersal routes (pinch-points). The model study also assessed the impact of potential grey squirrel control beyond the Central Lowlands of Scotland that will act as a contingency should squirrelpox reach the Central Scotland populations, the impact of squirrelpox at the interface between red and grey populations in Highland Scotland and the viability of control measures at regional strongholds that support red squirrel populations. The model results were presented at the SSRS Steering Group meetings in 2013 and were fundamental in shaping an options paper [10] that outlined the proposed strategies for protecting red squirrels from 2014. The options paper reports that 'Grey squirrel control is responding to the modelling work … where control in the identified pinch-point areas is already taking place', and the SSRS preferred option intends to 'increase resourcing to allow greater coverage of the remaining pinch-point areas' outlined by the model study. Thus, the model results are fundamental in shaping current and future policy and for planning the allocation of resources.

A key strategic stronghold for red squirrel conservation is the Isle of Arran. In 2012 the Arran Red Squirrel Assessment, FCS [11] stated that research should 'evaluate the risk of disease spread on Arran through the use of modelling approaches. The paper [1] highlighted the threat posed by squirrelpox on the population abundance of red squirrels. They showed that a squirrelpox epidemic could lead to the rapid reduction in red abundance.' The Maxwell Institute is assisting FCS with the development of modelling strategies to assess the disease risk posed to red squirrel populations on Arran. The investigation extends the mathematical framework developed in [1] and designs strategies that limit the spread and severity of squirrelpox outbreaks.

5. Sources to corroborate the impact

[2] Williams, F., *et al.*, The Economic Cost of Invasive Non-Native Species on Great Britain, CABI Report, (2010). http://www.maths.ed.ac.uk/~mthdat25/conservation/The_Economic_Cost_of_Invasive_Non-Native_Species_to_Great_Britain

[3] 'UK Red Squirrel Drop: Are Gray Squirrels to blame.' *National Geographic*, May 2 (2003). http://news.nationalgeographic.co.uk/news/2003/05/0502_030502_redsquirrels.html

[4] 'Conquest by Disease Carriers.' Editor's research highlights, *Science*, **299**, 1947 (2003). http://dx.doi.org/10.1126/science.299.5615.1947c

[5] 'Counting on squirrels for help.' *The Scotsman*, January 14, page 42 (2005). http://www.scotsman.com/news/sci-tech/counting-on-squirrels-for-help-1-671374

[6] 'New research may be able to save the declining red squirrel population - and it's all done with maths.' *The Guardian*, 22 February, (2005). http://www.theguardian.com/education/2005/feb/22/highereducation.workinprogress

[7] Poulsom, L., Griffiths, M., Broome, A. and Mayle, B, Identification of priority woodlands for red squirrel conservation in North and Central Scotland: a preliminary analysis, *Scottish Natural Heritage Commissioned Report No. 089* (ROAME No. F02AC334) (2005). http://www.snh.org.uk/pdfs/publications/commissioned_reports/f02ac334.pdf

[8] Scottish Red Squirrel Action Plan 2006-2011. Forestry Commission Scotland, Scottish Executive, Scottish Natural Heritage. http://www.snh.gov.uk/docs/A40765.pdf

[9] A Modelling Assessment of Control Strategies to Prevent/Reduce Squirrelpox Spread. This is a partnership project between Heriot-Watt University and Scottish Natural Heritage. Copies available from SNH employee who can also corroborate the factual claims of the impact of this modelling work on policy.

[10] Project Manager, SWT can provide details of the options paper presented at the SSRS steering group meetings in 2013 and corroborate how the mathematical modelling results are being used inform current policy and practice in Scotland.

[11] Arran Red Squirrel Assessment. 2012. Forestry Commission Scotland. Available from Ecological Consultant to the Forestry Commission Scotland and/or District Forrester, Forestry Commission Scotland.

Note: should links to web pages be broken, please use the website http://www.maths.ed.ac.uk/~mthdat25 to access pdf versions of the pages