

# A spatially explicit population model to compare management using culling and fertility control to reduce numbers of grey squirrels

S. Croft<sup>\*</sup>, J.N. Aegerter, S. Beatham, J. Coats, G. Massei

National Wildlife Management Centre, Animal and Plant Health Agency, Sand Hutton, NY, UK

## ARTICLE INFO

### Keywords:

Contraception  
Cost  
Individual-based model  
Invasive alien species  
Population management

## ABSTRACT

In the UK the now widespread non-native grey squirrel produces problems for the forestry industry through damage from bark stripping and threatens the survival of native species most notably the red squirrel which, mainly as a result of resource competition and transmission of infection, has suffered dramatic declines. Reducing grey squirrel numbers is essential to decrease this species' ecological and environmental impact.

Using an individual-based model operating in a fine scaled landscape of well-mixed woodlands with reliable seed production we develop novel effort-based mechanisms explicitly representing the probabilistic interaction of individual squirrels with either traps or bait hoppers to capture the density-dependant efficiency of culling and fertility control respectively. We also integrate a habitat-based resistance to inter-patch movement to describe more realistically the source-sink dynamics in regional scale populations.

We use this new framework to compare the relative effort of population management at a landscape scale using both culling and fertility control, alone and combined as part of an integrated, sequential, approach. We also exploit our spatially-explicit framework to demonstrate how we might identify neighbourhoods within our study area where management may be easier (quicker and cheaper) or more difficult (sub-populations resistant to management), to enable the prediction of an optimal spatial and temporal deployment of management effort.

Our results agree with previous studies on the relative efficiency of culling in eradicating squirrels, as well as on the substantial "costs" of this approach. Despite an assumption of lower deployment costs, our findings suggest that, at least for the initial squirrel densities assumed, fertility control alone is unlikely to achieve rapid enough reduction to prove a viable cost-effective alternative to completely replace culling. However, when applied to the low density populations following short-term culling, eradication could be achieved within the same timescales as continuous culling alone but with substantially lower costs.

## 1. Introduction

In the UK non-native grey squirrels (*S. carolinensis*) occupy most of mainland England and Wales and cause substantial economic and environmental impacts. These include widespread damage to forestry through bark stripping (Mayle and Broome, 2013; Nichols et al., 2016) as well as potential predation on birds (Bonnington et al., 2014). At more local scales, the species poses an ongoing threat to the native red squirrel (*Sciurus vulgaris*), mainly through resource competition and transmission of diseases, such as the Squirrelpox virus, leading to substantial population decline (Rushton et al., 2000; Gurnell et al., 2004). Reducing the density of grey squirrels is key to mitigating their national or regional scale impacts (Bertolino et al., 2014; Schuchert et al., 2014; Goldstein et al., 2016). Concurrently, a reduction in local squirrel

densities is a pre-requisite to managing the re-colonisation of red squirrels across parts of their former range.

Although most previous modelling studies (e.g. Rushton et al., 2002) have focused on grey squirrel management in support of red squirrel conservation other aspects of population control merit attention. These include the costs of achieving and maintaining low density populations of grey squirrels at large scales (e.g. regions), to minimise the economic or environmental burdens of this species. In addition, very few studies have explored where, within extensive regions subject to integrated grey squirrel management programmes, local eradication is quick to achieve and cost-effective to maintain, and where resistance to the removal of grey squirrels is likely to be greatest, justifying the deployment of additional management tools or resource.

Culling, traditionally used to reduce grey squirrel numbers, using

<sup>\*</sup> Corresponding author.

E-mail address: [simon.croft@apha.gov.uk](mailto:simon.croft@apha.gov.uk) (S. Croft).

marksmen, kill trapping, or live-trap and despatch is generally recognised as expensive and laborious and ill-suited to simultaneous deployment across large geographical scales. For instance, the cost of culling 6397 grey squirrels for 17 years in Anglesey, in addition to removing approximately 3200 animals from the adjacent mainland population and implementing habitat restoration and translocation of red squirrels, was around £1 million (Derbridge et al., 2016). Poisoning grey squirrels, using anticoagulants, once employed to protect tree crops, is now illegal in the UK. Culling alone has failed in most areas to bring grey squirrels under control and as a result, the UK harbours a population of approximately 2.5 million (Croft et al., 2017; Mathews et al., 2018) which continues to spread. In addition, public antipathy towards lethal methods of squirrel control has increased demand for alternative options, particularly in contexts such as urban areas where lethal control may either be impractical, or opposed by local communities (Barr et al., 2002; Bremner and Park 2007; Dunn et al., 2018). For example, in a recent survey on the UK public's acceptability of several population control methods for grey squirrels, Dunn et al. (2018) found that traditional lethal methods were regarded by the public as least acceptable, whilst contraception was the preferred method, supported by 63% of the 3758 respondents.

Fertility control has the potential to reduce population size and the rate of population recovery after culling (Shi et al., 2002; Massei and Cowan 2014). Ideally, this method should be based on delivering oral contraceptives in baits that are accessible to the target species only (Fagerstone et al., 2010; Massei and Cowan 2014). Although oral contraceptives are not available for grey squirrels, work is in progress to develop these drugs. In contexts where culling or delivery of injectable contraceptives are not feasible or economically viable, the availability of oral contraceptives would add considerably to the options available for wildlife managers. This study is part of a larger 5-year project aimed at developing and delivering oral contraceptives for grey squirrels (Massei 2018), both as a management tool in the absence of red squirrels, and also where they are in sympatry with red squirrels. This programme includes the development of new oral contraceptives delivered in baits, and the refinement of existing species-specific bait delivery devices (e.g. feed hoppers; Pepper and Stoker 1993).

Spatially-explicit population modelling offers a tool to test a variety of management options (variations in method, timing and intensity of deployment) and landscape scenarios (open/closed etc.) at scales beyond those practical for empirical assessment. In this context, as long as parameter estimates are well supported by experimental observation such models are invaluable in assessing the potential effects of fertility control on grey squirrel populations, alone or in conjunction with culling, and the effort and costs associated with regional population control strategies. The effect of fertility control and culling on non-native squirrel populations has been explored in previous studies (Rushton et al., 2002; Krause et al., 2014; Goldstein et al., 2016), though often methods are compared separately, or in simple combination rather than sequentially. Furthermore, little attention has been paid to how the distribution of woodlands across extensive landscapes might affect management outcomes. The specific aim of the initial study we present here was to apply a spatial population model to assess the relative effort required to manage and eradicate grey squirrels through culling, fertility control, or their integration, using a novel combination of modelling tools supported by parameter estimates from recent fieldwork.

## 2. Methods

### 2.1. Model landscape

For this study we nominally based our model landscape on a 600 km<sup>2</sup> region of north Cumbria which, through the analysis detailed in Appendix A, we identified to be relatively isolated with any immigration/emigration likely to be slow and therefore could reasonably be considered as being closed. Within this study area we defined distinct habitat

patches as contiguous blocks of woodland using a 25 m resolution land cover map (LCM2007; Morton et al., 2011); each explicitly represented by a fixed measure of its value to squirrels (carrying capacity), the area of the patch and a list of individual squirrel inhabitants.

Population carrying capacity for each patch was assigned based on the specific composition of deciduous and coniferous woodland, computed by applying type-specific estimates from the literature (Mathews et al., 2018) and our own field data (Appendix C). In a comprehensive literature review Mathews et al. (2018) reported mean densities of 1.9 ( $n = 21$ ) and 0.31 ( $n = 38$ ) squirrels/ha for deciduous and coniferous woodlands respectively. Beatham et al. (see Appendix C) recorded densities of 3.9 and 6.6 squirrels/ha estimated using capture-mark-recapture (CMR) in two 8 ha blocks of mixed deciduous woodland. Calculating the weighted mean of all estimates yielded a new mean density of 2.2 squirrels/ha which we applied for our description of mixed-deciduous woodland, the density applied to coniferous woodland remained 0.31 squirrels/ha. The landscape matrix surrounding woodland patches provided no contribution to squirrel numbers. This included urban areas where non-zero densities have been reported (Mathews et al., 2018) but are strongly correlated to the availability of greenspace (i.e. woodland) (Bonnington et al., 2014) which we suggest is accurately encapsulated within our definition of woodland at a 25 m resolution.

The reader should note that we do not consider inter-annual fluctuations in squirrel population as a result of seed production. The frequency and impact of masting on squirrel populations can vary greatly across individual tree species (Slade et al., 2019). However, within the broad classifications available for much of Britain (England) it is difficult to accurately describe this variation as different compositions of trees will inherently produce different patterns. Here, we consider tree species within a class to be well-mixed (this is relatively typical of British woodland, particularly broadleaf) such that the asynchrony in masting maintains relatively stable food resource and therefore populations of squirrels; see Appendix A for further justification of this modelling choice.

To model squirrel movements, each patch also required information about its local surroundings; specifically, a list of neighbouring patches and corresponding likelihood of movement between them. Rushton et al. (1997, 2002) defined this likelihood based on Euclidean distance alone assuming that squirrels can disperse up to a fixed maximum distance. Recent novel approaches investigating dispersal pathways (Stevenson-Holt et al., 2014; Flaherty 2016a; Flaherty et al., 2016b) offer an opportunity to incorporate considerations for how the composition of the landscape matrix between patches may also influence connectivity, refining definitions of dispersal. Following the process outlined by such studies we fitted a species distribution model (SDM; e.g. Phillips and Dudík, 2008) and applied the output to inform resistance scores for various non-woodland land classes (expressed as the equivalent distance that would be travelled in woodland per unit travelled in non-woodland); see Appendix A for full details. We used the derived resistance scores (Table 1) to calculate inter-patch cost-distances reflecting the porosity of the landscape in relation to woodland. To account for the finite dispersal distance of squirrels we delineated surfaces according to a maximum cost-distance threshold; this defined the local neighbourhood for each patch. Other patches intersecting this neighbourhood formed the list of neighbours for a patch. Corresponding likelihoods of travel to these neighbours was computed as the relative proportion of summed cost-distance across the neighbourhood that lay within the footprint of a neighbouring patch.

### 2.2. Population model

#### 2.2.1. Overview

To simulate grey squirrel populations we adapted the agent-based modelling approach outlined by Rushton et al. (1997, 2002) describing the life histories of individual squirrels, represented with an

**Table 1**  
Predicted habitat suitability and landscape resistance.

Class	Description	Suitability	Resistance Expert opinion	Estimated from suitability
1	Woodland (habitat)	0.72	0 – 5	1
2	Arable/Horticulture	0.22	20	13
3	Improved/Amenity grassland	0.44	10	4
4	Semi-natural grassland (inc. Fen, Marsh and Swamp)	0.29	10 - 20 (Swamp 100)	9
5	Mountain, Heath and Bog	0.07	20 - 50	50
6	Water margin	0.44		4
7	Coastal	0.07	50	48
8	Urban	0.65	5	2

assigned gender (sex ratio assumed 50:50 at birth), an age and life stage (juvenile, defined as <1 year or adult), the habitat patch where they live and whether they have been subject to successful contraception. Individuals were updated simultaneously on an annual time step by applying algorithms (Fig. 1) to represent various ecological processes (survival, reproduction, dispersal) and population management methods (culling and fertility control) as described below.

2.2.2. Ecological processes

Individual survival was tested at each time step by comparing a value selected from a random uniform distribution on the interval [0,1] against a fixed threshold of success. Any individuals failing this test (random numbers greater than the fixed threshold; see Parameterisation for threshold value) were considered dead and removed. As offspring are initially dependant on their mothers, we performed this test prior to any relating to reproduction to account for the consequent loss of reproductive effort for maternal fatalities realised throughout most of the

year.

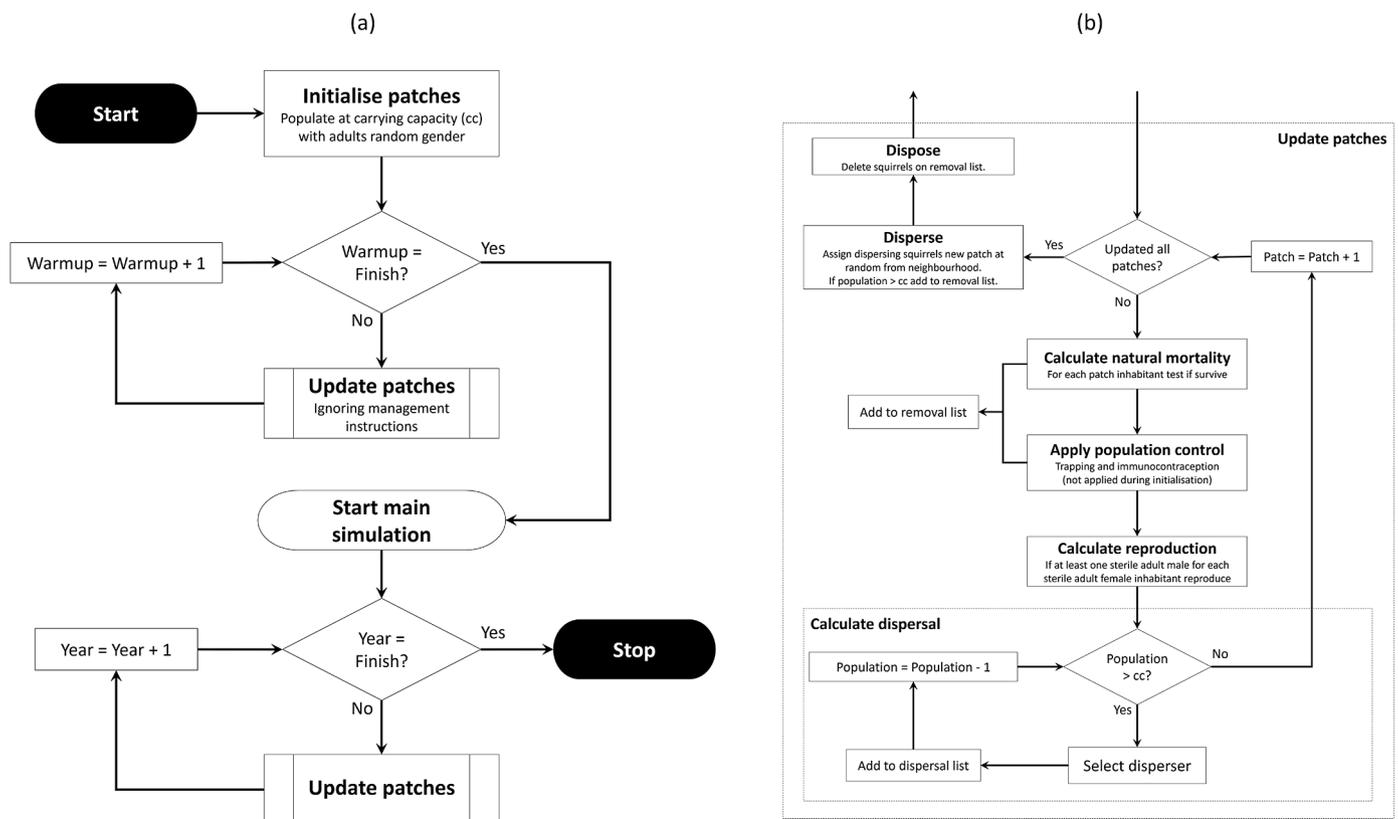
Only fertile adult females were considered to reproduce and to do so required at least one fertile adult male to be present in the same patch. Each candidate female could produce up to two litters per year with fixed parameter values defining the probability of either zero, one or two. For each litter produced, we chose a litter size at random from a truncated Poisson distribution, limited between one and eight offspring (Koprowski et al., 2016), with defined mean (Table 2).

As argued by Rushton et al. (1997, 2002) dispersal only occurred when a patch was above carrying capacity forcing individuals to either disperse or endure increased levels of mortality as a result of the lack of resources. Juveniles were considered most likely to disperse and were selected at random according to a sex-based bias (Goldstein et al., 2016). If patch populations still exceeded the patch carrying capacity, adults were randomly subjected to the same routine until the patch capacity was realised. All of the dispersing squirrels from every patch were added to a single list and shuffled to produce a random dispersal order. The destination of each squirrel was selected at random from those available (i.e. the list of neighbours for their current patch) according to a weighted distribution based on connection strength such that dispersal is most likely to close neighbours (Rushton et al., 2002). If a squirrel's destination patch was at or above its own carrying capacity dispersal was considered unsuccessful and the animal was assumed to die.

Animals accumulated their chronological age with each time step, and for grey squirrels in the UK juveniles could be assumed to have reached reproductive maturity in the year following their birth. Squirrels exceeding a maximum age (Table 2) were removed from the population.

2.2.3. Population management methods

We considered two management methods: removal using single-capture live cage traps; and oral contraception using bait hoppers. Unlike other models, we did not simulate control as a fixed proportionate



**Fig. 1.** Model diagram. Conceptual illustration of the model framework detailing: (a) the overall algorithm; (b) the subroutine used to update patch populations.

**Table 2**  
Parameter values used in simulations.

Parameter	Range	Value	References
Adult survival probability	0.4 - 0.8	0.7	Rushton et al. (2002, 2006); Goldstein et al. (2016)
Juvenile survival probability	0.2 - 0.6	0.4	Rushton et al. (2002, 2006); Goldstein et al. (2016)
Probability of adult female reproducing	0.5 - 1.0	0.9	Rushton et al. (2002, 2006)
Probability of adult female producing second litter	0.1 - 0.67	0.4	Rushton et al. (2002, 2006); Goldstein et al. (2016)
Litter size	2 - 8	3	Rushton et al. (2002, 2006); Goldstein et al. (2016); Koprowski et al. (2016)
Female to male dispersal ratio		1:1.5	
Maximum lifespan (years)		9	Koprowski et al. (2016)
Average home range size (hectares)		5	Koprowski et al. (2016)
Maximum dispersal distance (km)	1 - 20	3	Lurz et al. (2001); Rushton et al. (2002); Stevenson-Holt et al. (2014)
Trap encounter probability		0.05	Beatham et al. (Appendix C)
Hopper encounter probability	0.05 - 0.1	0.05	Beatham et al. (Appendix C)
Hopper competition (probability of access at one hopper per squirrel)		0.775	Beatham et al. (Appendix C)
Control effort (traps or hopper per day)	0.5 - 4		Mayle et al. (2007); Schuchert et al. (2014); Gurnell & Pepper (2016)
Control duration (total trapping days per year not including baiting)	36 - 45	45	Rushton et al. (2002); Mayle et al. (2007); Gurnell & Pepper (2016)
Probability of sterilisation	0 - 1		
Probability of recovery from fertility control (per year)		1	

reduction in the population (Rushton et al., 2002; Goldstein et al., 2016) but instead explicitly describe an effort-dependant mechanism, thereby allowing a more responsive and accurate reflection of interaction rates across changing densities or contrasting patches. For both culling and fertility control we defined “efficacy” based on the probability of an individual squirrel interacting with a particular device (trap or hopper) on any given day (from here on referred to as “encounter probability”), and “effort” by the density of devices and the duration of their deployment per year. Based on our empirical data (Appendix C) this probability of interaction remained constant during removal despite less competition for resources suggesting that our necessary simplification regarding seed production is unlikely to impact this aspect of the model.

To account for the use of single-capture traps we simulated interactions with squirrels from the perspective of the trap so as to realistically represent reductions in availability as traps are filled before being reset every day (Mayle et al., 2007). For each specified trap day, we performed a stochastic test against the density-dependant probability of a successful capture defined as  $1-(1-e_t)^s$  where  $e_t$  is the encounter probability for a trap and  $s$  is the average number of squirrels within a home range of the trap, i.e. the population which are likely to interact with it, computed as the product of the average squirrel density within the patch and the average area describing a squirrel home range. If capture was successful then we selected a squirrel at random to remove from the population.

Unlike traps, hoppers can be used by many squirrels. As such we instead simulated interactions with hoppers, and by proxy consumption of oral contraceptive, from the perspective of a squirrel. We performed a stochastic test against a variable probability of success to determine if an individual became infertile. The probability of successful contraception was the product of several components. Firstly, the delivery effort i.e. the number and period of hopper deployment (hopper days) which affects the likelihood and speed, with which individuals fed from hoppers.

This was reflected in a similar equation to trapping as  $1-(1-e_h)^h$  where  $e_h$  is the encounter probability for a hopper and  $h$  is the number of hopper days within an average squirrel home range (Table 2). Once squirrels find hoppers, experimental evidence indicates frequent and repeated re-use during a deployment (Appendix C) supporting the prospect of the delivery of an effective dose of contraceptive across a single deployment. Secondly, unlike trapping where population structures are perturbed by removal, the use of hoppers is not considered to interfere with squirrel social dynamics or competition for resources, which might result in some subordinate individuals being denied access to hoppers. This type of behaviour was observed by Beatham et al. (Appendix C) during field trials using a rhodamine bait marker to track hopper use suggesting a clear relationship between the maximum proportion of animals frequently using hoppers and the ratio of squirrels per hopper. We represented this by fitting an equation of the form  $(1-p)^{s:h}$  where  $p$  is the probability of a squirrel being denied access to all hoppers at a squirrel to hopper ratio of 1:1, and  $s:h$  is ratio of squirrels to hoppers (density of squirrels within a patch divided by the density of hoppers). Finally, we considered scenarios where a putative contraceptive may not be completely effective and included a component representing the probability of successful contraception given sufficient dose. Combining these components the probability of infertility for each individual was therefore calculated as  $S(1-p)^{s:h}(1-(1-e_h)^h)$ . We make the conservative assumption (based on the lack of experimental evidence) that squirrels were only infertile for a year after treatment following which individuals, if not subsequently re-treated, were regarded as fertile and allowed to reproduce.

### 2.3. Parameterisation

Parameter values were selected from published literature and from previous modelling studies (Table 2). For simplicity and to mimic the boundary conditions of the wider GB squirrel population we adopted a maximum dispersal distance (Table 2) from within the range outlined by Lurz et al. (2001) such that our chosen study area could be considered closed. Realistically, we recognise it is unlikely that any populations within the current GB distribution are absolutely closed and indeed previous studies have suggested pathways through which the initial invasion of our chosen region may have occurred (Stevenson-Holt 2012). We do not dispute the existence of such pathways but note that the cost of movement along them is sufficiently high, and therefore frequency of movement sufficiently low, that any leakages at the edges of our study area are so small they can be ignored without detriment to the experimental investigation.

Trap encounter probability, defined as the probability of an individual squirrel interacting with a trap on any given day, was derived from experimental data on the relationship between estimated population size (CMR) and trapping success (average proportion filled per day) collected by Beatham et al. (described in Appendix C). Since the probability of all squirrels failing to enter the trap is multiplicative we determined the probability of an individual squirrel failing, or avoiding, the trap as the probability of failure to the  $n^{\text{th}}$  root where  $n$  is the average squirrel population in the close vicinity of traps (home range; Table 2). This suggested a trapping probability for any given squirrel of 0.05. Conservatively, we assumed the same probability for equivalent interactions with hoppers although it should be noted that empirical work using PIT-tags to monitor hopper visits by squirrels suggests this probability may be greater (Appendix C), most likely due to the continuous accessibility of hoppers compared with single-capture traps which could only be accessed by one individual per day. The relationship between hopper use (proportion of squirrels testing positive for a rhodamine bait marker) against the ratio of squirrels to hoppers (Appendix C) suggested the proportion denied access to hoppers assuming a fixed ratio of one hopper per squirrel was 0.225 (consequently the maximum proportion able to access hoppers at this ratio was 0.775).

## 2.4. Simulation experiments

Simulations consisted of two phases: an initial “warm-up”, followed by a control phase in which various management strategies were applied. In the warm-up phase patches were initialised with a number of adult squirrels equal to their capacity, with their gender assigned at random. The model was then run for 10 years allowing sufficient time for the population demographic structure to stabilise. Specified management strategies were then applied and the population simulated for a further 50 years. For each strategy, we performed 100 repetitions, aggregating the results to produce comparative statistics reflecting the speed of population decline and by extension relative cost of different options. In this context “speed” of decline was primarily defined as the time (years) to achieve eradication but it also described the rate of population decline (percentage reduction in the first year of control). As Rushton et al. (2002) suggested that the main cost of culling is due to the requirement for staff to inspect each trap daily (this is not required during pre-baiting and as such we only consider time spent active trapping for relative comparison), we assumed the relative “cost” (reflecting an investment of resource either monetary or volunteer time) of fertility control to be a fifth of culling as hoppers might only need be checked weekly to replenish the bait. We therefore estimate the “cost” of fertility control, measured in cull years, to be 20% of respective times to eradication, beyond which management would no longer be required.

Initially we explored culling alone to establish the level of effort, expressed as density of traps deployed in each woodland, required to eradicate grey squirrels from the study area. The range of trap densities tested (specifically 0.125, 0.25, 0.5, 1, 2 and 4 traps/ha) was based on that recommended by best practice guidelines (4 traps/ha) (Mayle et al., 2007; Gurnell and Pepper 2016) and on the lower density of trap deployments used for the eradication on Anglesey (Schuchert et al., 2014) which employed an average of between 0.2 and 1 traps/ha, depending on woodland type, across an area similar to North Cumbria. Our calculations also assumed 4–5 days active trapping per month for each of the 9 months between February and October (standard guidelines; Gurnell and Pepper 2016) for a total of 45 days/year. Next, we explored replacing culling with fertility control. For comparison of relative costs as well as control efficacy (rate of decline) we assumed equal densities of hoppers as traps deployed for the same period (45 days per year), choosing to consider densities of 0.5/ha similar to that used at landscape

scale in Anglesey. As no data are available on the effectiveness of oral contraceptives, we tested a range of rates of induced infertility, i.e. 50%, 75%, 90% and 100%. Finally, we tested a sequential approach, culling for one year followed by fertility control using the same fixed density of traps and hoppers as employed for fertility control alone, again considering a range of contraceptive efficacy.

## 3. Results

For culling (Fig. 2), trap densities greater or equal to 0.25 traps/ha guaranteed eradication within 50 years (100% percentile across repetitions) with the median (50% percentile across repetitions) time taken ranging from 12 years for 0.25 traps/ha to 8 years for 4 traps/ha (Table 3). Initial rates of population reduction were rapid compared with fertility control alone (Figs. 2 and 3), with mean percentage decreases after the first year of control between 50% for a trap density of 0.125 traps/ha to more than 98% for trap densities greater than 0.5 trap/ha (Fig. 2 and Table 3), assuming trapping was carried out for 5 day/month and 9 months/year, i.e. 45 days per year.

Conversely, employing fertility control alone assuming 0.5 hoppers/ha (Fig. 3) failed to guarantee eradication within 50 years, even when assuming an effective oral contraceptive (100% reduction of fertility). This is not to say that eradication using fertility control never occurred, but it was unlikely to be within 50 years, only occurred in a few simulations (approx. 5%), and required the use of the most effective contraceptive (Table 3). Initial rates of population reduction were substantially slower than for culling with percentage decreases after the first year of control of 10%, 6%, 3% and 1% for contraceptive efficacies of 100%, 90%, 75% and 50% respectively (Fig. 3 and Table 3).

Applying an initial year of culling prior to fertility control assuming identical trap and hopper densities of 0.5 device/ha (Fig. 4) notably increased the probability of eradication within 50 years with contraceptive efficacies greater than 75% guaranteeing this outcome. For these efficacies (90% and 100%) the median time eradication was 10 years (Table 3); identical to the equivalent scenario using culling alone but with greater reliability (maximum time to eradication for culling in any simulation was 39 years whereas when replaced with fertility control after one year it was 26 and 21 years assuming contraceptive efficacies of 90% and 100% respectively).

The model identified neighbourhoods within the study area which

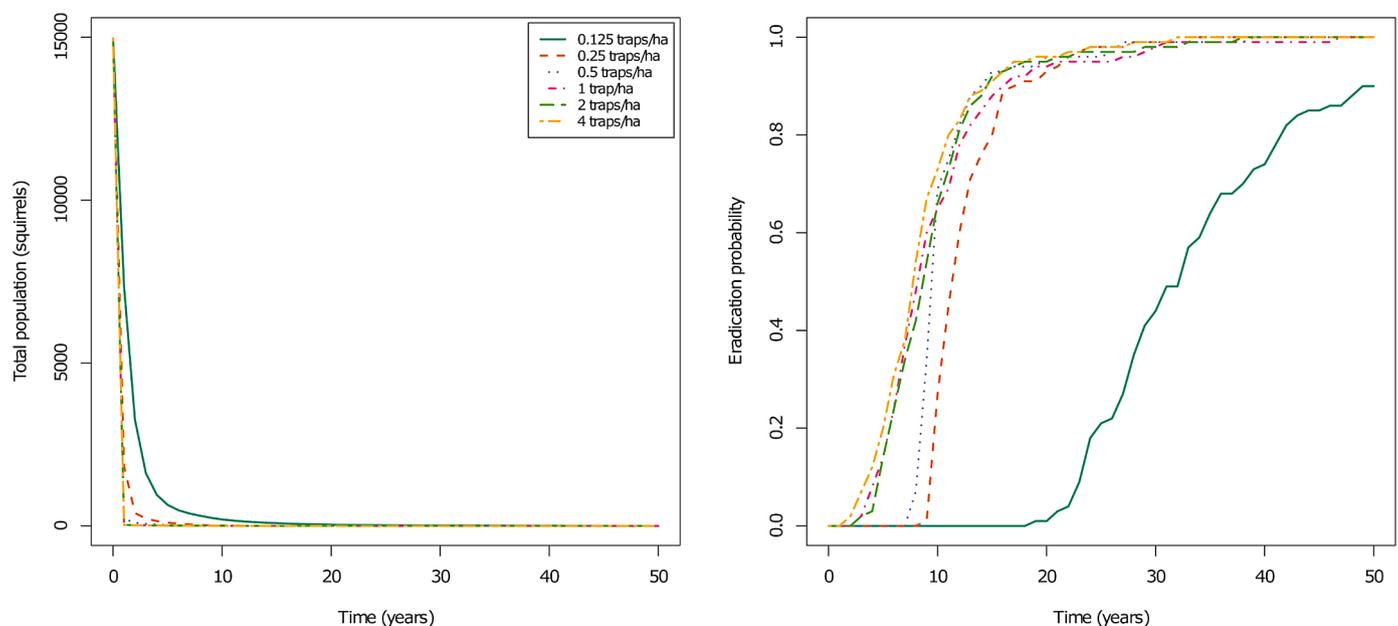


Fig. 2. Eradication timings for culling. Effects of different levels of trapping effort (traps per hectare) on grey squirrel numbers from a starting population of 15,500 individuals at year 0. Trapping was applied for 45 days per year, assuming 5 days of active trapping per month from February to October.

**Table 3**  
Summary of model simulation results obtained by employing culling, fertility control or both sequentially (one year culling followed by ongoing fertility control).

Management scenario	Mean population reduction in year 1 (%)	Time to eradication (yrs)	
		Median	Range
<b>Culling</b>			
0.125 traps/ha	50.73	33	[19,>50]
0.25 traps/ha	87.73	12	[9,34]
0.5 traps/ha	98.53	10	[8,39]
1 trap/ha	99.65	9	[3,47]
2 traps/ha	99.77	9	[3,38]
4 traps/ha	99.80	8	[2,32]
<b>Fertility control (0.5 hoppers/ha)</b>			
50% contraceptive efficacy	1.46	>50	[>50,>50]
75% contraceptive efficacy	3.26	>50	[>50,>50]
90% contraceptive efficacy	6.22	>50	[>50,>50]
100% contraceptive efficacy	10.31	>50	[49,>50]
<b>1 year culling followed by ongoing fertility control (0.5 devices/ha)</b>			
50% contraceptive efficacy	98.53	>50	[9,>50]
75% contraceptive efficacy		11	[9,>50]
90% contraceptive efficacy		10	[9,26]
100% contraceptive efficacy		10	[9,21]

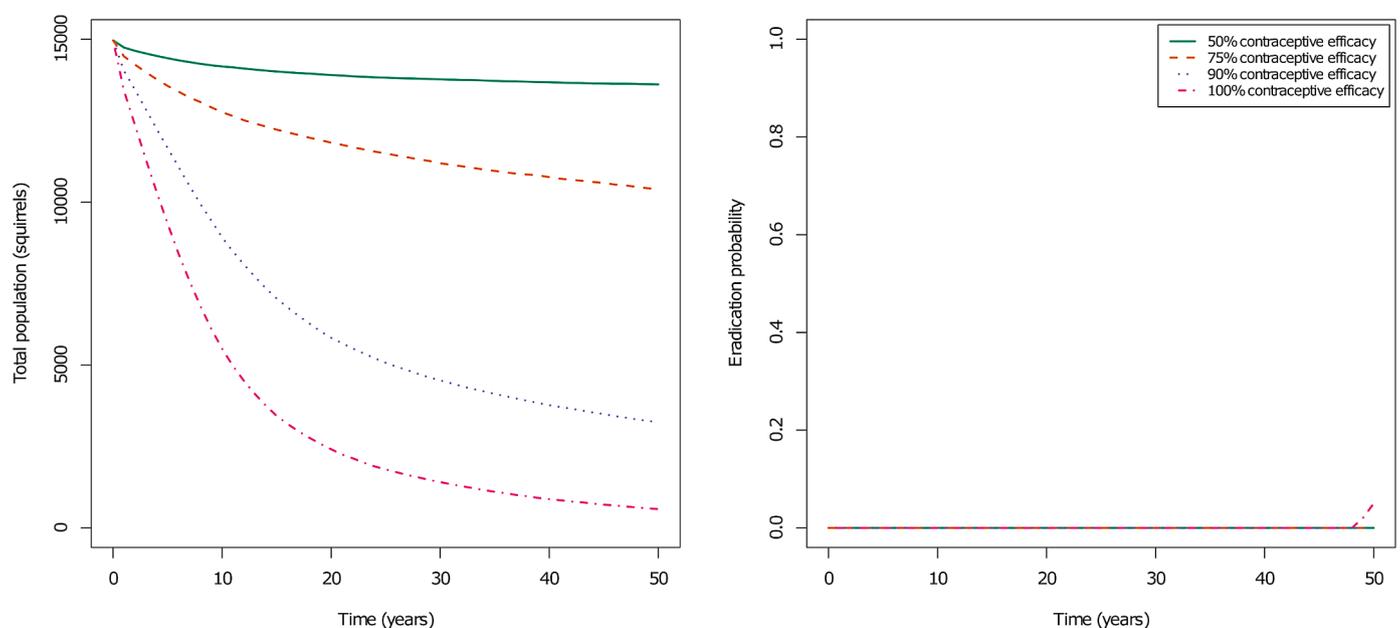
are more or less susceptible to the effects of management. We illustrate this using a simple and plausible fertility control only scenario (75% effective) showing well described areas of local eradication often close to similar areas still hosting populations resistant to management. Eradicated areas feature sparse networks of well separated small patches, whilst resistant areas feature well connected networks of larger woodlands (Fig. 5b). Our model suggests this proximate co-existence is not persistent (eradication of even resistant neighbourhoods is likely, albeit slow) and is produced by the suppression of emigration from neighbourhoods of large and productive patches. Our illustration was

chosen to accentuate the differences between neighbouring patches but does support two key observations. Similar spatial patterns in response would be observed in the more rapid approaches, but for a number of the scenarios, (e.g. culling only or mixed approaches) this pattern would have only been observed following the initial year of operations, with eradication likely to be subsequently imminent across most of the study extent. Secondly, we note that whilst our plausible and moderate fertility control scenario (Fig. 5b) produces a distinct heterogeneity in management outcomes, multiple benefits accrue. After 20 years considerable areas of the extent are free of grey squirrels, and the areas where they appear resistant to management are spatially limited, and host reduced populations, potentially below any broad threshold for economic damage and reducing other harmful effects squirrels may have on the environment.

#### 4. Discussion

For the first time, we describe a model for simulating grey squirrel populations incorporating effort-based management using probabilistic interaction rates between individual animals and either traps or bait hoppers. This study is informed by experimental data, to capture realistic spatial and temporal variations in the relative efficacy of each control method (specifically, density-dependence). We compare different options based on culling, fertility control and, uniquely, a sequential integration of the two approaches considering short-term culling followed by multi-year fertility control. Distinct from previous studies, we explore how management activity might permit the maintenance of low densities of grey squirrels to mitigate their economic and environmental impacts across extensive landscapes. We also illustrate how co-ordinated management programmes can exploit the refined description of grey squirrel movement used here to identify local neighbourhoods within extensive landscapes for which differing combinations of population management methods might be deployed to optimise the speed and cost-effectiveness of grey squirrel eradication.

Our results agree with previous work in suggesting that culling can rapidly reduce squirrel numbers and that even a low density of traps (0.125 traps/ha) reduces the population by 50% in the first year. However, at least 0.25 traps/ha must be maintained for at least 45 days per year to guarantee eradication in 50 years. With an average of 0.5 traps/ha, the simulated median eradication time was 10 years,



**Fig. 3.** Eradication timings for fertility control. Effects of fertility control on grey squirrel numbers, assuming various efficacies for the oral contraceptive (effort set at 0.5 hoppers per hectare for a total of 45 days per year).

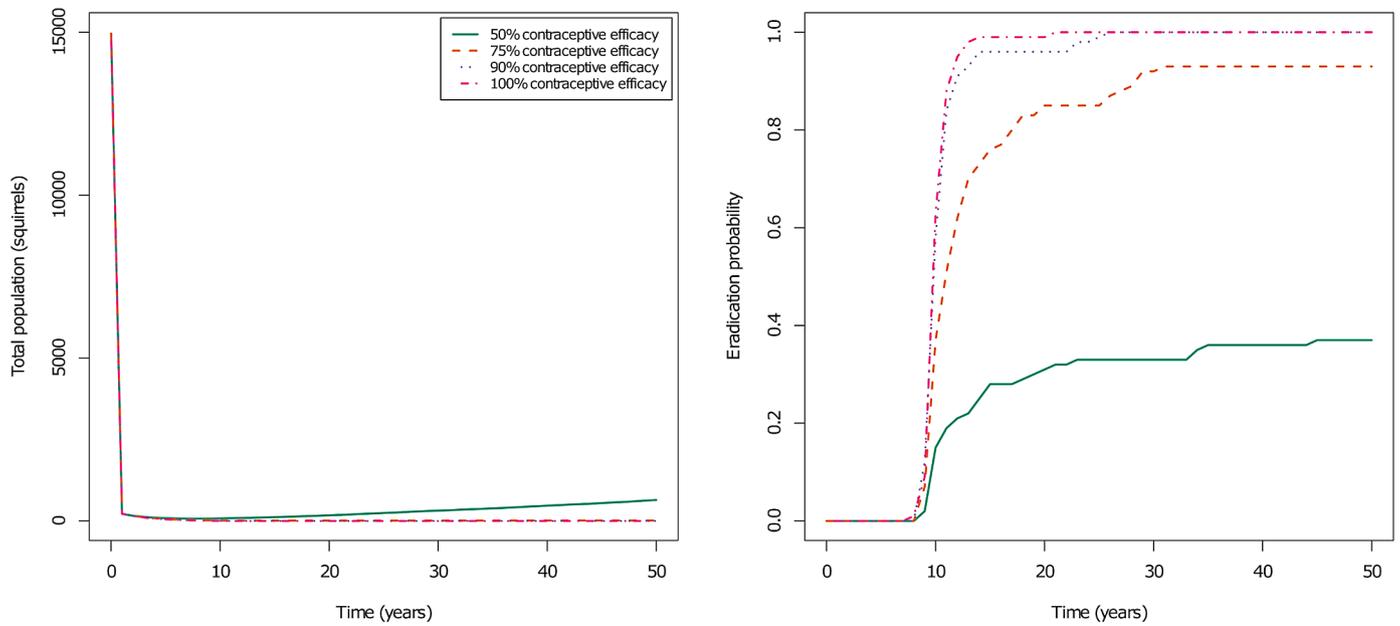


Fig. 4. Eradication timings for an integrated, sequential, management approach. Effects of fertility control following one year of culling on grey squirrel numbers, assuming various efficacies for the oral contraceptive (effort set at 0.5 devices per hectare for a total of 45 days per year).

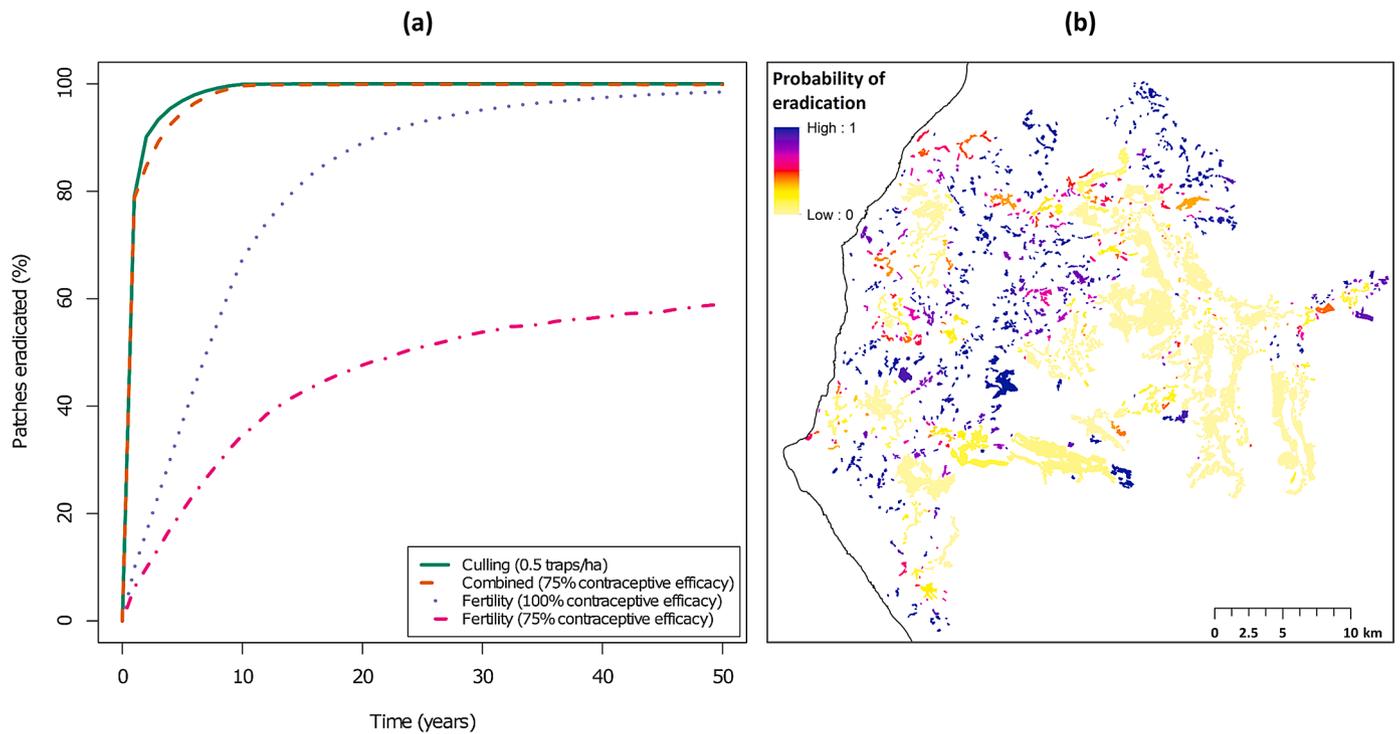


Fig. 5. Spatial pattern of eradication. Plot (a) shows the proportion of patches in the model landscape from which squirrels had been eradicated over time for several management strategies assuming a fixed device density (trap and hopper) of 0.5/ha. Map (b) shows the probability of eradication in patches after 20 years of fertility control assuming a hopper density of 0.5/ha and a contraceptive efficacy of 75%.

comparable to that reported on Anglesey (Schuchert et al., 2014). Comparing our results across all trapping densities indicates that at higher trap densities there were only minimal improvements in both the rate of population reduction in the first year and the eventual time to eradication but that the likelihood of a faster eradication is generally higher (shorter maximum time to eradication across all simulations; 100% percentile) offering greater certainty of achieving this outcome.

As expected, the model showed that fertility control alone is slower

than culling to reduce populations; even with a completely effective contraceptive (100% reduction in fertility) only reducing populations by around 10% in the first year. Eradication across the study area using this method alone is unlikely to be considered more cost-effective than culling assuming equivalent numbers of traps as hoppers but would be achieved eventually, and would occur much sooner in landscape scale neighbourhoods (Fig. 5). This indicates that fertility control alone would not provide a practical solution to eradicate grey squirrels, but may

prove invaluable at maintaining low densities, sufficient to mitigate most economic and environmental problems grey squirrels produce. However, we note that dependant on the formulation and mode of delivery, oral contraceptives may eventually become much more cost-effective than assumed here. For instance, we have conservatively assumed that induced infertility lasts only one year, inhibiting one or possible two reproductive cycles in grey squirrels. In other squirrel species treated with single-dose injectable contraceptive vaccines infertility may last several years. In the closely related fox squirrel (*S. niger*) such vaccines maintained infertility in 100% of treated animals for at least 17 months, with results suggesting that infertility was likely to persist much longer (Krause et al., 2014). In the California ground squirrel (*Spermophilus beecheyi*) the proportion of lactating females were reduced by 91% the first year and 96% in the second year (Nash et al., 2004). This might encourage deployments of fertility control in alternate years further reducing cost and effort. Further, extending the period between hopper refills with bait, from our conservative assumption of 5 days is likely to produce substantial reductions in costs. Refilling intervals are dependant on the nature of the bait formulation and hopper size. Current experimental work uses a highly palatable paste bait delivered in hoppers which requires refilling at 5 day intervals. Alternative formulations (e.g. a liquid), or intelligent delivery devices (e.g. regulating access to bait) may permit the use of much larger hoppers and extend servicing intervals.

Our modelling demonstrates that rapidly reducing squirrel densities using one year of culling followed by ongoing fertility control could achieve eradication in similar time to culling alone; even if the efficacy of the oral contraceptive were only 75% this sequential approach represents the most cost-effective option. This approach has the added benefit that for much of the period of management, before eradication is achieved, squirrel densities will be low, potentially below any threshold associated with damage to trees. In addition, whilst a combination of culling and fertility control might still not be popular with stakeholders that oppose culling, it might be preferable to culling as the sole method for squirrel control.

It should be recognised that, within the scope of this comparative study, we make several simplifying assumptions which may limit the immediate application to inform real-world scenarios. Firstly, similar to other modelling studies (e.g. Rushton et al., 2002, Jones et al., 2016), we do not consider annual fluctuations in seed production which have been shown to affect squirrel numbers (Gurnell 1996). We have outlined in Appendix A the substantial uncertainties involved in representing local seed production without a patch by patch description of tree species and their abundance (i.e. composition of the patch). For the purposes of our relative assessment this experimental choice does not affect our general conclusion, that short-term culling to reduce squirrel densities followed by fertility control provides a more cost effective strategy than culling alone (see Appendix A), but does limit the model's ability to accurately predict absolute timescales and locations for removal given different management strategies; for instance a good mast year may allow previously culled populations to bounce back sufficiently so as to require a more adaptive management approach interspersing long-term fertility control with additional periods of culling. This would need to be addressed for the model to be used as a practical tool for woodland managers. Secondly, we deliberately model a region in the landscape which may reasonably be considered, at least relatively, closed (i.e. any reinvasion is likely to be slow) containing a stable population of squirrels. Our conclusions are therefore limited to these conditions and may not translate to situations with more open or unstable (invading) populations. Finally, here we consider a "best" case scenario with ubiquitous control across the landscape. In reality, even where management is co-ordinated (Schuchert et al., 2014) landowner participation is more variable. As with the other assumptions we make this scenario does not affect the validity of our relative comparison but will clearly be a key factor in the development of a practical management strategy. Future work will focus on this aspect of the model to better inform decision

making.

Even though our description of the value of patches (to squirrels) is crude, producing little heterogeneity in value (carrying capacity), our refined description of squirrel movement between patches allows our spatially-explicit model to identify neighbourhoods across our extent where management is easier (i.e. more rapid and cost effective) and eradication more likely within a limited time-frame. This is driven by the complexity of the inter-patch networks within these neighbourhoods in our modelled landscape and the source-sink dynamic they produce. This observation promotes two possible benefits. Firstly, red squirrels might be reintroduced into woodlands emptied of grey squirrels much sooner than the date of removal of the last grey squirrel anywhere in the study area (our measure of eradication success), although the cost of checking traps in areas where red squirrels occur will increase as these traps must be checked at least twice per day. The model could be used to identify the neighbourhoods of competitor-free space suitable for the recolonisation of red squirrels. Secondly, we note that Fig. 5 also identifies neighbourhoods across the study area where spatially differential management strategies may produce even faster and more effective outcomes. For example, had one year of culling been deployed only in those neighbourhoods considered resistant to management, typically large blocks of woodland able to support high densities of squirrels for which culling would be essential, even moderately effective fertility control programmes across the whole landscape may offer cost-effective and rapid resolutions to the problems caused by the presence of grey squirrels. Such programmes, tailored to the character of patches, or patch neighbourhoods, suggest that regional scale grey squirrel management, principally to reduce their density and minimise their economic and environmental impact, could be extended at a relatively reasonable cost to support the targeted conservation of the red squirrel.

#### Credit statement

**Simon Croft:** Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing, Visualisation. **James Aegerter:** Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing. **Sarah Beatham:** Conceptualization, Investigation, Resources, Data curation, Writing - Review & Editing, Project administration. **Julia Coats:** Investigation, Resources, Data curation. **Giovanna Massei:** Conceptualization, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Acknowledgement

This work was funded by the Department for Environment, Food and Rural Affairs (Defra) under project code WMA2BC60. In addition to this support we would also like to thank the UK Squirrel Accord for their majority contribution to funding the empirical studies described in Appendix C without which the work presented in this manuscript would not have been possible.

#### Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109386](https://doi.org/10.1016/j.ecolmodel.2020.109386).

## References

- Barr, J.J., Lurz, P.W., Shirley, M.D., Rushton, S.P., 2002. Evaluation of immunocontraception as a publicly acceptable form of vertebrate pest species control: the introduced grey squirrel in Britain as an example. *Environ. Manage.* 30, 342–351.
- Bertolino, S., Di Montezemolo, N.C., Preatoni, D.G., Wauters, L.A., Martinoli, A., 2014. A grey future for Europe: *sciurus carolinensis* is replacing native red squirrels in Italy. *Biol. Invasions* 16 (1), 53–62.
- Bonnington, C., Gaston, K.J., Evans, K.L., 2014. Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. *Urban Ecosyst.* 17 (2), 533–546.
- Bremner, A., Park, K., 2007. Public attitudes to the management of invasive non-native species in Scotland. *Biol. Conserv.* 139 (3–4), 306–314.
- Croft, S., Chauvenet, A.L.M., Smith, G.C., 2017. A systematic approach to estimate the distribution and total abundance of British mammals. *PLoS ONE* 12 (6), e0176339.
- Derbridge J.J., Pepper H., Koprowski J. (2016). Economic Damage by Invasive Grey Squirrels in Europe. In: Shuttleworth et al. (eds) (2016), 393–405.
- Dunn, M., Marzano, M., Forster, J., Gill, R.M., 2018. Public attitudes towards “pest” management: perceptions on squirrel management strategies in the UK. *Biol. Conserv.* 222, 52–63.
- Fagerstone, K.A., Miller, L.A., Killian, G., Yoder, C.A., 2010. Review of issues concerning the use of reproductive inhibitors, with particular emphasis on resolving human-wildlife conflicts in North America. *Integr. Zool.* 5, 15–30.
- Flaherty, M., 2016a. Developing Optimal Strategies for Limiting the Spread of Grey Squirrels (*Sciurus Carolinensis*) and Conservation of Reds (*Sciurus Vulgaris*) in Ireland. NUI Galway, Ireland. PhD Thesis.
- Flaherty M., Goldstein E.A., Lawton C. (2016b). Predicting Grey Squirrel Spread in Ireland; Spatial Tools For Future Management of an Invasive Species. In: Shuttleworth et al. (eds) (2016), 37–56.
- Goldstein, E.A., Butler, F., Lawton, C., 2016. Modeling future range expansion and management strategies for an invasive squirrel species. *Biol. Invasions* 18, 1431–1450.
- Gurnell, J., 1996. The effects of food availability and winter weather on the dynamics of a grey squirrel population in Southern England. *J. Appl. Ecol.* 33 (2), 325–338.
- Gurnell, J., Lurz, P.W., Shirley, M.D., Cartmel, S., Garson, P.J., Magris, L., Steele, J., 2004. Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mamm. Rev.* 34, 51–74.
- Gurnell J., Pepper H. (2016). The Control and Management of Grey Squirrel Populations in Britain. In: Shuttleworth et al. (eds) (2016), 407–436.
- Jones H.E., White A., Lurz P.W.W., Boots M., Shuttleworth C.M. (2016). Mathematical Models of Grey Squirrel invasion: a Case Study On Anglesey. In: Shuttleworth et al. (eds) (2016), 235–254.
- Koprowski J., Munroe K., Edleman A. (2016). Gray Not Grey: Ecology of *Sciurus Carolinensis* in Their Native Range in North America. In: Shuttleworth et al. (eds) (2016), 1–18.
- Krause, S.K., Kelt, D.A., Van Vuren, D.H., Gionfriddo, J.P., 2014. Regulation of tree squirrel populations with immunocontraception: a fox squirrel example. *Human-Wildlife Interact.* 8 (2), 3.
- Lurz, P.W.W., Rushton, S.P., Wauters, L.A., Bertolino, S., Currado, I., Mazzoglio, P., Shirley, M.D.F., 2001. Predicting grey squirrel expansion in North Italy: a spatially explicit modelling approach. *Landscape Ecol.* 16 (5), 407–420.
- Massei, G., Cowan, P., 2014. Fertility control to mitigate human-wildlife conflicts: a review. *Wildlife Res.* 41, 1–21.
- Massei, G., 2018. Oral contraceptives for grey squirrels. *Q. J. Forestry* 112, 39–41.
- Mathews, F., Kubasiewicz, L.M., Gurnell, J., Harrower, C.A., McDonald, R.A., Shore, R.F., 2018. A Review of the Population and Conservation Status of British Mammals. A report by the Mammal Society Under Contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough, UK. ISBN 978-1-78354-494-3.
- Mayle, B., Ferryman, M., Pepper, H., 2007. Controlling Grey Squirrel Damage to Woodlands. [https://www.forestry.gov.uk/pdf/fcpn004.pdf/\\$FILE/fcpn004.pdf](https://www.forestry.gov.uk/pdf/fcpn004.pdf/$FILE/fcpn004.pdf). Accessed: 6th March 2017.
- Mayle, B., Broome, A.C., 2013. Changes in the impact and control of an invasive alien: the grey squirrel (*Sciurus carolinensis*) in Great Britain, as determined from regional surveys. *Pest Manag. Sci.* 69, 323–333.
- Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., et al., 2011. Final Report For LCM2007 - the new UK Land Cover map. CS Technical Report No 11/07 NERC/Centre for Ecology & Hydrology (CEH Project number: C03259).
- Nash, P.B., James, D.K., Hui, L.T., Miller, L.A., 2004. Fertility control of California ground squirrels using GnRH immunocontraception. *Proc. Vertebrate Pest Conf.* 21, 274–278.
- Nichols, C.P., Drewe, J.A., Gill, R., Goode, N., Gregory, N., 2016. A novel causal mechanism for grey squirrel bark stripping: the Calcium Hypothesis. *For. Ecol. Manage.* 367, 12–20.
- Pepper, H., Stoker, D., 1993. Grey Squirrel Control Using Modified hoppers. Forestry Authority Research Information Note 232. Forestry Commission, Edinburgh, UK.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31 (2), 161–175.
- Rushton, S.P., Lurz, P.W.W., Fuller, R.M., Garson, P.J., 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. *J. Appl. Ecol.* 34, 1137–1154.
- Rushton, S.P., Lurz, P.W., Gurnell, J., Fuller, R., 2000. Modelling the spatial dynamics of parapoxvirus disease in red and grey squirrels: a possible cause of the decline in the red squirrel in the UK? *J. Appl. Ecol.* 37, 997–1012.
- Rushton, S.P., Gurnell, J., Lurz, P., Fuller, R.M., 2002. Modeling impacts and costs of gray squirrel control regimes on the viability of red squirrel populations. *J. Wildlife Manag.* 66, 683–697.
- Rushton, S.P., Lurz, P.W.W., Gurnell, J., Nettleton, P., Bruemmer, C., Shirley, M.D.F., Sainsbury, A.W., 2006. Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiol. Infect.* 134, 521–533.
- Schuchert, P., Shuttleworth, C.M., McInnes, C.J., Everest, D.J., Rushton, S.P., 2014. Landscape scale impacts of culling upon a European grey squirrel population: can trapping reduce population size and decrease the threat of squirrelpox virus infection for the native red squirrel? *Biol. Invasions* 16, 2381–2391.
- Shi, D., Wan, X., Davis, S.A., Pech, R.P., Zhang, Z., 2002. Simulation of lethal control and fertility control in a demographic model for Brandt’s vole *Microtus brandti*. *J. Appl. Ecol.* 39, 337–348.
- Slade, A., White, A., Lurz, P.W.W., 2019. Part 1: Evaluation of Red Squirrel Stronghold Forest Management. Forestry Commission Scotland, UK.
- Stevenson, C.D., 2012. Modelling Habitat Networks and Dispersal in the Grey Squirrel *Sciurus carolinensis*. Lancaster University, UK. PhD thesis.
- Stevenson-Holt, C.D., Watts, K., Bellamy, C.C., Nevin, O.T., Ramsey, A.D., 2014. Defining landscape resistance values in least-cost connectivity models for the invasive grey squirrel: a comparison of approaches using expert-opinion and habitat suitability modelling. *PLoS ONE* 9, e112119.