



Red Squirrels United - Evolving IAS grey squirrel management techniques in the UK and Ireland

D3 – Ecosystem function restoration assessment:
Outcomes of monitoring evaluations on conservation actions, Year 3 review.

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Summary

Reporting on the Conservation Actions is limited to simple data summaries as most partners provided their data in bulk at the end of year 3.

Models to assess the conservation actions include removal models which were assessed using simulated data (developed in year 2).

The limitations of this model led to the development of a hierarchical Bayesian approach to model the grey squirrel removal data. The model aims to include spatially explicit data, control strategies and population traits. This approach can accommodate sparse data and allows multiple management measures to be assessed.

The model will allow the joint assessment of the impact of control operations on populations, the spread of the grey squirrels between sites and the natural population growth.

The occupancy modelling approach to assess the red squirrel distribution and abundance was tested on the complete dataset produced by camera monitoring by Northumberland Wildlife Trust partner but is inconclusive likely due preferential sampling protocols, targeted towards grey removals and geographically contained within administrative and project boundaries.



SUMMARY OF OBJECTIVES AND PROGRESS

Actions included in deliverable D3	5
Evaluate and inform the implementation of grey squirrel management	5
Provide an ecosystem restoration assessment for project areas	5
Progress of Action D3 in Year 3	6
Current status within global modelling framework	6
Progress in Year 3	6

OVERVIEW OF ANALYTICAL APPROACHES AND DATA AVAILABILITY

Ecological models, assumptions and requirements	7
Data Provision to end of data collection	8

PROGRESS TOWARDS EVALUATING THE IMPLEMENTATION OF GREY SQUIRREL MANAGEMENT

Rates of grey squirrel removal per unit control effort through time	9
Quantifying control effort	9
Removals by trapping	10
Trapping success through time	10
Captures in relation to traps*days, annually	11
Removals by shooting, through time	12
Assessing the effect of management interventions on grey squirrel abundance/range	13
Conceptual model overview	14
System dimensions	14
Model overview	16
Data input	18
Model sub-systems	18
Removals: assessing detection probabilities and total local populations	18
Population change: natural deaths and recruitment in remaining local populations	19
Movement: population available for dispersal	19
Potential integration of economics estimation	20

PROVIDING AN ECOSYSTEM RESTORATION ASSESSMENT FOR PROJECT AREAS

Change in abundance and range size of native red squirrel in response to control operations	21
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Data limitations in assessing detection probability	21
Potential of RSU data in assessing changes in Red Squirrel distribution	22
Impact of management on the proportion of grey squirrels carrying infections	24
Tissue sampling data	24
Least cost pathway analysis	26

NEXT STEPS

Analytical steps to complete by the end of the project	27
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SOFTWARE AND METADATA REFERENCES

Literature cited	28
Analytical packages and software references	28



SUMMARY OF OBJECTIVES AND PROGRESS

Actions included in deliverable D3

There are two main areas of work being coordinated and assessed by NU within Action D3: Ecosystem function restoration assessment, both of which are dependent on the provision of data from project partners in Conservation Actions C1- C4.

EVALUATE AND INFORM THE IMPLEMENTATION OF GREY SQUIRREL MANAGEMENT

The aim of this action is to use data collated on grey squirrel control, including live capture and shooting, to assess current control practises with the aim of optimising control in time and space, specifically to assess:

- (1) rates of grey squirrel removal per unit control effort through time
- (2) effect of management interventions on grey squirrel abundance/range

PROVIDE AN ECOSYSTEM RESTORATION ASSESSMENT FOR PROJECT AREAS

To assess the impact of the control of greys squirrels on the conservation of the red squirrels we planned to combine monitoring, sightings and control effort data in an assessment of:

- (3) change in abundance and range size of native red squirrels in response to grey culling
- (4) impact of management on the proportion of grey squirrels carrying infections

The revised focus of the D3 objective is to evaluate the overall conservation actions to inform future IAS management.

Progress of Action D3 in Year 3

CURRENT STATUS WITHIN GLOBAL MODELLING FRAMEWORK

The global modelling framework was set out in the first year of the project; it was described in the report A6 and is summarised in Table 1. Step 1 was completed in the Prep Action A6. However, difficulties in obtaining high quality data has led to changes to the framework. Due to delays in data provision Step 5 and 6 are longer feasible. Instead more time has been spent on developing modelling structures to suit the available data.

Table 1: Global modelling framework.

1. Assemble data	2. Standardize datasets	3. Develop model structure	4. Assess impact of control	5. Rerun, update	6. Transfer, replicate
Review data, identify strengths and weaknesses, and develop methods to address objectives for each site.	Determine specific requirements for data collection with regards to environmental factors and control effort, produce data accordingly.	Occupancy models, removal data models, cost-benefit models.	Models progressively improved by adjusting for natural and site-specific variations with increasing amount of high quality data.	Update models using high quality data, produce more precise inferences.	High quality data representative of natural variations and control effort allow transferring inferences from conservation actions to other areas.

PROGRESS IN YEAR 3

The revised focus of the D3 objective is to evaluate the overall conservation actions to inform future Invasive Alien Species (IAS) management.

Data provision continued to be the main constraint on progress with Action D3. June 2019 was agreed the last data collection point and final datasets were shared with Newcastle University (NU) at the end of July 2019, so only data summaries and initial analyses are presented for year 3.

We continued to explore alternative analyses of the grey squirrel removal data. The structure for a data simulation model from in year 2 was developed to improve inference about different control strategies and their effectiveness. This led to the development of a Bayesian model in year 3. The model attempts to accommodate variable data quality and make a use of removal data that is more exhaustive than existing removal models in that it combines spatially explicit data, control strategies and population traits, through time.

The resulting inferences aim to jointly address the impact of control operations on populations, the spread of the grey squirrels between sites and the natural population growth. This alternative modelling framework is complex but may allow for more robust inference from the available data.

The suitability of occupancy modelling of red squirrel populations is limited due to the non-systematic recording of red squirrel observations in the field by some partners, and preferential sampling strategies so alternative methods of assessing the impact of control on red squirrels have been explored.

OVERVIEW OF ANALYTICAL APPROACHES AND DATA AVAILABILITY

Ecological models, assumptions and requirements

The role, assumptions and requirements of ecological modelling to evaluate aspects of the conservation actions specific to the RSU objectives were investigated and described in detail in the first year review document titled *D3 – Ecosystem function restoration assessment: Outcomes of monitoring evaluations on all year 1 conservation actions* produced by NU in October 2017.

Ecological models allow the integration of multiple types and scales of data to investigate and understand the dynamics of complex ecological systems. We use models to improve our understanding of the changes in grey squirrel populations brought about by culling and the consequent impact on red squirrels.

More specifically to the RSU project, it means that squirrel count data (*e.g.* numbers observed or captured) can be used to gather information about their overall abundance (given that we can't accurately count them all). However, in order to consider count data as an index of abundance and to investigate changes in abundance through time, specific models are used that come with precise assumptions that condition their applicability.

(1) Count data must be standardised or standardisable across datasets

A standardised methodology would record all animals observed during a fixed duration at diverse locations, however it is not practical or feasible to standardise methodologies across all RSU partners as practices, protocols and priorities vary.

Instead, count data obtained by all partners must be standardised according to the methodology used to obtain the data (*e.g.* observation or trapping). The effort involved in data collection must be also be described precisely in time and space, so that count data can be adjusted to reflect differences between methods.

(2) Input data must allow a good estimate of the probability of detection

Whatever method we use to count squirrels, *e.g.* sighting or captures, will not be completely accurate. In our models we also need to estimate the abundance of animals that are not observed or captured. To do this we assess the probability that we will detect an animal using a given methodology. The probability of detection will vary with habitat and through time and with variation in management practises (*e.g.* the use of baiting) and these factors need to be recorded so they can be used in the models.

Accurate representation of control effort is essential for developing models; the RSU project and initial analytical plan were designed so that this is achieved via the systematic and accurate recording of effort in space and time.

Data Provision to end of data collection

The RSU data received by NU from the start to end of the RSU data collection period are summarised in Table 2. The summary is of all submitted datasets, not all of which were suited to analyses as some contained missing data and/or uncorrected errors.

Table 2: Summary of data reported in the agreed format to NU by partners, by end August 2019.

	NWT	LWT	UW	RSTW
Data collection start	2016-12-01	2017-01-03	2017-01-10	2016-01-07
Data collection end	2019-06-25	2019-05-24	2019-06-28	2019-06-28
Total duration	936 days	871 days	899 days	1350 days
N grey killed	1148	756	664	8930
N grey seen	389	642	0	0
N red recorded	297	170	0	68
N control sessions	951	510	387	3705
N monitoring sessions	545	92	0	0
N sessions per method				
Camera	510	0	0	0
Feeder	26	0	0	0
Shoot	569	217	187	6
Sighting	9	0	0	0
Trap	382	293+trap loans	203	3699
Number greys recorded in individual data	359	742	784	2054

The quality of data provision remained an issue throughout the project and the final dataset have a number of known errors, including missing data. Examples of discrepancies are summarised in Table 3. Data submitted on the recording template (Northumberland Wildlife Trust (NWT) and Lancashire Wildlife Trust (LWT) partners) were overall higher quality data in terms of both accuracy and completeness, allowing fast and systematic compiling by NU.

Table 3: Examples of discrepancies contained in the data submitted by RSU partners to NU (data up to early 2019, Ulster Wildlife (UW) not included).

	NWT	LWT	RSTW
N of unique session IDs *	1230	482	1729
N of sessions recorded	1230	483	2114
Missing or wrong records of effort (<i>inc.</i> coordinates, date, duration, number of devices)	No record of area covered (74 shooting sessions)	Duration missing (12 sessions), Coordinates errors (92 sessions)	Trap locations missing (129 traps), 11 null coordinates, area covered not estimable (100 sessions)

No linking possible, error, or incomplete record in reference lists	Various typos/ alternative spellings amended in the NWT-specific clean-up script	2 sites not recorded in reference list	Woodland name missing (4 sessions + 39 in reference), 3 trap locations missing
N of squirrel records for which the data validation cell reads 'check data'	6 squirrels	0 squirrels	706 squirrels
Number greys recorded: ** in session tab / in individual data	884 / 863	702 / 667	4957 / 1580
Number reds recorded: *** in session tab / in individual data	241 / 11	201 / 80	169 / 72

* The number of unique session IDs and the total number of sessions recorded by each partner did not match when partners submitted incomplete data. The template used woodland name, method and date to produce a unique session ID automatically. When any of those essential variables was not recorded, the ID generation failed and associated data were not possible to match.

** The session tab contains session level data (e.g. ten captures in session A), the individual tab contains biometrics data (e.g. ten biometrics records expected for session A).

*** Biometrics were not expected for red squirrel observations.

PROGRESS TOWARDS EVALUATING THE IMPLEMENTATION OF GREY SQUIRREL MANAGEMENT

The aim of this action is to use data collated on grey squirrel control to assess current control practices with the aim of optimising control in time and space, to assess:

- (1) rates of grey squirrel removal per unit control effort through time
- (2) effect of management interventions on grey squirrel abundance/range

Rates of grey squirrel removal per unit control effort through time

QUANTIFYING CONTROL EFFORT

To assess potential changes in the number of grey squirrel captures, either between project areas or through time, data must be standardised to account for differences in management practise. We report removal data as the rate of grey squirrel removal per unit control effort. This is needed to allow meaningful comparisons of the number of captures. For example trends may be of interest at various scales such as through time or between sites, operators, or methods. Standardisation also allows an assessment of cost, as resource allocation is an important part of control strategies and is directly related to effort variables such as time, methods and operators.

REMOVALS BY TRAPPING

Trapping success through time

For trapping operations, the rate of grey squirrel captures per unit control effort is computed as the ratio of the total number of captures over the total number of trapping occasions, also referred to as traps*days (*i.e.* the number of times the traps were set daily, multiplied by the number of days the traps were set for, multiplied by the number of traps set). Rates of grey squirrel removal per unit control effort were computed using session data; trapping success for all RSU partners is displayed weekly for each trapping session, along with monthly and quarterly means variations (Figure 1).

Missing data were handled with the aim to minimise the amount of records to be omitted from the analysis; assumptions were made when possible (*e.g.* duration for which traps were set daily was assumed to be 12h for Red Squirrel Trust Wales (RSTW)). Other variables did not allow for systematic correction and lead to complete omission of observations (*e.g.* date, location). When trapping success was computed to be above 100%, the value displayed on the figure is 100%, and the associated variables are unreliable.

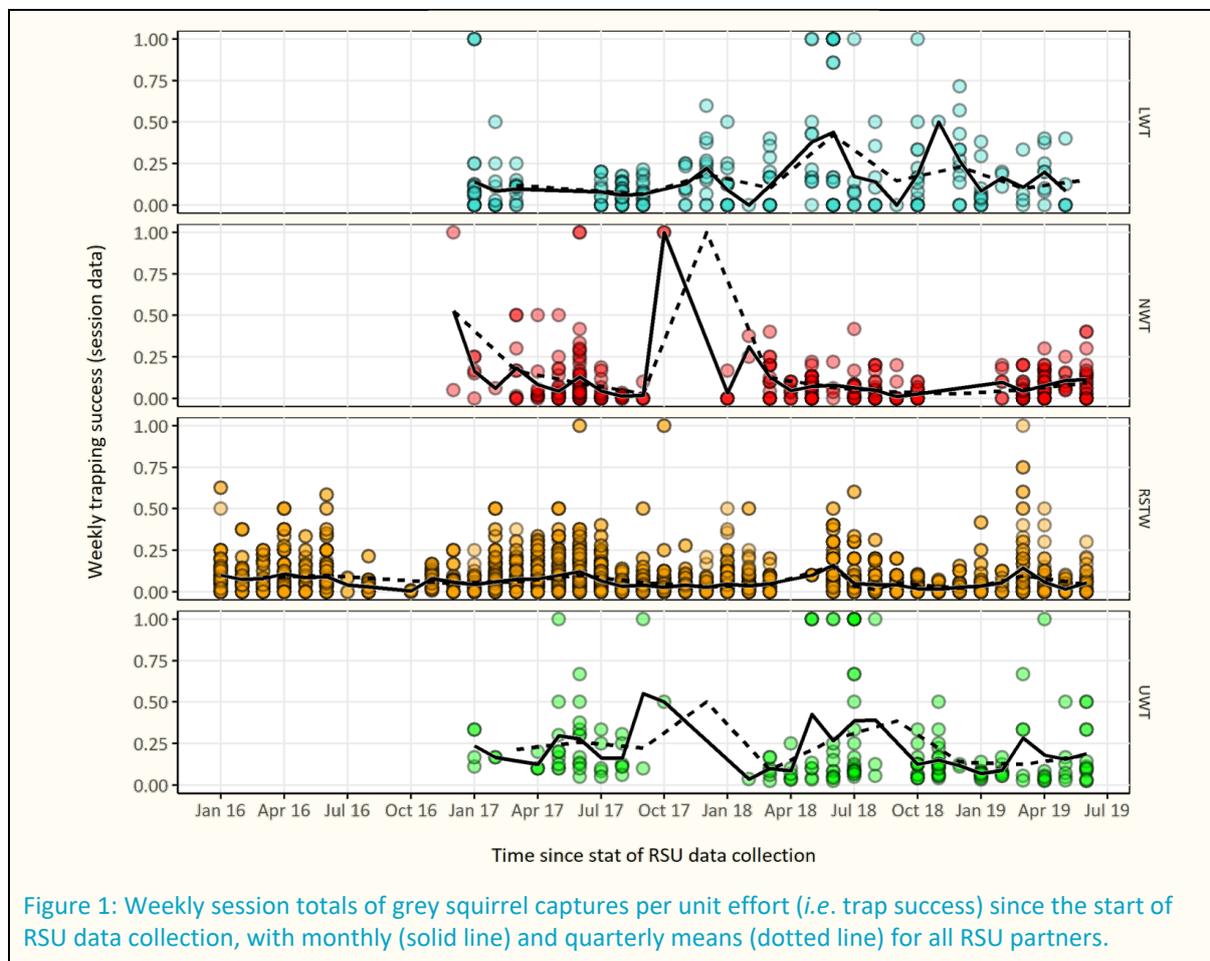


Figure 1: Weekly session totals of grey squirrel captures per unit effort (*i.e.* trap success) since the start of RSU data collection, with monthly (solid line) and quarterly means (dotted line) for all RSU partners.

Captures in relation to traps*days, annually

Weekly totals of grey squirrels captures are presented in Figure 2, this time in relation to the weekly number of traps*days associated with the trapping operations. The trends are presented annually and for each partner, to allow visualisation of the trends despite the different scales of removals and effort (note both free-scaled axes).

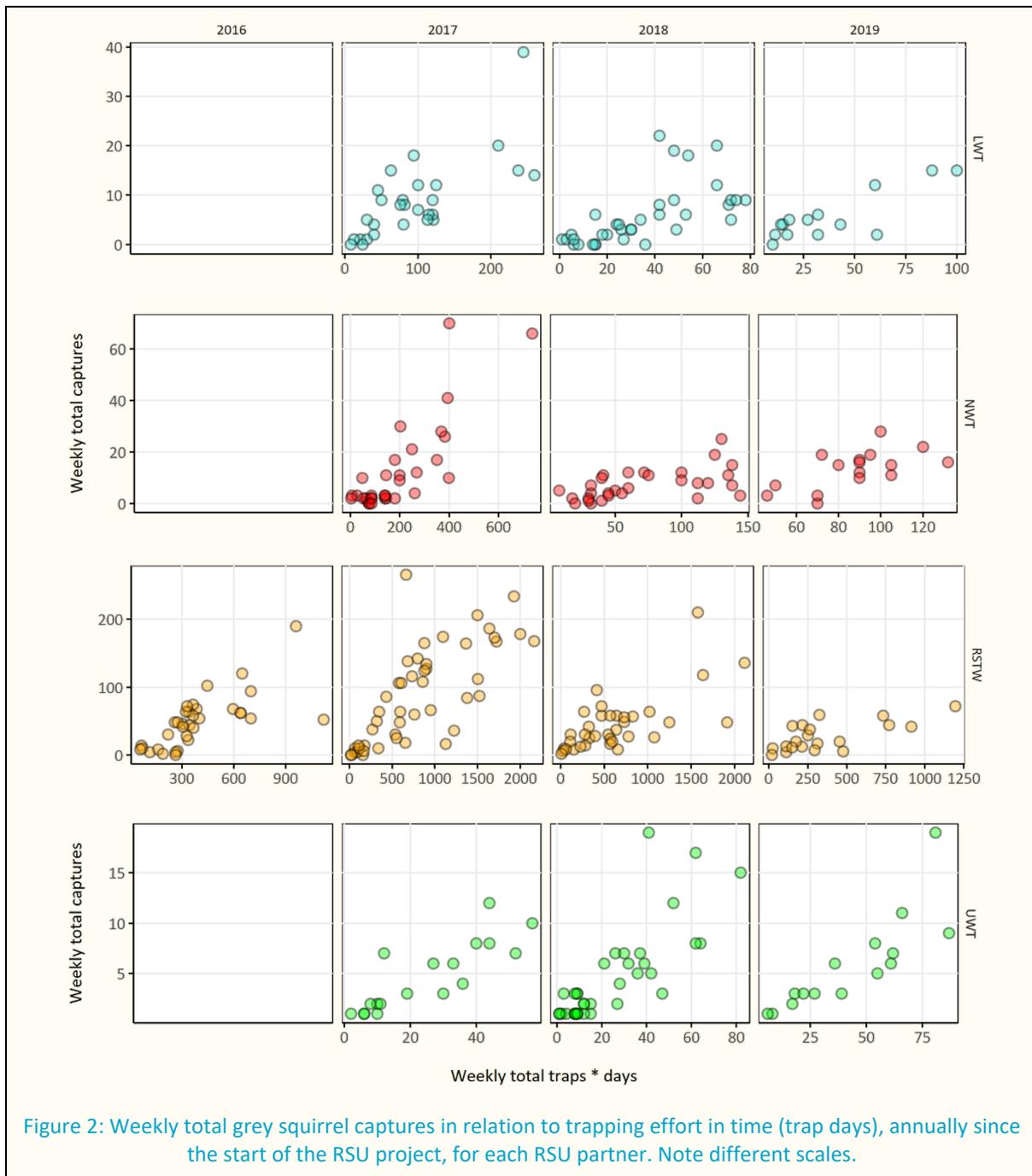


Figure 2: Weekly total grey squirrel captures in relation to trapping effort in time (trap days), annually since the start of the RSU project, for each RSU partner. Note different scales.

The relationship between total captures and trapping effort is overall positive; it varies in size both between RSU partners, and between years since start of the RSU project. The assessment of those trends will be completed as part of the next and final analytical step of the project.

Removals by shooting, through time

For shooting operations, the rate is computed as the ratio of the total number of captures over the total number of consecutive days constituting a session, multiplied by the number of shooters. Trends in time since the beginning of the project are displayed on for all RSU partners.

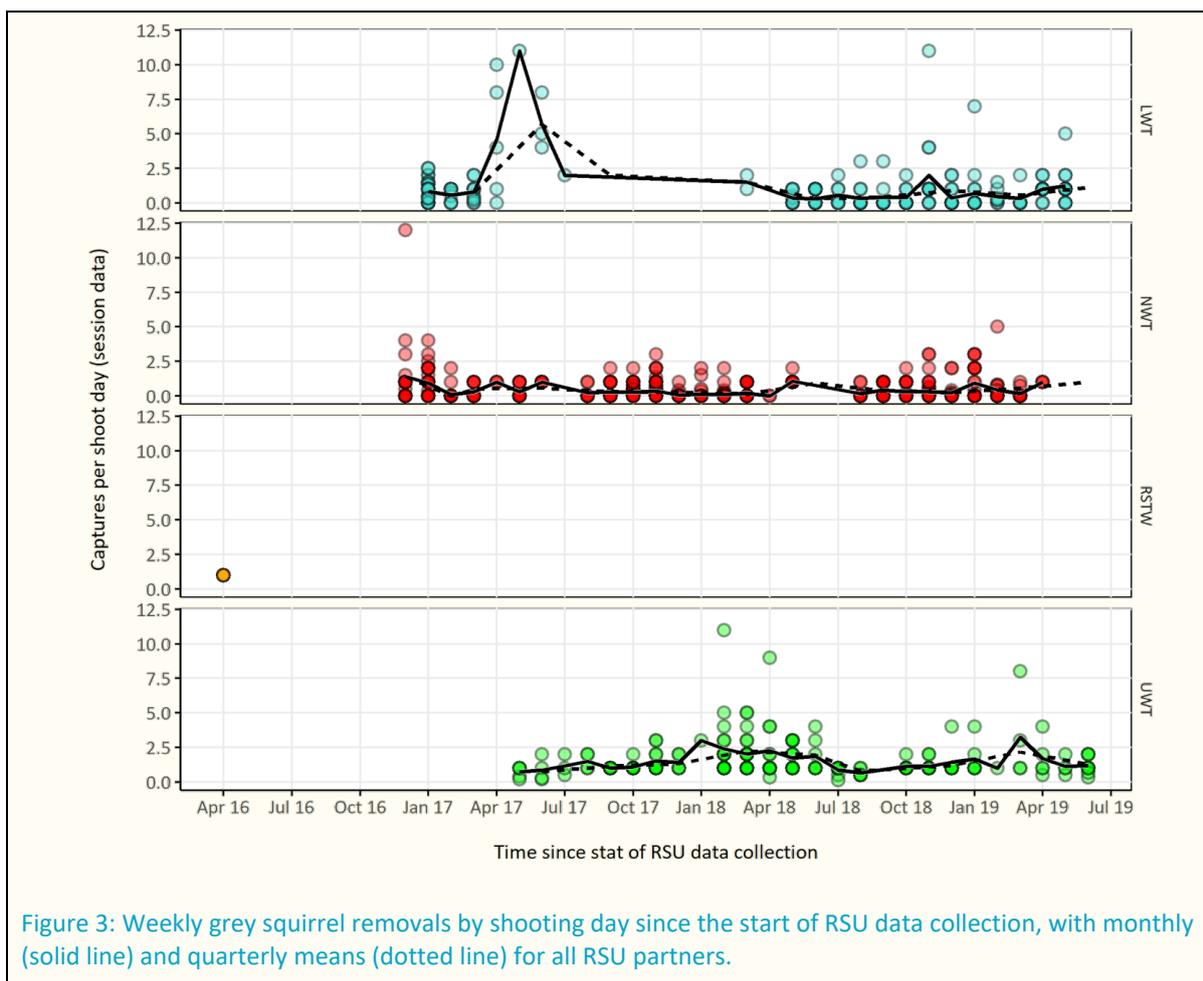


Figure 3: Weekly grey squirrel removals by shooting day since the start of RSU data collection, with monthly (solid line) and quarterly means (dotted line) for all RSU partners.

Assessing the effect of management interventions on grey squirrel abundance/range

The simulation model from year 2 modelled squirrel life history and management interventions at a timescale that was used in the field sampling which meant that multiple events could co-occur in the same time-step of the model for an individual squirrel. This had implications for the utility of the model because simultaneous events were difficult to include and the precise sequence of events has impacts on the model outputs. In year 3 a modelling approach which catered for multiple events in any time period was developed using a hierarchical Bayesian MCMC model structure.

A new study by Link *et al.* (2018) uses an analytical structure that integrates several aspects of interest to the RSU analytical objectives and constitutes a strong basis for further model development. The Link *et al.* (2018) model structure was adapted to incorporate several additional elements that reflect the RSU objectives, as well as specific data collection designs, landscapes, and species' behaviour. For instance, the structure in development allows estimating detectability for four control methods simultaneously, using the effort variables relevant to each method in relevant units that may differ between methods, which is a recurring limitation in classic removal models. The three approaches explored since the start of the RSU project are compared in Table 4.

Table 4: contrasting the structures of removal model, data simulation, and MCMC model in their ability to cope and represent varying sampling features as undertaken by the RSU partners.

Sampling feature	Relevant implications	Can the model be applied despite, or incorporate the associated data properties?		
		Removal model	Simulation structure	MCMC model structure
Multiple collection methods	The average detection probability value varies with the sampling method.	No.	Yes, but iteratively.	Yes, simultaneously.
Both control and monitoring methods	The outcome of the method is an individual that contributes to next iteration of population growth or does not.	No.	Yes, but iteratively.	Yes, simultaneously.
Multiple collection methods used simultaneously	The impact of several methods is simultaneous at the population level (<i>e.g.</i> co-occurring sessions of monitoring, trapping, shooting) but control methods only apply once per individual (<i>i.e.</i> a squirrel seen and trapped, cannot be shot).	No.	Yes, but iteratively.	Yes, simultaneously.
Unequal effort in space within site	Control areas change, so must be informed for each session, but are sometimes missing.	No.	Yes,	Yes,

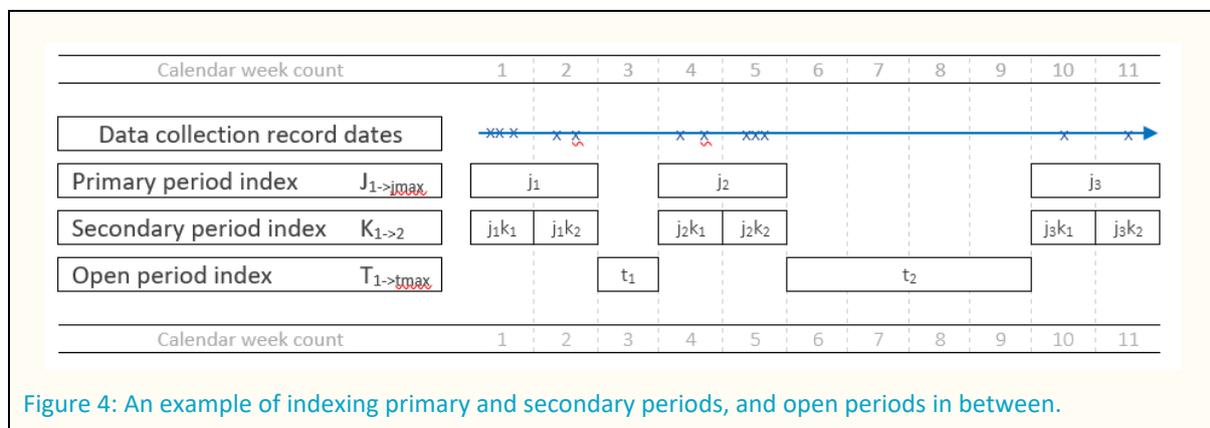
			average per method can be used when NA.	average per method can be used when NA.
Non-repeated / Irregular sampling	Temporal trend within sessions are not representative or estimable.	No.	Yes.	Yes.
Irregular sampling frequency and duration	Primary periods are separated by open periods of varying durations.	No.	Yes, but iteratively.	Yes, simultaneously.

CONCEPTUAL MODEL OVERVIEW

System dimensions

The definition for sites (dimension I) was specific to the type of landscape covered by each RSU partner. For instance, in the North Merseyside where the landscape is patchy, woodlands are clearly delimited and separated by urban or agricultural areas; for LWT partners, woodlands are considered as individual sites. However other landscapes such as the Mournes for Ulster Wildlife (UW) partners and Kielder forest for NWT partners are continuous woodland with gradients of habitat density. Those landscapes are to be divided into grids inclusive of the whole RSU area.

The chronology of data collection was assimilated to a timeline with a regular weekly time-step (Figure 4). For all partners, primary periods (J) were of two weeks duration and contained two secondary periods (K) of one week each. The system allowed for the open periods (T) to be of any duration, reflecting periods during which no data were collected by a given partner. The start and end weeks were specific to each partner’s data collection timeline.



The system’s dimensions reflect the hierarchical structure of the processes investigated in the model, as well as the level of resolution available from partners’ data. The weekly time-step is in line with the pattern of the control operations which generally take place during weekdays; it is also consistent with the assumption of population closure with regards to population dynamics, and relevant to the scale of estimation of dispersal probabilities between sites within RSU areas.





Model overview

The model uses Markov Chain Monte Carlo (MCMC) methods to estimate Metropolis acceptance probabilities, within a Bayesian framework. Each concept, along with hyper parameters estimation and model outputs, will be described in the final RSU report. Here, the conceptual model is presented.

The model includes several hierarchical processes which are spatially interconnected and considered to occur either simultaneously or sequentially along a weekly time-step. The scope and chronology of the processes incorporated in the suggested model are illustrated on Figure 5 and described below for a given site within a landscape where RSU control operations take place.

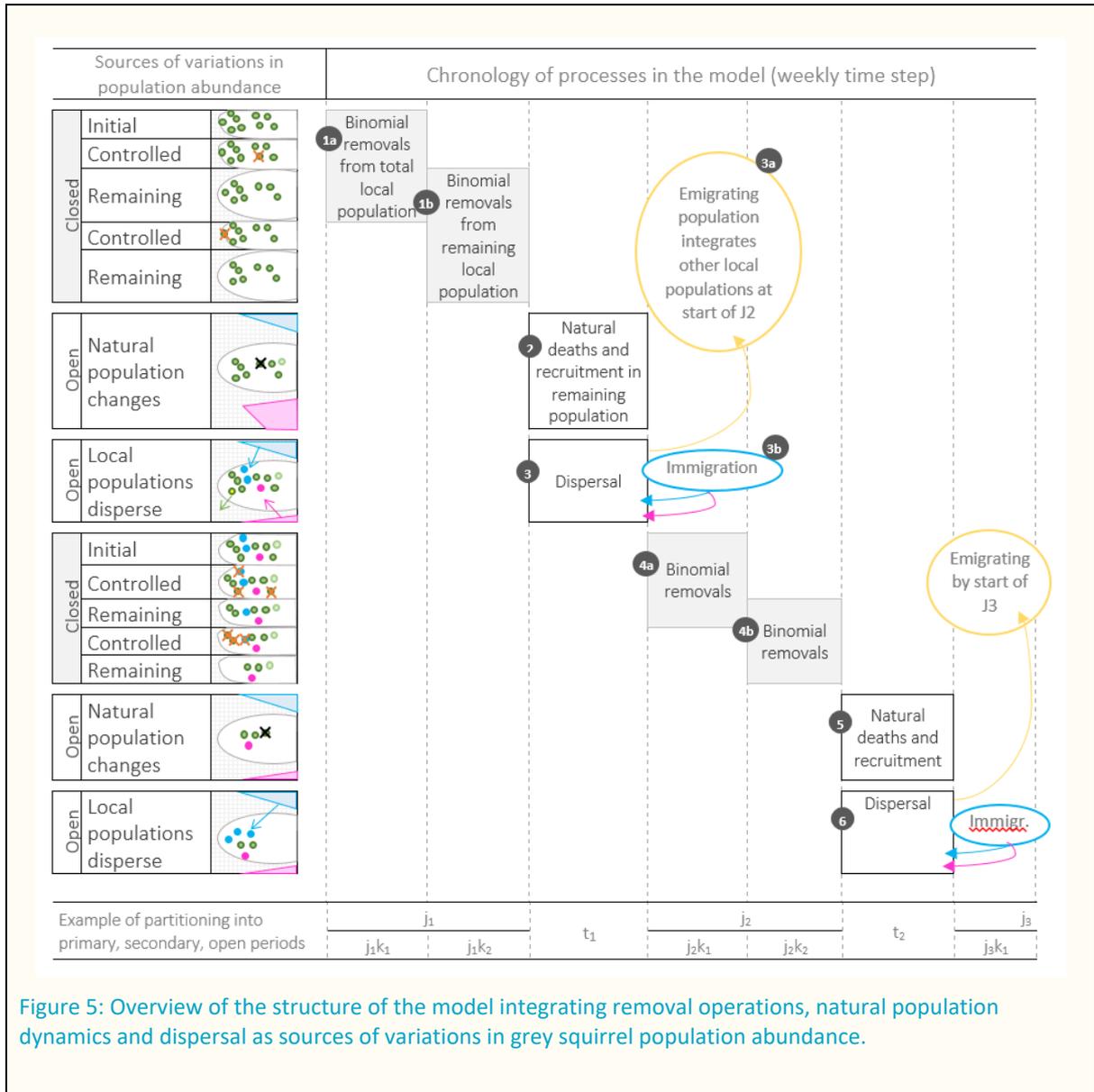
The local population is initially considered closed, assuming no significant changes in natural dynamics occurs during the duration of the primary period. During the first secondary period, (1a) RSU control operations take place within the initial local population, resulting in individual grey squirrels being removed. Control is again applied to the remaining population (1b), potentially resulting in more removals. Captures are expected to vary primarily with method-specific probabilities of detection and local population abundance.

The population is then considered open for the duration of the time interval, *i.e.* until the next primary period. The model first estimate (2) the population changes related to natural deaths (unrelated to control operations) and recruitment, in the remaining population post-removal. Values estimated within this population growth model are expected to be verifiable in literature and may allow distinguishing the local natural population growth from the abundance trends observed which is biased by continuous removal of individuals.

Then (3) the updated population is considered in relation to the other surrounding sites. Given the conditions, a proportion of the local population may disperse to other sites (3a); those individuals will be integrated as part of the initial population at other sites accordingly at the start of the primary period that is relevant to the estimation. Individuals may also disperse from other sites to the local population (3b) or they may remain within the local population (*i.e.* not disperse). Those individuals are integrated to the initial population for the subsequent processes. Dispersal is expected to vary with local habitat criteria, level of woodland isolation, and time of year in relation to mating season.

Changes in local abundance are expected to vary with various variables such as the duration of the open period, site isolation, habitat quality, time of year, population density.

The following primary period starts with the local initial population as the product of those three distinct processes: removals, natural changes, and dispersal. Individuals are removed during the first (4a) and second (4b) secondary periods. Natural population changes are estimated for the remaining population (5), which is then considered able to disperse to and from other sites or remain local.



Data input

Data collected by LWT partners were processed in the formats below and used for initial model development. All input variables were partitioned into regular weekly time-steps, with partner-specific start and end dates and open period durations. Grey squirrel captures were formatted as weekly totals for each method of collection, resulting in 4 arrays of dimensions (I*J*K) as the response variable.

Data collection effort variables were also aggregated weekly for each method, resulting in 7 arrays of dimensions (I*J*K) such as:

- Total number of control days for all methods (4 arrays)
- Total control area covered for roaming methods (2 arrays)
- Mean trap density for trapping roaming (1 array)

Continuous values were all scaled between 0-1 accordingly to the range contained in each partner's record. The duration of open periods is integrated as a (J-1) vector with the values in days.

A distance matrix must be computed for each partner, relating all sites by the distance separating them (in km), resulting in one (I*I) array each. The development of the model structure aims to make the model applicable to the other RSU locations and data. However, the level of landscape fragmentation differs highly between RSU locations; for instance, LWT partners cover clearly delimited woodlands while NWT operate within a larger forest. It is anticipated that different requirements in terms of formats and aggregations will have to be considered to produce a representative description of the sites and distance between them.

MODEL SUB-SYSTEMS

Removals: assessing detection probabilities and total local populations

Grey squirrel captures recorded by the RSU partners constitute the population removed. The values are incorporated in the model as weekly totals per method and woodland for each partner. In a similar way to the removal model concept, the population removed is considered a fraction of the total local population that is sampled via a binomial value that represents detection probability. In this model, detection probabilities are described by a set of effort variables that is method-specific (Table 5).

The four control methods are trapping and shooting, both as roaming methods and as point operation (*i.e.* single trap and shooting at feeder). A candidate value is generated and tested for admissibility for each of the effort variable included for each method (*i.e.* a total of 11 equations required for detectability).

Table 5: Name of the effect estimated for each effort variable per control method.

	Intercept (value in average conditions)	Duration (N of days)	Area covered (proportion of woodland)	Trap density (N of devices.ha ⁻¹)
Trapping – roaming	α	β	γ	Trpd
Shooting – roaming	α_2	β_2	γ_2	.
Trapping - point	α_3	β_3	.	.
Shooting - point	α_4	β_4	.	.



The effects included in the detectability equations were defined as specific to the effort variable, the method, and the woodland. The combination of the three dimensions results in entirely transferable inferences as it eliminates the need for a standardised interpretation of effort units. For instance, it is not required for a day of shooting at feeder to take similar meaning to a day of trapping roaming, as in each case a day is a method-specific unit. This presents a clear advantage with regards to the cost estimation of the control operations.

Additionally, considering the control area as a proportion of woodland covered rather than an absolute squared metric has for advantage to implicitly include additional information, including for example on the proportion of woodland not controlled, potential management strategies or limitations linked to woodland sizes in the landscape. The proportion of woodland covered is also more meaningful in terms of squirrel dynamics, as a hierarchical structure implies clustering by woodland which is not biased by the area covered within it (*i.e.* similar population growth assumed per woodland regardless of the size of the control area within it).

Missing records were replaced by average values per method per woodland per site. This allowed incomplete records to be included with minimal bias (albeit lowering the possible level of precision).

Population change: natural deaths and recruitment in remaining local populations

When a primary period ends, the population is considered to be open. The local population initially consists of the individuals that remain after the control operations and are available for dispersal to other sites before the start of the following primary period. The population change model considers an additional quantity in the gains and losses of the local population that are due to natural population changes (birth and deaths), expressed as proportional to both the local population and to the duration of the time interval before the next data collection records. The use of a Skellam distribution as in Link *et al.* (2018) allows modelling local per capita loss and gain as a difference between the two populations' Poisson distributions. By using two parameters λ^+ and λ^- that are involved in describing both the distribution of the pre-changes population and the additional loss and gain population (mean and variance components).

Movement: population available for dispersal

The local population available for dispersal is then allowed to disperse from and to other sites. A distance matrix is developed that computes the distance between all sites of interest. The aim is to include all sites of relevance to grey squirrels, so also including suitable sites not covered by RSU operations. Estimation for sites where no data collection occurred is computationally demanding however it is required to reflect the population movements accurately, and potentially predicts areas that are not currently surveyed but where additional sampling effort may be justified, to improve model precision or accuracy if the lack of data leads to high uncertainty, or to adjust control strategies.

Probability of dispersal amongst each local population is estimated as a function of the distance between woodlands and the duration of the open period. Current work on the further developments on this model to include additional variables such as the time of year in relation to breeding season



(during which individuals are less likely to disperse), an index of carrying capacity (to be determined), and potentially an element reflecting the proximity to river corridors which have been said to facilitate grey squirrel dispersal.

Potential integration of economics estimation

The initial approach considered that by quantifying control effort precisely, expenditures could be computed for the operations for a given scenario. Variables of relevance are both material (*e.g.* number of traps, bait) and related to operator time use. The suggested model aims to relate control effort to population trends; however, its structure is designed to adjust for a lack of precision in the control effort records. The quality of output will be directly influenced by the precision of data input. Costs associated with each element of control operations can be matched to model outputs.

PROVIDING AN ECOSYSTEM RESTORATION ASSESSMENT FOR PROJECT AREAS

To assess the impact of the control of grey squirrels on the conservation of the red squirrels we aimed to combine monitoring and control effort data to assess:

- (3) change in abundance and range of native red squirrel in response to control
- (4) impact of management on the proportion of grey squirrels carrying infections

Change in abundance and range size of native red squirrel in response to control operations

DATA LIMITATIONS IN ASSESSING DETECTION PROBABILITY

In Year 2, we found that the estimation of detectability of red squirrels was essential to developing an occupancy model but is complicated by three elements that are inherent to the partners' collection methods (details can be found in the Year 2 report); those elements are, varying control strategies between rangers, and by each ranger:

- Landscape partitioning between rangers: limits the ability to estimate whether the probability of detecting a red squirrel relates to the location and the environmental parameters describing it, or to ranger-specific skills or technique in observing or recording sightings.
- Varying control strategies between rangers: control strategies can be highly ranger-specific in the effort invested into control operations, as well as seasonal. For instance, a ranger may cover larger areas for shorter sessions, while another applies the opposite strategy. Systematic variation between rangers and through time confound the assessment of the effects of covariates (time of year, area and duration), so that including them in an occupancy model partly reflects ranger-specificity.
- Varying control strategies by each ranger: red squirrels are mostly detected while leading control operations. The probability of detection of red squirrels may be influenced by the presence of grey squirrels because 1) an ecological process makes red squirrels more elusive where grey squirrels are present 2) rangers are more focussed on grey squirrels (*e.g.* dispatch) than detection of red squirrels. To separate these processes, we explored the effort devoted in time and space for the three operators, in situations when the grey squirrel was detected versus not and found that when grey squirrels were detected, rangers conducting shooting operations were likely to either cover more ground or revisit a site for one or two consecutive days more than when no grey squirrel was detected.

Variations in management strategies likely aim to optimise control effort across the landscape and resources. However, those changes are systematic and introduce systematic biases, that are confounded with the factors that influence the detectability of red squirrel and therefore hinder their estimation. The lack of consistency in the control efforts across the landscape challenges the estimation of those effects, while no repeated sampling or crossed information in the data allows adjusting for the resulting bias.



POTENTIAL OF RSU DATA IN ASSESSING CHANGES IN RED SQUIRREL DISTRIBUTION

Occupancy models can estimate the probability of an individual's presence given particular environmental conditions, while accounting for imperfect detection (*i.e.* individuals may be present yet unseen), and was therefore the approach of choice to assess the change in abundance and range of the native red squirrel in response to culling of grey squirrels.

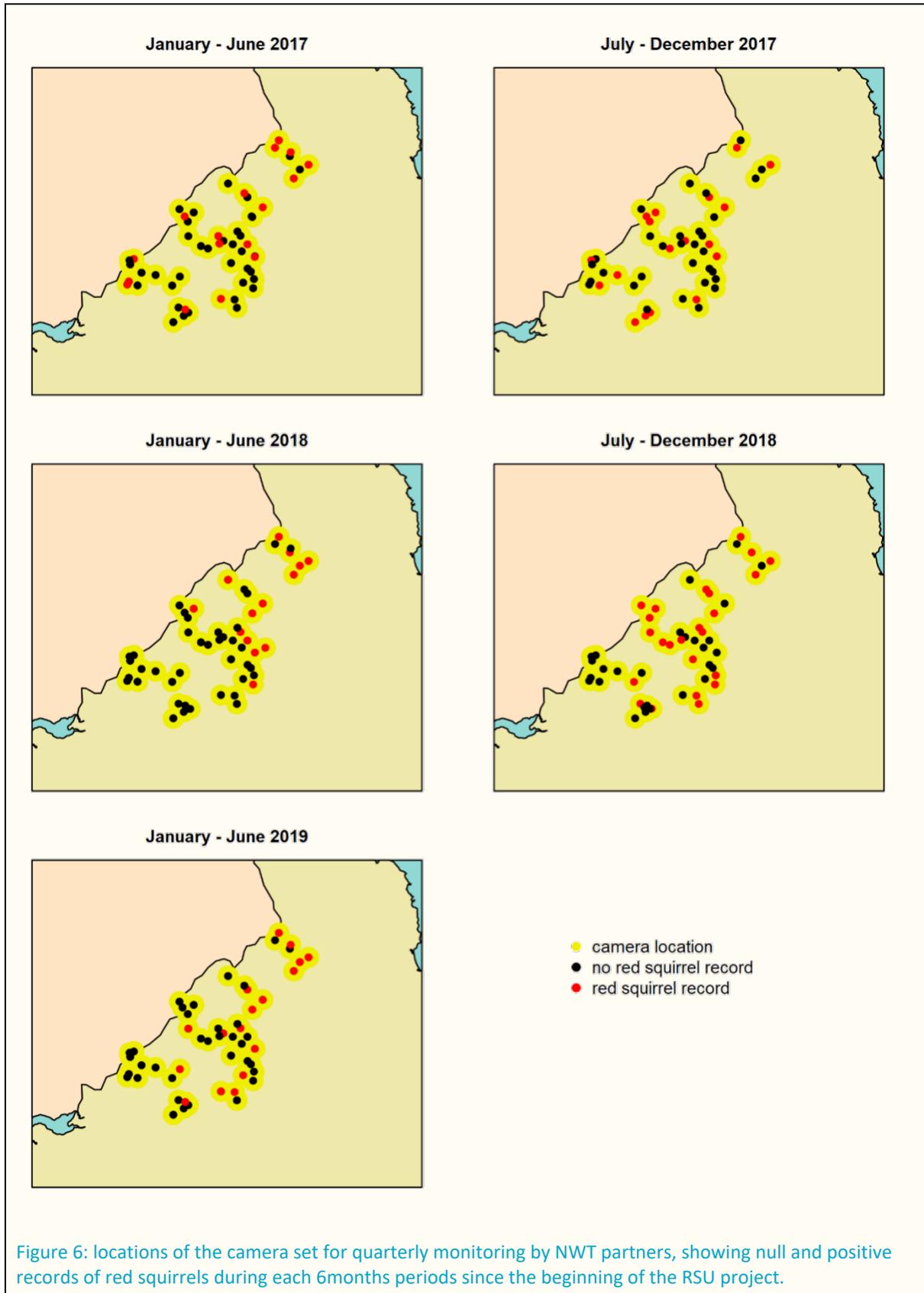
As detection is imperfect, it is important to determine which environmental parameters influence the detection probability and in what way. Data from multiple visits to sites, through different times of year and conditions are usually used to assess detectability in varying conditions; probability of detection likely varies throughout the year, at different sites, and accordingly with method-specific sampling effort. The annual report in Year 2 presented different types of systematic variations in detection effort within the data, and detailed ways in which the resulting biases hinders inferences on Red squirrel occupancy before reaching a more representative dataset.

NWT partners record red squirrel sightings during any type of field visit, including all methods of control and monitoring. Sightings are also specifically recorded by camera traps during each quarterly early warning monitoring. The systematic presence/absence records constitute a set of repeated observations through time at a given location, with a monitoring effort that may potentially be considered constant for the use of analysis. The camera locations and observations are presented for each six months period since the start of the project in Figure 6.

The apparently similar effort involved in the data production from camera traps allowed neglecting effort variables. Dynamic occupancy models were fitted to the quarterly monitoring records (R-package *unmarked*), that included variables descriptive of the sites (National Forest Inventory habitat classification), as well as camera coordinates (to allow detection of a geographical trend) and the time of observation (year, season, month). The model structure incorporated the processes of colonization, extinction, covariate-dependent rates, initial population and detection probability. The models produced estimates that did not allow inferences on trends in time or space regarding Red Squirrel occupancy. Several factors are likely to contribute to the inconclusive outputs, including:

- the overall area covered by camera monitoring may be unrepresentative of the animals' presence and movement; the set-up reflects administrative boundaries and zones drawn by NWT partners, as well as doubles as an early warning system for grey squirrel invasion which it targets.
- the protocol in processing camera data may lead to biased and/or a lack of information.

It is expected that the RSU dataset will not be extensive enough to fully explore the influence on detection probability to allow the application of occupancy models.



Impact of management on the proportion of grey squirrels carrying infections

TISSUE SAMPLING DATA

Data recording templates were updated in Year 2 to accommodate and automate tissue sample data to other information previously collected on individual squirrels.

NU reviewed the biometrics records of the individuals available for disease analysis to the end of 2018. UW and RSTW had collected the highest number of samples (Figure 7). Where possible the biometric data were matched to the cull records which allowed further data to be explored (e.g. body weight, Figure 8).

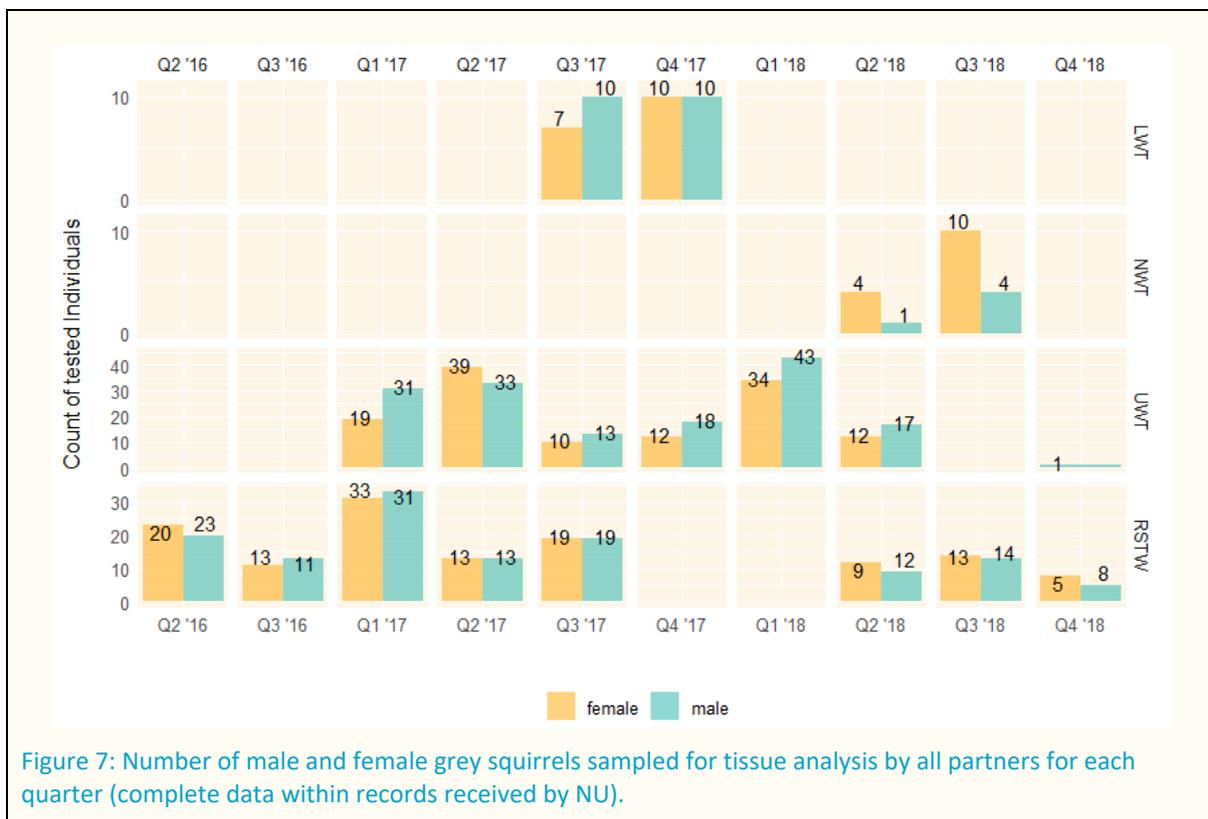


Figure 7: Number of male and female grey squirrels sampled for tissue analysis by all partners for each quarter (complete data within records received by NU).

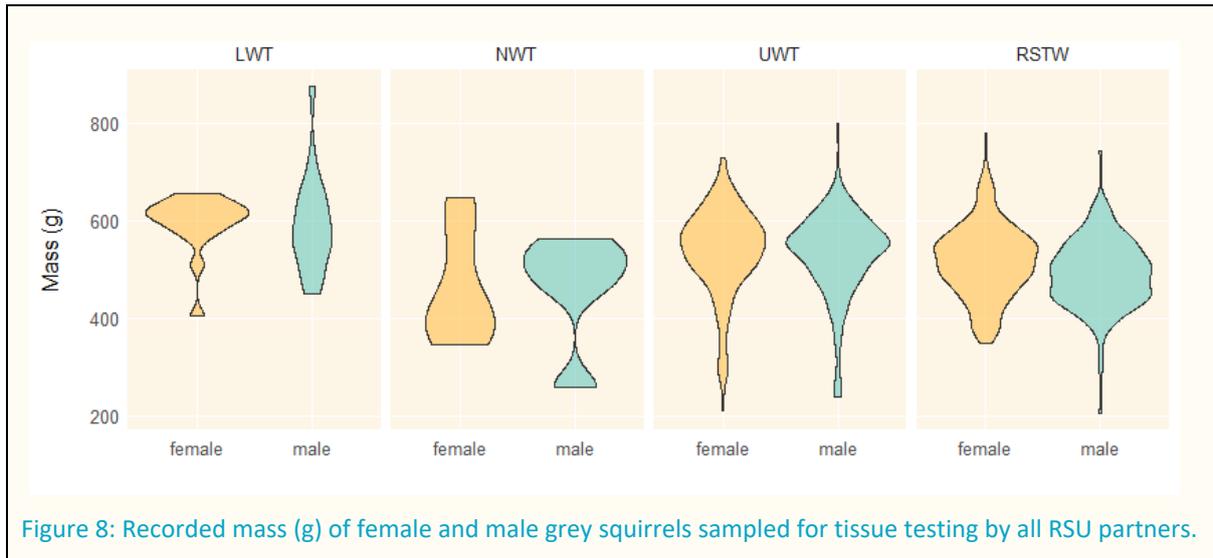


Figure 8: Recorded mass (g) of female and male grey squirrels sampled for tissue testing by all RSU partners.



Least cost pathway analysis

The monitoring network of camera traps implemented by NWT partners aims to optimise the early detection of both red and grey squirrels and provide important insight to inform local species management. It is not known to what extent the grey squirrel will utilise the conifer forest, so corridors and paths into the forest must be monitored. As the monitoring design was not supported or assessed analytically, NU developed a study to determine the optimal location of the camera network based on predicted probabilities of squirrels' movement.

Records of red and grey squirrel presence were used to build habitat suitability models to identify movement corridors favoured by grey and red squirrels across a range of habitats. The relationship between habitat suitability and recorded presence was computed via Maxent algorithm to produce local least cost pathway networks for each species and highlight areas of dense connectivity.

Dense connectivity corridors were identified for each species. Important areas were in line with the locations of Kielder early warning system cameras suggesting the placement for early detection of red and grey squirrels was suitable.

The model outputs highlight the crucial importance of broadleaved woodland in driving the grey squirrel movements into the landscape, suggesting that these areas represent key points which need to be monitored systematically to prevent further incursion and to protect red squirrel presence areas.

The main woodland block made up of Sitka and Norway Spruce appeared less suitable for grey squirrel than for red which supports Kielder Forest as a site of importance for reds recruitment /stronghold and justifies putting conservation efforts in preserving a viable red squirrel population and maintaining this area grey-squirrel free, by implementing an efficient detection system.

However important caveats remain. Landscape resistance values are based on literature and expert knowledge in part, and unknown in part of the landscape, leading to a level of uncertainty that is difficult to quantify. Presence records modelling includes the assumption that data come from random or representative sampling. The lack of records in less visited parts of the landscape also introduces an observer bias that is not accounted for but may be improved with further data collection.

The main findings of this study are currently being prepared for publication before the end of the year.



NEXT STEPS

Analytical steps to complete by the end of the project

- Summarising the usable control effort data for inference, and test for trends in the relationship between total captures and trap days, annually for each RSU partner
- Develop useful maps showing the progression of red squirrel records since the start of the RSU project
- Clean and format all relevant RSU data to fit in to the Bayesian removal model in progress of development
- Complete the development of the Bayesian removal model, fit, draw inferences, investigate potential for applicability at larger scales
- Integrate a cost analysis if possible
- Analysis the disease data from the tissue testing when available.
- The analysis of least cost pathways networks for the grey squirrel in the Kielder forest is currently in preparation for publication.

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Analytical packages and software references

All models are developed within the R environment:

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Specialised packages used in the modelling process include:

- to read shapefiles and process spatial data: geosphere, spdep, raster, rgdal, rgeos, maptools, sp, tmap, dismo
- to read and compile RSU partners' records: readxl, reshape, tidyr, rnrf, plyr, dplyr
- for data illustration: ggplot2, raster, geosphere, RColorBrewer
- for modelling: unmarked, pscl, lme4
- for data editing: stringr, zoo, lubridate, ggpubr, scales, chron, zoo



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