Institution: Maxwell Institute for Mathematical Sciences		
Unit of Assessment: UoA 10 – Mathematical Sciences		
Title of case study: Mathematical modelling of the UK squirrel system directs conservation and forest management policy and practice to protect endangered red squirrels.		
Period when the underpinning research was undertaken: 2003-2020		
Details of staff conducting the underpinning research from the submitting unit:		
Name(s):	**Role(s) (e.g. job title):**	**Period(s) employed by submitting HEI:**
Andrew White	Professor of Mathematics	1999 - date
Period when the claimed impact occurred: 1 Aug 2013 – 31 Dec 2020		
Is this case study continued from a case study submitted in 2014? No		

1. Summary of the impact

Mathematical modelling research by Prof White at the Maxwell Institute has been used to direct policy and practice to conserve red squirrels – a protected species in the UK – from squirrelpox virus carrying invasive grey squirrels. The research demonstrated that the red squirrel conservation policy used up to 2015 would not be sufficient to contain squirrelpox in the UK. Working with stakeholders, his research was the trigger for a radical change in policy to protect red squirrels in priority areas in the UK, directly informing the 'Scottish Strategy For Red Squirrel Conservation (2015)' and the Red Squirrel Survival Trust policy to protect red squirrels on Anglesey.

Prof White's research has also evaluated red squirrel population viability under different forest management scenarios. This research underpins commissioned reports produced by Prof White for the Forestry Commission that have had a direct impact on current and future forest management practice in the UK that balance timber production and red squirrel conservation.

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 red squirrel is a protected species in the UK (Wildlife and Countryside Act 1981) and was one of the first species identified for conservation under the UK Biodiversity Action Plan (Conserving Biodiversity – The UK Approach, DEFRA 2007). In addition to the threat grey squirrels cause to red squirrel conservation, they also negatively impact the health of the UK's trees and woods through bark stripping, with greys causing significantly more damage than red squirrels. This has an impact on forestry and the UK's policy to expand woodland cover. A European Squirrel Initiative report conservatively estimates a 'GBP40 000 000 per annum timber loss from grey squirrels' in England alone.

Prof White leads a research group based at the Maxwell Institute for Mathematical Sciences that works with ecological, conservation and forest management partners to develop spatial, deterministic and stochastic mathematical frameworks that can be used to address key issues related to red squirrel conservation. The mathematical modelling research provided evidence that squirrelpox infection was a key driver of the rapid replacement of red squirrels by greys in the UK (3.1). 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. The deterministic model of competition and disease for the UK squirrel system (3.1) underpins a spatial, stochastic model that includes a representation of the real habitat composition taken from up-to-date digital habitat inventory maps (3.2-3.5). The models were developed in collaboration with conservation agencies and facilitated through a NERC Innovations Project Grant (NE/MO21319/1), allowing the modelling research to inform key policy and management decisions to protect red squirrels. This research work has been able to predict the spread of squirrelpox throughout Scotland and advise how grey squirrel control practice can be modified and targeted to specific locations to prevent squirrelpox expansion (3.2). The model

system was also used to show that the exclusion of grey squirrels from priority regions for red squirrel conservation would be sufficient to protect reds from replacement (3.3). These novel results also showed that squirrelpox can spread from greys outside to reds inside a priority region leading to periodic outbreaks of infection (but not endemic persistence) in the red populations and that the red squirrel population density could return to pre-infection levels following an outbreak of infection (3.3).

The model complexity was increased to represent seasonal demographics for red squirrels and to include tree seed crop dynamics and was used to assess red squirrel population viability under different forest management (felling and restocking) scenarios for red squirrel reserves in England (3.4). Results highlighted how red squirrel survival could be significantly increased by felling and restocking adjustments, and improving connectivity between the adjacent forests. The research provided an exemplar of how modelling can help managers objectively balance the differing pressures of multipurpose forestry. The model was further enhanced by comparing results to field data from Anglesey, Wales in which grey squirrels were removed and red squirrels reintroduced (3.5). This allowed the model to include a validated representation of grey squirrel population control and results could be interpreted in terms of 'trapping effort hours' which is the practical resource unit used for grey squirrel control management. This development led to commissioned research to assess the level of control required to protect red squirrels in key locations in the UK.

3. References to the research

(3.1): Tompkins, D. M., White, A. R. & Boots, M. (2003). Ecological replacement of native red squirrels by invasive greys driven by disease. Ecology Letters. 6: 189-196. (doi.org/10.1046/j.1461-0248.2003.00417.x, Journal Impact factor (JIF) - 8.7).

(3.2): White, A., Lurz, P. W. W., Bryce, J., Tonkin, M., Ramoo, K., Bamforth, L., Jarrott, A. & Boots, M. 2016. Modelling disease spread in real landscapes: Squirrelpox spread in Southern Scotland as a case study. Hystrix, the Italian Journal of Mammalogy 27: 1. (doi.org/10.4404/hystrix-27.1-11657, JIF - 1.5).

(3.3): White, A., Bell, S.S., Lurz, P.W.W. and Boots, M. 2014. Conservation management within strongholds in the face of disease-mediated invasions: red and grey squirrels as a case study. Journal of Applied Ecology. 51: 1631-1642. (doi.org/10.1111/1365-2664.12274, JIF - 4.6).

(3.4): Jones, H. E. M., White, A., Geddes, N., Clavey, P., Farries, J., Dearnley, T., Boots, M. & Lurz, P. W. W. 2016. Modelling the impact of forest design plans on an endangered mammal species: the Eurasian red squirrel. Hystrix, the Italian Journal of Mammalogy 27: 1. (doi.org/10.4404/hystrix-27.1-11673, JIF - 1.5).

(3.5): Jones, H.E.M, White, A., Lurz, P.W.W., & Shuttleworth, C.M. 2017. Mathematical models for invasive species management: Grey squirrel control on Anglesey. *Ecological Modelling*. 359: 276-284. (doi.org/10.1016/j.ecolmodel.2017.05.020, JIF - 2.5).

4. Details of the impact

Impact on Red Squirrel Conservation Policy in Scotland

The mathematical research in (3.2,3.3) led to commissioned reports [5.1,5.2] undertaken by Prof White for Scottish Natural Heritage and the Forestry Commission Scotland which delivered management advice for the protection of red squirrel populations exposed to squirrelpox virus. Prior to this work, conservation policy had focussed on control in regions where grey squirrels tested positive for squirrelpox. This had reduced grey numbers in local areas but had not prevented disease spread or increased red squirrel numbers. The work showed that it is extremely challenging to prevent the spread of the squirrelpox into areas where grey squirrels are already well-established and, importantly, that squirrelpox will not persist in red squirrel (only) populations. Saving Scotland's Red Squirrels (SSRS), who are responsible for red squirrel conservation in Scotland, state [5.3] that Prof White's work "*had impact both on policy through inclusion in the Scottish Strategy for Red Squirrel Conservation (2015) [5.4] and practice as SSRS recognised the difficulty in containing squirrelpox as the trigger for a radical change of strategy that protects remaining red squirrel populations in Priority Areas for Red Squirrel Conservation (PARCs) in southern Scotland*". Furthermore, SSRS indicate that our

"*mathematical modelling work adds a scientific underpinning and rationale for the use of grey squirrel control to protect red squirrel population"* which is coordinated by local communities in and around PARCs and has led to an increase in red squirrel distribution and abundance [5.3]. The modelling work continues to direct red squirrel conservation policy in Scotland through commissioned research undertaken by Prof White for Saving Scotland's Red Squirrels in 2017 [5.5] to determine the level and location of grey squirrel control to prevent further spatial expansion of the grey squirrel distribution beyond the Highland protection line in Scotland and for the Forestry Commission Scotland in 2018 [5.6] to examine the level of grey control required to protect red squirrels in Southern Scotland. The modelling research (3.2,3.3),[5.1,5.2,5.8] was promoted by stakeholders and led to extensive coverage on BBC radio, BBC online and in national newspapers (The Times, The Herald, The Scotsman) [5.7].

Impact on Forest Management Practice in Northern England

Prof White's modelling research (3.2,3.3) was extended to answer specific red squirrel conservation issues faced by forest management practitioners. Working with Stakeholders in the Forestry Commission (FC), future felling and restocking scenarios for Kidland and Uswayford forest (2962 ha of forest in north-east England) were used to drive the mathematical model and led to predictions of red squirrel population viability (3.4). Quoting from the Planning and Environment Manager for the North England Forest District of the Forestry Commission [5.8] "*The findings in the report (3.4) highlighted how the (original) proposed forest design plans could lead to a risk of red squirrel extinction (particularly in Uswayford). As a result alternate felling and restocking regimes were developed by FC and tested in the model. The model results had a direct impact on the final forest design plans for the Uswayford and Kidland forest (for 2017 - 2041) which are outlined in the Cheviot Forest Plan (FC 2015) and which represent the optimum in terms of silviculture and red squirrel viability. The combined FC and Maxwell Institute modelling study therefore played a key role in the red squirrel conservation strategy in these forests.*"

Impact on Grey Squirrel Control Strategy on Anglesey

Prof White further developed the model to include a realistic representation of grey squirrel control effort by fitting the model to field observations for the removal of grey squirrels and reintroduction of red squirrels on the Isle of Anglesey, Wales (3.5). The model showed that the most effective strategy to remove grey squirrels would focus the initial trapping effort on high density regions and then spread the trapping effort to all regions where greys are present. The model also showed that the best strategy to prevent grey squirrel re-invasion of Anglesey would focus trapping efforts on the mainland side of the Britannia bridge and use high levels of targeted trapping on Anglesey when grey squirrel sightings are reported. The research findings were adopted by the Red Squirrel Survival Trust (RSST) in 2017 as the strategy to protect red squirrels on Anglesey who state [5.9] that "*the modelling work continues to be used to determine the optimal strategy to prevent the re-invasion of Anglesey by grey squirrels and has therefore had an impact on the RSST conservation practice to protect red squirrels on Anglesey – which are still thriving. The modelling work also played a key role in providing evidence-based research to convince the public of the ongoing need to control grey squirrels*". The applicability of our mathematical research is emphasised by Dr Craig Shuttleworth of the Red Squirrel Survival Trust who states [5.9] that "*the collaboration between ecologists, conservation practitioners and mathematical modelling provided a template for how interdisciplinary research can provide solutions to real world problems for the protection of endangered species and therefore the maintenance of biodiversity in the UK*."

Impact on Forest Management Practice in Scotland

Forest and Land Scotland (formally the Forestry Commission Scotland) commissioned Prof White to adapt the model (3.4,3.5) to determine the viability of 19 designated red squirrel strongholds in Scotland [5.10,5.11]. The model compared red squirrel viability under stronghold forest management (SHM) plans (where tree species composition is altered to discourage grey squirrels) and UK forest standard (UKFS) management plans. The research showed that some designated strongholds were unsuitable for red squirrel protection, that other regions may provide natural strongholds (where reds are protected under UKFS plans) and that north of the Highland red squirrel protection line there was no benefit to red squirrel abundance under SHM compared to UKFS. Forestry and Land Scotland state [5.12] that "*reconciling the SHM policy*

with other management objectives, fluctuating timber markets and wind-blow events, requires significant additional management input and can affect income from timber sales. Furthermore, the single-species focus of the SHM policy has consequences for other environmental work that aims to increase ecosystem diversity. The results of the research by Professor White are therefore important for Forestry and Land Scotland and will have a direct impact on management across large parts of the national forest estate. The research findings will allow a future focus on natural strongholds under the UKFS approach and this will afford more flexibility to conserve red squirrel populations whilst simultaneously delivering other forest management objectives."

5. Sources to corroborate the impact

[5.1] White, A. and Lurz, P.W.W. 2014. A modelling assessment of control strategies to prevent/reduce Squirrelpox spread. Scottish Natural Heritage Commissioned Report No. 627 (see summary pp i-ii). https://www.nls.uk/e-monographs/2014/627.pdf

[5.2] Lurz, P.W.W., White, A., Meredith, A., McInnes, C. and Boots, M. 2015. Living with pox project: Forest management for areas affected by squirrelpox virus. Forestry Commission Scotland Commissioned Report (see Exec. Summary, pp 3-6). http://www.macs.hw.ac.uk/~awhite/LivingWithPoxReport.pdf

[5.3] Letter of support from the Project Manager for Saving Scotland's Red Squirrels and the Manager of the Wildlife Management Team for Scottish Natural Heritage.

[5.4] Scottish Strategy for Red Squirrels. 2015. Scottish Squirrel Group (see Section 2.2) https://www.nature.scot/scottish-strategy-red-squirrel-conservation-june-2015

[5.5] White, A., Lurz, P.W.W and Boots, M. 2017. Grey squirrel control along the highland line. Report for Scottish Natural Heritage and the Scottish Wildlife Trust (see Exec Summary, p 3). http://www.macs.hw.ac.uk/~awhite/SWT_SNH_HighlandLine_FinalReport.pdf

[5.6] White, A. and Lurz, P.W.W 2018. Grey squirrel control in southern Scotland: A model analysis. Forestry Commission Scotland Commissioned Report (see Exec. Summary, p 3). http://www.macs.hw.ac.uk/~awhite/FES_SouthScotlandReport.pdf

[5.7] Media coverage. Weblinks at http://www.macs.hw.ac.uk/~awhite/squirrels/media.html

[5.8] Letter of support from the Planning and Environment Manager for the North England Forest District, Forestry Commission.

[5.9] Letter of support from the Conservation Advisor to the Red Squirrel Survival Trust.

[5.10] Slade, A. White, A. and Lurz, P.W.W 2019. Evaluation of Red Squirrel Stronghold Forest Management. Forest and Land Scotland Commissioned Report (see Exec. Summary, pp 1-2). http://www.macs.hw.ac.uk/~awhite/FLS_Stronghold_Evaluation_Report_Part1.pdf

[5.11] Slade, A. White, A. and Lurz, P.W.W 2019. Identification of Natural Red Squirrel Strongholds. Forest and Land Scotland Commissioned Report (see Exec. Summary, pp 1-2). http://www.macs.hw.ac.uk/~awhite/FLS_Stronghold_Evaluation_Report_Part2.pdf

[5.12] Letter of support from the Wildlife Ecologist for Forest and Land Scotland.