

England Red Squirrel Recovery Strategy

A structured decision-making approach

April 2026

Natural England Commissioned Report NECR669

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Foreword

Red squirrels are a declining species in England, now lost from most of their former range. It is thought that their range has contracted by 95%. In England the species is confined to the North with extant populations on islands. The red squirrel is listed as a species of principle importance, S41 of the NERC Act (2006) and endangered on Britain's Red List for Terrestrial Mammals (Mathews et al 2020).

Causes of decline are multiple; major drivers include loss and fragmentation of habitat, introduction of the grey squirrel, and squirrelpox virus. The situation continues to worsen as small, fragmented populations suffer growing intrinsic threats e.g. genetic factors. While these factors present challenges to red squirrel persistence, there is a belief that recovery is possible with the appropriate management support.

Following pilot workshops held in 2020 it was agreed that a Structured Decision Making process could aid the approach to red squirrel recovery in England. A subsequent series of workshops and webinars were held with over 60 key stakeholders to help determine the local conditions under which red squirrel recovery is possible. Alongside determining which of the alternative strategies that allow red squirrel recovery are most suitable across the objectives.

As part of the process, a model was built to capture interactions between competing species as well as between hosts and parasites. Those interactions were combined with a population model, then adapted to project outcomes across a range of alternative management scenarios. This model factored in the non-biological elements of the problem leading to a comprehensive biological and socio-economic presentation of opportunities in a chosen conservation strategy for the recovery of red squirrels in England.

The production of this report is a crucial first step to assist Natural England working with its partners to recover the red squirrel in England.

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Executive summary

Why this work was needed

Red squirrels (*Sciurus vulgaris*) have disappeared from most of their former range in England, largely due to squirrelpox virus and competition from invasive grey squirrels (*Sciurus carolinensis*) and habitat loss. To help identify the best way forward for red squirrel conservation in the face of uncertainty and conflicting stakeholder values, this project used a **Structured Decision Making** (SDM) approach. We, the Strategy Team (i.e. the report authors), combined scientific modelling with the values of over **60 stakeholders** to support evidence-based, transparent conservation decision-making for red squirrel recovery in England.

What methods we used

We followed the five main stages of the SDM process:

1. Define the problem

We agreed a problem statement with stakeholders that clearly defined the scope and scale of the decision needing to be made.

2. Set objectives

Through workshops and working groups, we engaged with stakeholders to define six core objectives relating to: **red squirrel recovery**, **cost**, **public acceptability**, **animal welfare**, non-target **species bycatch**, and wider **socio-economic benefits** such as people's connection to nature and tree damage from grey squirrel bark stripping.

3. Develop strategies

We designed **18 alternative management strategies** combining different types of lethal grey squirrel management, red squirrel translocations, and possible future technologies (grey squirrel fertility control and a squirrelpox vaccine) at different geographic scales (regional vs. England-wide).

4. Evaluate consequences

We predicted how each strategy performed against the six core objectives by:

- Building a **biological model** to simulate squirrel populations and disease spread over 25 years under the 18 alternative management strategies.
- Conducting an **expert elicitation** exercise to score the welfare impacts of various methods on red and grey squirrels.
- Running a **survey-based model** to estimate national and local public acceptability of different grey squirrel management methods.

5. Explore trade-offs and guide decisions

Consequences were summarised in tables to allow comparison across all objectives,

thus helping to **clarify the key trade-offs between conservation outcomes and wider ecological, social, and economic concerns**. We elicited people's relative preferences towards improving different objectives during a 1-day workshop. These preferences were used to individually solve trade-offs and examine which of the strategies performed best for each person and the group.

What we found

- Strategies incorporating **England-wide suppression of grey squirrels** offer the best potential for large-scale red squirrel recovery and reduced tree damage by grey squirrels. However, they are also the most expensive, have the greatest welfare impacts, the greatest potential for species bycatch, and the lowest predicted public support.
- The **regional strategies** we modelled for Northern and South West England that include red squirrel translocations offer similar benefits for red squirrel persistence, with an expressed preference among stakeholders towards the **Northern England** strategies. The regional strategies are more targeted, thus are potentially more feasible and incur fewer costs for other objectives than the England-wide strategies.
- **Doing nothing**, continuing with the current **status quo**, and switching from **lethal to non-lethal** management of grey squirrels result in a high chance of red squirrel extinction across mainland England over the next 25 years. These strategies also fail to protect trees from grey squirrel bark stripping damage. However, the **'Do nothing' strategy** does perform best for many of the other objectives highlighting that taking action to recover red squirrels comes with value costs.

What this means for decision-makers

This report does not prescribe a chosen 'optimal' strategy. Instead, it offers a transparent, structured, and evidence-based framework to help inform red squirrel recovery in England with the next step being a decision on a national strategy to take forward. We have shown that despite huge volunteer effort, continuing with the status quo will most likely lead to the extinction of red squirrels across mainland England. Red squirrel recovery is only achievable with significantly increased grey squirrel management across England or at targeted regional levels. Additionally, strategies including red squirrel translocations often performed better than those without. As this process is iterative, it can be reapplied at smaller spatial scales to support more nuanced local decision-making.

Ultimately, red squirrel recovery looks possible — but it requires clear priorities, national co-ordination, and long-term commitment to balancing ecological needs with economic constraints and societal values.

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Background on structured decision making

Making decisions around environmental management is often a complex task involving the engagement of varied stakeholder groups and evaluation of many potential actions that could be implemented. Managers are often required to make decisions with limited information and little opportunity to gather more data before acting. Decision support tools can help managers make the best decisions with the information available.

Structured decision making (SDM) is a collaborative and facilitated approach used for problem solving (Gregory et al., 2012; Hemming et al., 2022). It is increasingly used in fields such as environmental management and public policy and is recommended by DEFRA's code on reintroductions in England (DEFRA, 2024). The process is based on an iterative cycle (**Figure 1**), commonly referred to as the ProACT cycle, in which the decision **P**roblem is clearly defined, **O**bjectives are explicitly stated, **A**lternative management strategies are defined and evaluated in terms of their predicted **C**onsequences on each objective, and **T**rade-offs are evaluated to inform a decision—all while explicitly accounting for uncertainty (Gregory et al., 2012; Hammond et al., 1999).

The implementation and monitoring of the decision provides insights that can be used to update the underlying information and assumptions during further iterations of the process. The SDM process also recognises that decisions are values-focused and, therefore, it explicitly integrates both science and values. Whilst SDM does not guarantee favourable outcomes, it increases the likelihood of achieving the best outcome.

Stages of SDM

- 1) **Clarify the decision problem.** This is achieved by creating a 'problem statement' that clearly defines the focus and scope of the decision problem and why it has arisen.
- 2) **Define objectives and performance attributes.** The SDM process is values-based, integrating the preferences and values of the decision-makers and stakeholders to identify the optimal management strategy. This process recognises that a strategy is simply a way of achieving a suite of given objectives; thus, no 'best' strategy can be defined unless the objectives are clearly stated alongside clear ways to measure each objective. Furthermore, success is also then best evaluated by how well an implemented strategy achieves stated objectives.
- 3) **Develop alternative strategies.** Once the objectives are clearly established, it is possible to define the potential management actions that could best achieve the objectives. Candidate strategies that include different combinations of actions are then constructed (i.e. alternative strategies). Given the biological and non-biological complexity of most environmental management, several alternative strategies with differing combinations of actions will inevitably be available and worth evaluating.

- 4) **Model & predict consequences.** Alternative strategies are then compared in terms of their expected outcomes with regard to the objectives. Outcomes, or consequences, can be predicted in different ways, including using models of the biological system and eliciting expert knowledge.
- 5) **Evaluate trade-offs & make a decision.** Objectives can often conflict with each other. It is necessary to understand how much each objective is valued relative to the others to make a decision that explicitly addresses the trade-offs at hand. In addition, it can be difficult to decide which strategy to choose when the outcomes of each strategy are uncertain. Acknowledging and quantifying uncertainty and evaluating its influence on the expected outcomes of alternative strategies improves transparency and provides decision-makers with a more complete assessment of the problem to aid in the decision making. SDM can draw from a wide array of tools to account for uncertainty, especially when there is a risk of negative outcomes, and help to trade-off competing objectives.
- 6) **Implement, monitor & review.** Once a strategy is chosen and implemented, it is important to monitor the outcomes to improve the information base for future decisions. A review mechanism should also be included in implementation so that new information can be incorporated into future decisions.

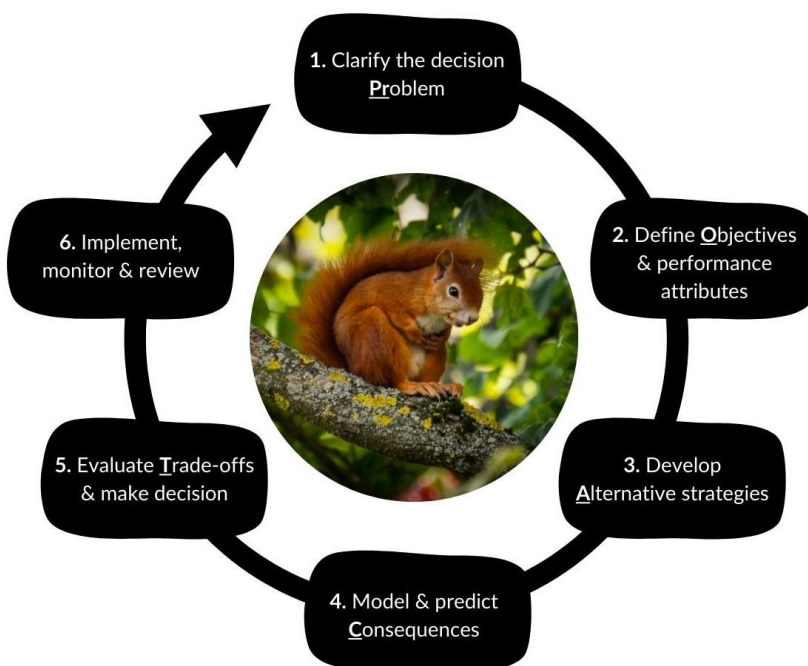


Figure 1. The structured decision making cycle, or PrOACT cycle, showing how the decision space can be navigated by clarifying the decision problem, defining objectives, developing alternatives, predicting consequences, and evaluating trade-offs before coming to a decision.

Stakeholder workshops

Stages 1-3 of the PrOACT cycle were developed and refined during in-person workshops and a series of online working group meetings. These are outlined below, with the process and outcomes for each stage described in more detail thereafter.

As first steps, two similarly structured two-day workshops were conducted in 2023 to approach the decision of how best to recover populations of red squirrels in England. The first workshop took place at the Zoological Society of London on 27–28 June 2023. The second workshop took place in Newcastle on 18–19 October 2023. Each workshop was attended by a different group of stakeholders.

In total, these workshops brought together 32 different stakeholders to discuss, and ensure inclusion of, their aspirations and concerns regarding red squirrel conservation. Stakeholders represented a broad range of interests and sectors, including academia, veterinary professionals, forestry, landowners, government organisations, NGOs, and volunteers from several red squirrel conservation groups across the country. A full list of workshop participants and their affiliations can be found in **Table A1** of **Appendix 1**.

The purpose of these first two workshops was to establish an agreed-upon problem statement, elicit objectives, and brainstorm potential management actions. Afterwards, we established five voluntary working groups that covered the fundamental objectives agreed upon in the workshops. In February 2024, we held a two-hour online meeting with each working group to further refine the performance attributes, the potential management actions, and start to build alternative strategies. These alternative strategies were then further refined by the Strategy Team throughout 2024. A full list of working group participants and their affiliations can be found in **Table A1** of **Appendix 1**.

Stage 1: Problem statement

The following problem statement was developed and agreed upon at the two workshops outlined above in **Stakeholder workshops**:

Red squirrels are an endangered native species in England that have experienced a major range contraction. The causes of their decline are multiple, but one major driver is the introduction of grey squirrels that outcompete red squirrels and are carriers of the squirrelpox virus. The squirrelpox virus is a fatal disease when contracted by red squirrels. Other drivers of red squirrel decline include the loss and fragmentation of habitat. In addition, there are potential demographic and genetic risks associated with small populations.

Although active conservation helps maintain stable populations, threats to red squirrels persist so the species is still of conservation concern and a priority to many. While there are challenges to red squirrel recovery, there is a belief that it is possible with the appropriate management support. Management actions are varied with some being less palatable to local/regional and national communities. There is a growing depth of knowledge from research into risks to red squirrels, but mitigation of these risks (including improving methods for grey squirrel management) remains uncertain. Furthermore, conflict exists between people who do not approve of management methods for various reasons, or do not see red squirrels as a priority.

Planning for red squirrel recovery needs to:

- 1) Determine the local conditions under which red squirrel recovery is possible and link to a national strategy.
- 2) Determine which of the available strategies to allow red squirrel recovery are most suitable across objectives, including the acknowledgement of conflict.
- 3) Understand the attitudes of involved stakeholders and relevant decision makers to the uncertainty and risk of a poor outcome across stated objectives.
- 4) Ensure any actions undertaken include learning to reduce key uncertainties.

Discussions around the hopes and challenges of red squirrel recovery in England have been long running. The outputs from this project will aid in making decisions around the best ways to implement actions addressed within the England Red Squirrel Action Plan. They will guide local recovery actions and inform a strategic approach to recovery at the national level, helping the government to achieve its national species recovery targets. Specifically the D4 abundance target and the D5 extinction target, which are reporting requirements under the Environment Act (2021). The outputs will help government to fulfil the aims of the Environmental Improvement Plan, which builds on, and is the first revision of, the 25 Year Plan. It is hoped that outputs from this project and structured process could complement other national strategies of Scotland and Wales.

Stage 2: Objectives

Background

In SDM, objectives are a statement of values, where the things that matter most to people are articulated as concise, context-specific statements. There are three main types of objectives: fundamental, means, and process.

- **Fundamental** objectives are those that people care about the most, regardless of how they are achieved.
- **Means** objectives are ‘intermediate’ objectives that are important because they help in achieving the fundamental objectives.
- **Process** objectives are those that describe how people want a decision to be made.

Fundamental objectives represent the criteria against which success should be judged, so it is necessary to determine a way to measure each objective. We refer to these measurement criteria as performance attributes.

Outcomes

Six fundamental objectives with 14 associated performance attributes were established through a process of workshops, working group meetings and refinement by the Strategy Team (**Table 1**). At this stage, the performance attributes still reflect the elements that the stakeholders care most about, rather than being specific measures of the objectives. The detailed performance attributes can be found in **Stage 4: Consequences**. The fundamental objectives, in no particular order, are:

- Maximise red squirrel recovery
- Maximise socioeconomic benefits
- Minimise non-target bycatch in grey squirrel traps*
- Minimise opposition to grey squirrel management actions**
- Minimise negative welfare impacts on squirrels
- Minimise cost

* Minimise non-target bycatch in grey squirrel traps was originally phrased as ‘Maximise wider ecosystem benefits’ with discussed performance attributes including species bycatch, carbon sequestration, and general knock-on effects to other species. However, throughout the project, it became clear that non-target bycatch was the most important factor, mentioned time and again by stakeholders in various meetings. As such, this became the focus of this objective. ** Originally referred to as maximise public support, but later framed as minimising opposition more specifically to the grey squirrel management actions being undertaken in each strategy.

Table 1. The six fundamental objectives that stakeholders agreed upon with how each should be evaluated (performance attributes) when deciding between strategies. The performance attributes were refined at a later stage, hence these are referred to as ‘draft’ performance attributes.

Fundamental objectives	Draft performance attributes
Maximise red squirrel recovery	<ul style="list-style-type: none"> 1) Population size 2) Distribution 3) Population viability
Maximise socioeconomic benefits	<ul style="list-style-type: none"> 1) Wellbeing 2) Forestry benefits
Minimise non-target bycatch in grey squirrel traps	<ul style="list-style-type: none"> 1) Bycatch of key species in kill traps 2) Bycatch of key species in live traps
Minimise opposition to grey squirrel management actions	<ul style="list-style-type: none"> 1) National opposition 2) Local opposition
Minimise negative welfare impacts on squirrels	<ul style="list-style-type: none"> 1) Impact of management on grey squirrels 2) Impact of translocations on red squirrels 3) Red squirrels suffering of squirrelpox
Minimise cost	<ul style="list-style-type: none"> 1) Total cost 2) Total cost per year

Process

Prior to the workshop, we circulated a questionnaire to the workshop participants that contained a set of six overlapping questions:

- 1) What do you hope to achieve for red squirrel recovery in England?
- 2) What do you think would be the **best** outcome(s) for red squirrel recovery in England?
- 3) What do you think would be the **worst** outcome(s) for red squirrel recovery in England?
- 4) Working towards red squirrel recovery in England, what issues/concerns would you address?
- 5) When developing and implementing a plan for red squirrel recovery in England, what actions/outcomes would you want to avoid?
- 6) What barriers do you think would hinder success for red squirrel recovery in England?

These questions allowed participants to express their aspirations and describe their concerns regarding red squirrel recovery in England. The responses to the questionnaire were used by the Strategy Team to develop a suite of values expressed as objectives, which were given to the participants during the workshop. To ensure independent discussions in each workshop, participants were only provided with the objectives that stemmed from that workshop's participants. Working in smaller groups of 3–4 people, participants used those answers as a prompt to identify their fundamental objectives (their core values) as well as categorising others as means or process objectives where possible. For each fundamental objective, groups suggested one or more performance attributes to provide a metric by which to compare potential conservation actions and strategies.

In each workshop, all the groups' fundamental objectives and performance attributes were consolidated into a set that was then discussed until agreed upon by the whole group. After the completion of both workshops, the Strategy Team consolidated the two agreed-upon sets into a set of five fundamental objectives with potential performance attributes. The Strategy Team also organised all objectives into an objectives hierarchy to visualise how each objective is linked to others and to the fundamental objectives (**Figure 2**). A summary of the key discussion points from both workshops can be found in **Appendix 2**. The full list of the original 77 objectives from both workshops, and how they are captured by the objectives hierarchy, can be found in **Table A2** in **Appendix 3**.

After the workshops, the objectives and performance attributes were refined during the online working group meetings. They have been further refined by the Strategy Team, in consultation with various stakeholders, throughout the course of the project. This included adding another fundamental objective, 'minimise negative welfare impacts on squirrels', that was overlooked during the workshops but raised by several different stakeholders and organisations afterwards. The final list of fundamental objectives, and how each was measured during this process, can be found in **Table 1**.

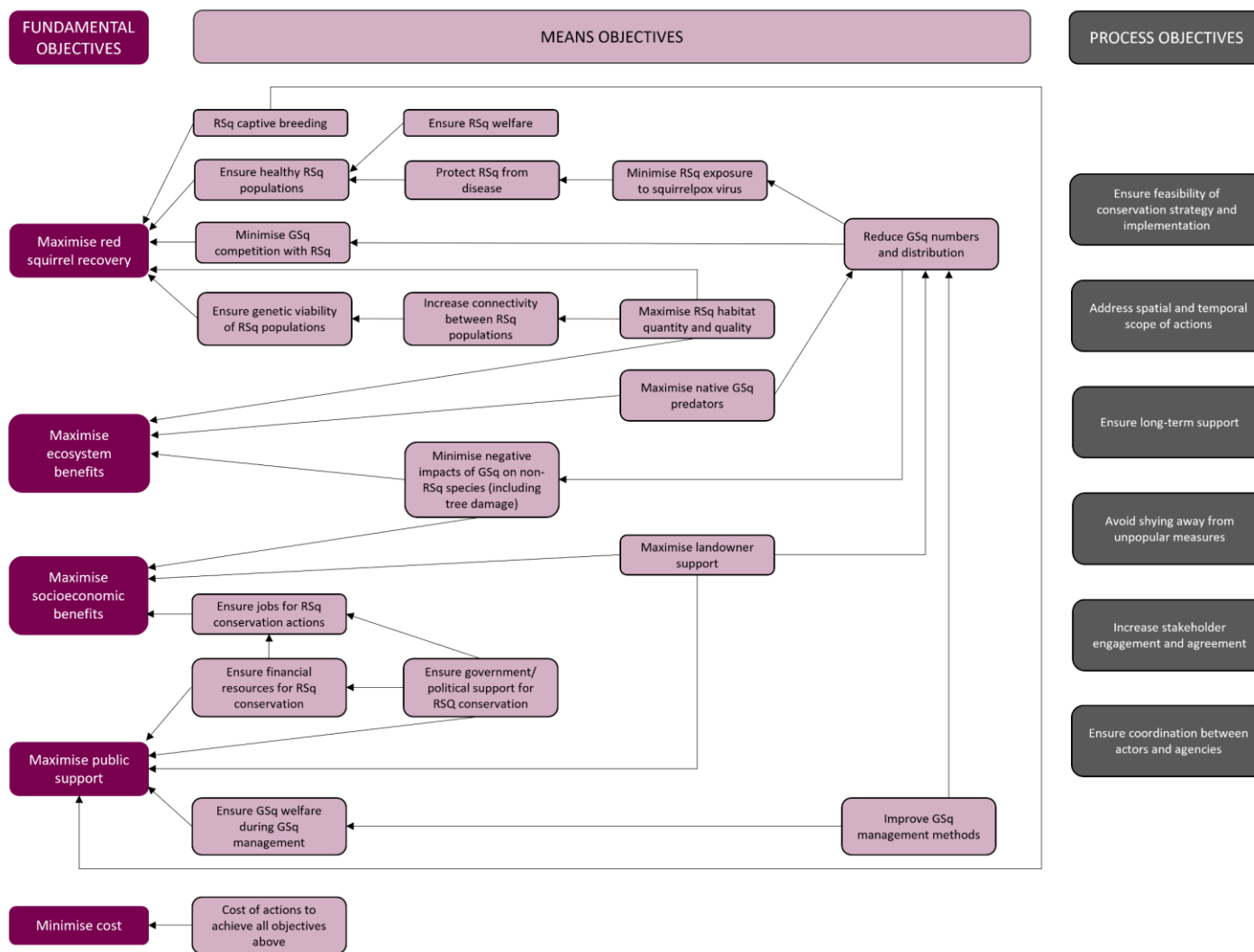


Figure 2. Objectives hierarchy showing the fundamental objectives (darker, left) and how the means objectives (lighter, central) link together to achieve the fundamental objectives. Process objectives (dark grey, right) determine how the actions and strategy should be formed, decided upon, and implemented. RSq = red squirrel, GSq = grey squirrel.

Stage 3: Alternative strategies

Background

From an SDM perspective, 'alternatives' are the possible actions that could be implemented to achieve the fundamental objectives. Alternatives are usually a suite of multiple actions rather than a single action. These suites of actions are referred to as 'alternatives', or in this case, we call them our 'alternative strategies'.

Outcomes

We built and compared a total of 18 alternative strategies. When building strategies, we considered four regions of England, that we self-determined and named, as shown in **Figure 3**:

- 1) **Northern England (NE)** – determined by current red squirrel distribution
- 2) **South West (SW)** – counties of Cornwall, Devon, Somerset, and Dorset, to complement ongoing pine marten reintroductions
- 3) **Rest of England (RoE)** – the rest of England not covered by our NE and SW region designations, except for the Isle of Wight
- 4) **Isle of Wight (IW)** – treated separately from the mainland due to being an island.

The actions within the strategies focus on lethal grey squirrel management (shooting, live traps and dispatch, and kill traps), non-lethal grey squirrel management (fertility control), red squirrel translocations (both reinforcements and reintroductions), and disease management (squirrelpox virus vaccine). An overview of each strategy is provided in **Table 2**, with a more detailed description of each below. Strategies are named according to where management takes place and what management takes place. Strategy names with a '+' indicate the addition of grey squirrel fertility control, and those with a '++' indicate the addition of both grey squirrel fertility control and a squirrelpox vaccine.

The first strategy (**Do nothing**), models what happens if all management is stopped. After this, there are three strategies that take the current level of management in Northern England and model what happens if this continues as is for 25 years (**Status quo**), what happens if this continues for 25 years with fertility control and a squirrelpox vaccine added when they become available (**Status quo++**), and what happens if this continues at current levels but all lethal grey squirrel management is stopped if fertility control becomes available (**Non-lethal**). The 'Non-lethal' strategy does not include a '+' in the name as the inclusion of fertility control is already indicated by the naming of the strategy unlike the rest of the strategies where this clarification is needed.

The rest of the strategies involve increased management efforts in the regions where they are focused. Three of the six strategies that focus on Northern England aim for local grey squirrel suppression using lethal grey squirrel management techniques only (**NE suppression**), using lethal management and fertility control (**NE suppression+**), and using lethal management, fertility control, and a squirrelpox vaccine (**NE suppression++**).

The other three strategies that focus on Northern England (**NE reinforcement**, **NE reinforcement+**, **NE reinforcement++**) include the same order of grey squirrel management effort but alongside opportunistic reinforcements of red squirrel populations in the current red squirrel range in Northern England.

To complement ongoing pine marten reintroductions in Devon and Somerset, we designed two strategies that, alongside increased management of grey squirrels in Northern England, aim for suppression of grey squirrels in the South West followed by reintroductions of red squirrels. These reintroduction strategies are modelled without (**SW reintroduction**) and with (**SW reintroduction++**) fertility control and squirrelpox vaccine options.

The last six strategies investigate increasing management effort across the whole of England (EN). The first of these three strategies aims for widespread grey squirrel suppression across England using only lethal grey squirrel management techniques (**EN suppression**), using lethal management and fertility control (**EN suppression+**), and using lethal management, fertility control, and a squirrelpox vaccine (**EN suppression++**). The other three strategies that focus on the whole of England include opportunistic reintroductions of red squirrels outside of their current Northern England range. Specifically, **EN reintroduction (RoE)** includes only lethal grey squirrel suppression with translocations of red squirrels to the area marked as the 'Rest of England' in **Figure 3**. **EN reintroduction++ (RoE)** is the same but with the inclusion of fertility control and a squirrelpox vaccine should they become available. The final strategy, **EN reintroduction+ (RoE + SW)**, includes England-wide suppression of grey squirrels via lethal management and fertility control, with opportunistic red squirrel reintroductions across the South West region as well as the Rest of England region.

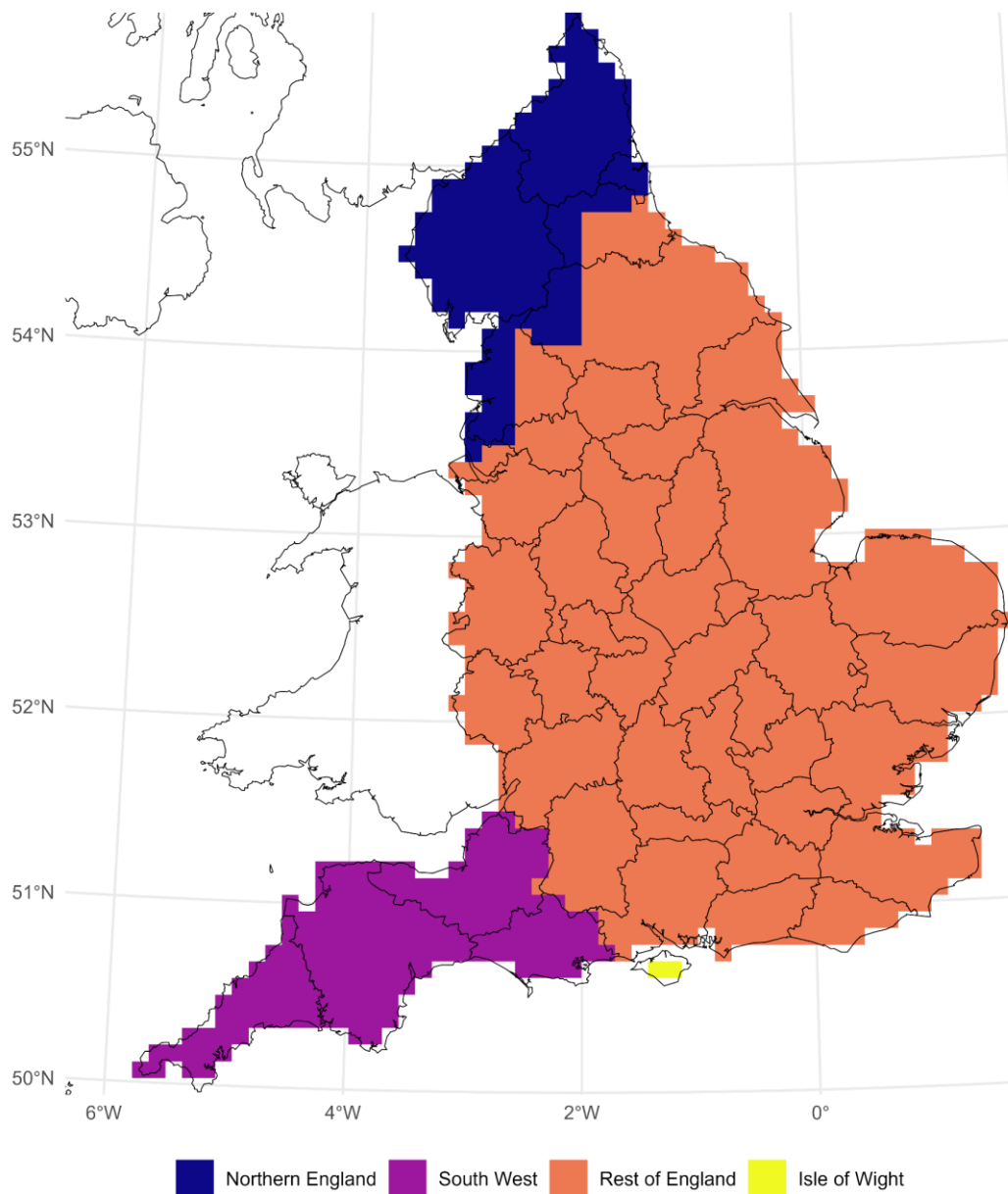


Figure 3. Spatial regions considered when building strategies. Blue = Northern England (where red squirrels are currently present); Purple = South West (counties of Cornwall, Devon, Somerset, and Dorset to complement ongoing pine marten reintroductions); Orange = Rest of England (everywhere else except the Isle of Wight), and Yellow = the Isle of Wight.

Table 2. Strategy table showing the combination of actions in each of the 18 strategies. For lethal grey squirrel (GSq) management, a single tick represents current levels of effort, while three ticks represent increased management efforts. For the ‘Non-lethal’ strategy, lethal management is undertaken at current levels, but ceases once fertility control become available (denoted with a single tick changing to a cross). The locations where management is conducted are denoted as: EN = England-wide; NE = Northern England; SW = South West; and RoE = Rest of England, as defined in Figure 3. In the strategy names, ‘+’ includes fertility control, and ‘++’ includes both fertility control and a squirrelpox virus (SQPV) vaccine.

	Lethal GSq management	Fertility control	SQPV vaccine	GSq management location	RSq translocations and location
1. Do nothing				EN	
2. Status quo	✓			NE	
3. Status quo++	✓	✓	✓	NE	
4. Non-lethal	✓ → ×	✓	✓	NE	
5. NE suppression	✓✓✓			NE	
6. NE suppression+	✓✓✓	✓		NE	
7. NE suppression++	✓✓✓	✓	✓	NE	
8. NE reinforcement	✓✓✓			NE	✓ NE
9. NE reinforcement+	✓✓✓	✓		NE	✓ NE
10. NE reinforcement++	✓✓✓	✓	✓	NE	✓ NE
11. SW reintroduction	✓✓✓			NE + SW	✓ SW
12. SW reintroduction++	✓✓✓	✓	✓	NE + SW	✓ SW
13. EN suppression	✓✓✓			EN	
14. EN suppression+	✓✓✓	✓		EN	
15. EN suppression++	✓✓✓	✓	✓	EN	
16. EN reintroduction (RoE)	✓✓✓			EN	✓ RoE
17. EN reintroduction++ (RoE)	✓✓✓	✓	✓	EN	✓ RoE
18. EN reintroduction+ (RoE + SW)	✓✓✓	✓		EN	✓ RoE + SW

For an accessible version of this table, please download the supplementary document from [the report page](#).

Strategy details

Management effort

The management effort in the strategies named **Status quo**, **Status quo++**, and **Non-lethal** is based on current grey squirrel management effort in Northern England. It is based on management conducted for red squirrel conservation and does not include grey squirrel management that is taking place for other purposes, e.g. tree protection from grey squirrel bark stripping. We took this decision as it is near impossible to estimate the baseline management of grey squirrels across the entirety of England by all parties due to a lack of data and data sharing. Whereas data exists in the current red squirrel range in Northern England thanks to ongoing efforts by volunteer groups. However, we also acknowledge that not all management efforts for red squirrel conservation in Northern England are recorded. As such, the management effort allocated in these three strategies is almost certainly an underestimate of the true effort and this should be considered when assessing the consequences of these strategies.

In contrast, all other strategies (except **Do nothing**), incorporate management efforts equivalent to those stated necessary for eradication, or at least large-scale suppression, of grey squirrels (Croft et al., 2021). Thus, management effort in these strategies is allocated independently from the estimates in status quo conditions, so they are not affected by the underestimation of current effort levels.

Translocations

It is recommended that a minimum of 19–20 red squirrels are translocated in the autumn for successful establishment of new populations (Poole, 2007). To prevent inbreeding, it is also recommended to reinforce populations with pairs of squirrels on four occasions over 50 years after the initial release (Poole, 2007). Although most translocations of red squirrels have used a process of delayed release (soft release) from intermediary enclosures (Lawton et al., 2015), some practitioners recommend immediate release (hard release) from nest boxes to reduce stress for translocated individuals (Dennis et al., 2009).

Given that there are no donor populations of red squirrels in England due to their low population numbers, we designed a translocation strategy that sources individuals from captivity. The translocation pathway we decided to incorporate in the model is an immediate (hard) release of 20 individual red squirrels from captivity in October, followed by reinforcements of 2 females every 4 years thereafter. This is similar to the Clocaenog Forest reinforcements in Wales (per. comm.). We allowed two translocations to take place per strategy but specified that neither could take place within the first 2 years of the strategy and that they had to be at least one year apart. This was determined after discussions with Judi Dunn (BIAZA Red Squirrel Focus Group / Wildwood Trust), Amy Wootton (Welsh Mountain Zoo) and members of BIAZA Red Squirrel Focus Group to ensure we designed feasible strategies that could be met by the current captive breeding facilities.

The locations for red squirrel reinforcements in Northern England, and reintroductions in the Rest of England, and the Rest of England plus the South West, were determined opportunistically during each model run (see **Stage 4: Consequences**). In contrast, the reintroductions in the two strategies specific to the South West only (**SW reintroduction** and **SW reintroduction++**) were assigned to specific hectads to complement pine marten reintroductions being undertaken by the Two Moors Pine Marten Project. Specifically, one hectad to the east of Dartmoor National Park in Devon (OS Grid Reference SX88) and one hectad to the east of Exmoor National Park in Somerset (OS Grid Reference SS94) were chosen due to having high predicted carrying capacities for pine martens and red squirrels. As well as higher relative carrying capacity for red squirrels than grey squirrels compared to surrounding hectads, due to the presence of coniferous woodland (**Figure 4**).

Fertility control and squirrelpox virus vaccine

Fertility control research is underway at the Animal and Plant Health Agency (APHA) with progress being made on the development and delivery of an oral contraceptive (Beatham et al., 2024). Research into developing a squirrelpox vaccine was previously started by Moredun with funding from the Wildlife Ark Trust but there is currently no oral vaccine under development. As such, both grey squirrel fertility control and a squirrelpox virus vaccine are not currently available for use and strategies that include these actions may never become an option. Hence, there is always a strategy that focuses on lethal management of grey squirrels with either fertility control included (strategy names with a '+') or both fertility control and a squirrelpox vaccine included (strategy names with a '++'). The **Non-lethal** alternative, whereby once fertility control becomes available all lethal grey squirrel management actions cease, was included as a means towards achieving the minimise public opposition objective as people have previously been found to be more supportive of fertility control than lethal control (Dunn et al., 2018).

Given the uncertainty around these methods becoming available and the timescales, for all model runs in alternatives that included fertility control and/or squirrelpox vaccine, we assigned both i) a probability that such technology will become available, and ii) the expected time until it does so. These values were elicited in the biological expert elicitation workshops (see **Stage 4: Consequences** and **Table 15**). As a result, the outputs from modelling these strategies are an average of possible futures where these methods take effect for different periods of time, or sometimes never become available at all. Thus, they should be considered as what the future could look like, given additional methods for red squirrel conservation become available, and not a strict outlook on exactly what the addition of fertility control or a squirrelpox vaccine means. Overall, this means a decision can be made now based on available actions, but with the knowledge of what might happen in the future, should one or both technologies become available.

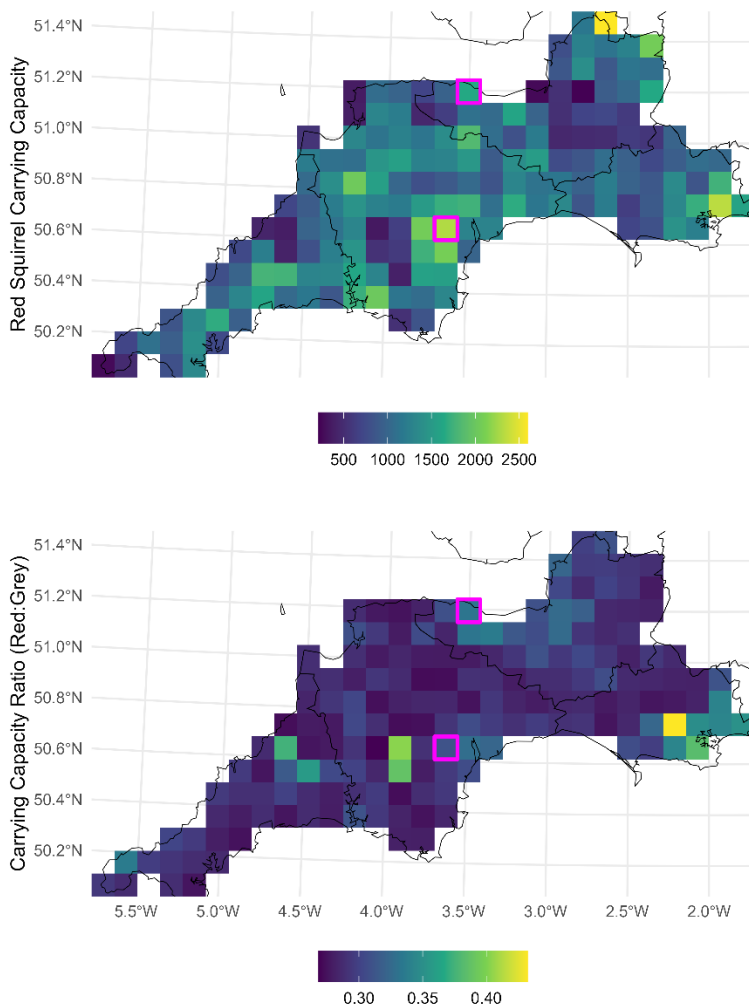


Figure 4. The South West region of England showing red squirrel carrying capacity (top) and the carrying capacity ratio between red and grey squirrels (bottom). The red squirrel release hectads that were specified in the model are those highlighted with a pink border, i.e. where red squirrel carrying capacity is high and where the ratio of red to grey squirrel carrying capacity is the highest of the hectads where pine martens are predicted to be present. Carrying capacities were taken from Slade et al. (2023). Predicted pine marten presence was supplied by Vincent Wildlife Trust and is not displayed here.

Process

Actions

Actions were initially brainstormed and evaluated in the two in-person workshops. Participants were asked to provide all the actions they could think of that would contribute towards achieving one or more of the fundamental objectives agreed upon in their workshop. They did this by writing their ideas on sticky notes and putting them onto flipcharts representing four different themes: Red Squirrel Conservation, Grey Squirrel Management, Habitat Management, and Other (to allow for any actions that did not fall under any of the first three themes). The workshop facilitators then aggregated the results and removed any duplicates or suggestions that were not considered to be actions related to achieving the objectives.

After aggregation of the actions, participants were asked to provide their judgement on how impactful these actions would be in relation to the fundamental objectives, and their confidence in that judgement. They were also asked to pick which actions from the complete set they would choose to implement if they were to create a red squirrel conservation strategy. This activity changed substantially between workshops.

Participants of workshop 1 provided their judgement of impact and confidence only on the actions they picked as part of their personal strategy and provided such judgements over all fundamental objectives (except for welfare, as this objective was added later). In workshop 2, participants only evaluated actions by their impact on the biological fundamental objective (maximise red squirrel recovery) but did so for all the actions available. After the evaluation exercise, the facilitators led an open discussion about the results, to help clarify whether and why some actions were preferred over others, and why there was uncertainty around the outcome of specific actions.

To aggregate the results for both workshops, the Strategy Team grouped the actions into more nuanced themes than the original four then rescaled the assessed impact and confidence to fit within the same constructed scales. For impact, all answers were fitted to a scale going from -2 to 2 (where -2 means "High negative impact", -1 "Low negative impact", 0 "No impact", 1 "Low positive impact" and 2 "High positive impact"). Confidence was fitted to a scale going from -1 to 1 (-1 being "Not very confident", 0 "Somewhat confident" and 1 "Very confident"). The results of this process are shown in **Table A3** in **Appendix 3**.

The list of candidate actions was clarified and refined in the working group meetings. The remaining actions and their purpose are presented in **Table 3**. A conspicuous absence from the list in **Table 3** is gene drive technology. Although this was considered as a potential action for grey squirrel management (see **Table A3**), it was considered too hypothetical at this stage for inclusion in planning for red squirrel recovery.

Table 3. Current and potential actions to aid red squirrel recovery in England alongside the purpose of each action, as discussed in workshops and working group meetings.

Theme	Type	Action	Purpose
Grey squirrel management	Lethal	Live trapping Single traps or multi-catch traps followed by shooting or cranial dispatch	Reduce number and distribution of grey squirrels
Grey squirrel management	Lethal	Kill trapping Varieties of spring traps or resetting traps such as GoodNature traps	Reduce number and distribution of grey squirrels
Grey squirrel management	Lethal	Shooting Free shooting; at bait stations; drey poking	Reduce number and distribution of grey squirrels
Grey squirrel management	Non-lethal	Fertility control if/when available	Reduce number and distribution of grey squirrels without lethal management
Grey squirrel management	Biological control	Pine martens	Reduce number and distribution of grey squirrels
Red squirrel conservation	Disease management	Squirrelpox virus vaccine if/when available	Reduce number of red squirrel deaths from squirrelpox virus
Red squirrel conservation	Disease management	Rapid squirrelpox response	Remove infected individual red squirrels from the population to prevent/reduce transmission of squirrelpox virus to other red squirrels, thus reducing number of red squirrel deaths

Theme	Type	Action	Purpose
Red squirrel conservation	Artificial structures	Rope bridges	Provide safe crossing of roads in red squirrel habitat to reduce red squirrel roadkill
Red squirrel conservation	Artificial structures	Nest boxes	Increase red squirrel nesting opportunities, and provide refuge from squirrel predators
Red squirrel conservation	Translocations	Wild-to-wild	Increase number of red squirrels in currently-occupied areas (reinforcements) or establish new populations in areas not currently occupied (reintroductions)
Red squirrel conservation	Translocations	Captive-to-wild	Increase number of red squirrels in currently-occupied areas (reinforcements) or establish new populations in areas not currently occupied (reintroductions)
Red squirrel conservation	Captive populations	Establish greater number of captive facilities more widely spread across England	Increase captive stock of red squirrels for potential translocations and improve public access so more people can see and learn about red squirrels
Habitat management	Restoration / creation of habitat	Commercial woodland planting	Increase and improve habitat available for red squirrels
Habitat management	Restoration / creation of habitat	Natural woodland planting	Increase and improve habitat available for red squirrels

Theme	Type	Action	Purpose
Habitat management	Restoration / creation of habitat	Hedgerow planting	Increase connectivity between fragmented habitats
Raising Awareness	Communications package	One full comms package including: outreach on social and mainstream media; inclusion of red squirrels in national curriculums; red squirrel ambassador scheme for local and national community outreach; dedicated PR/comms officers	Increase public support for red squirrel recovery and get more people involved in conservation efforts

Causal maps

Once the list of actions was agreed, the Strategy Team drafted causal maps, sometimes referred to as influence diagrams, which show the relationships between the actions and fundamental objectives. These were discussed and edited in each working group meeting. These diagrams are not exhaustive and depict the relationships and mechanisms deemed most important from the workshop and working group discussions. The causal map for the welfare objective was created by the Strategy Team alone, as this objective was added after the working group meetings had taken place. All six causal maps are shown in **Figure 5 – Figure 10**.

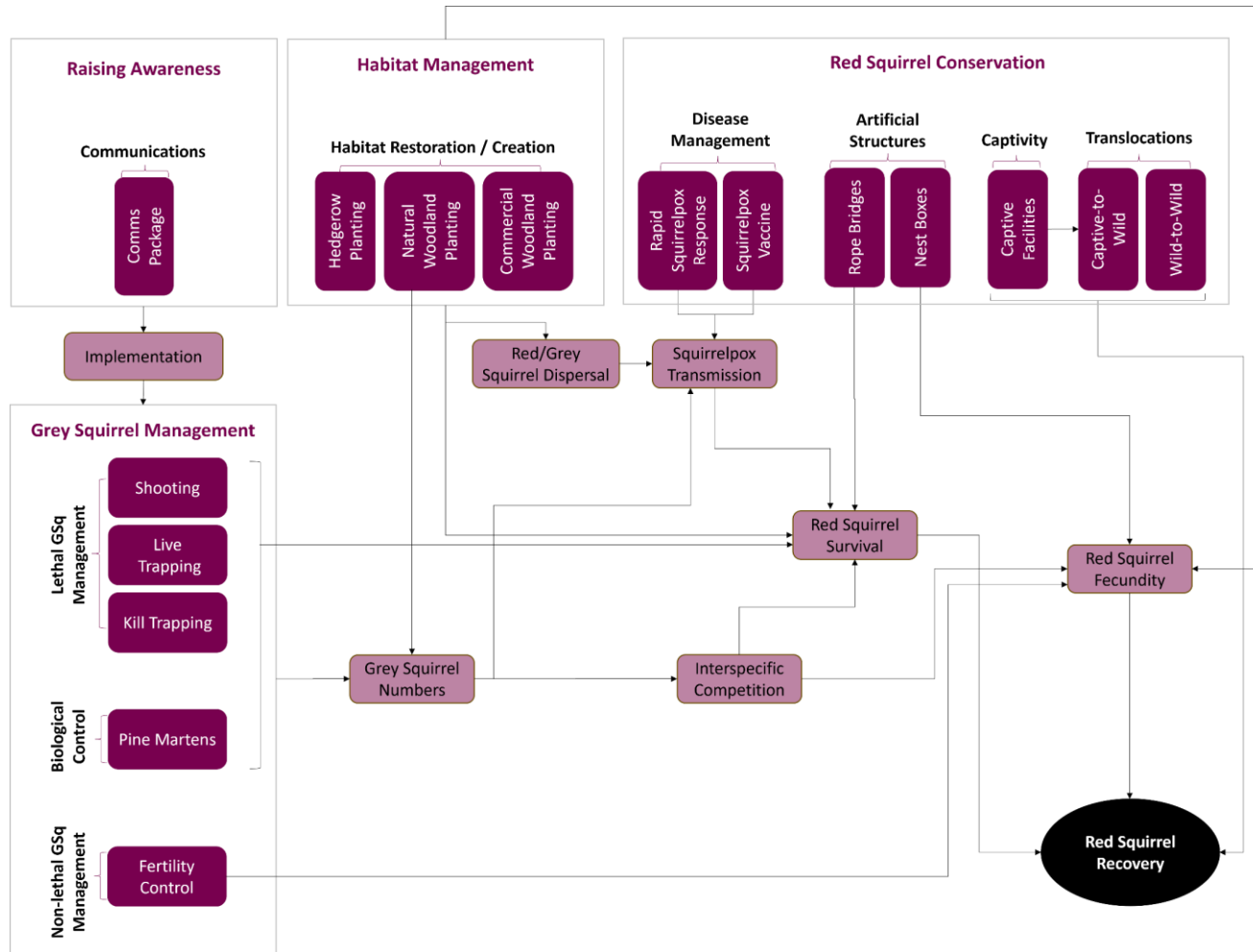


Figure 5. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of maximising red squirrel recovery.

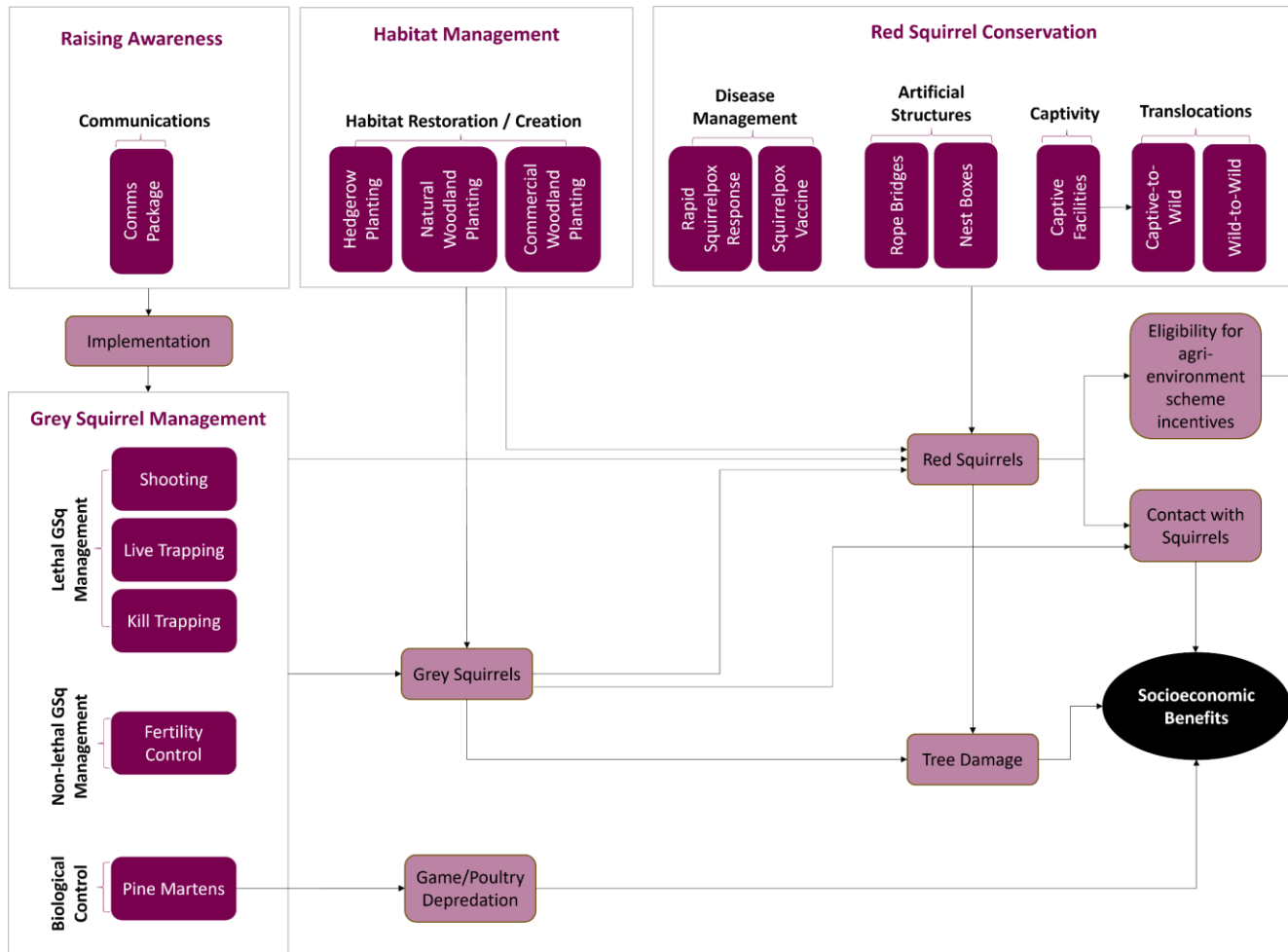


Figure 6. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of maximising socioeconomic benefits.

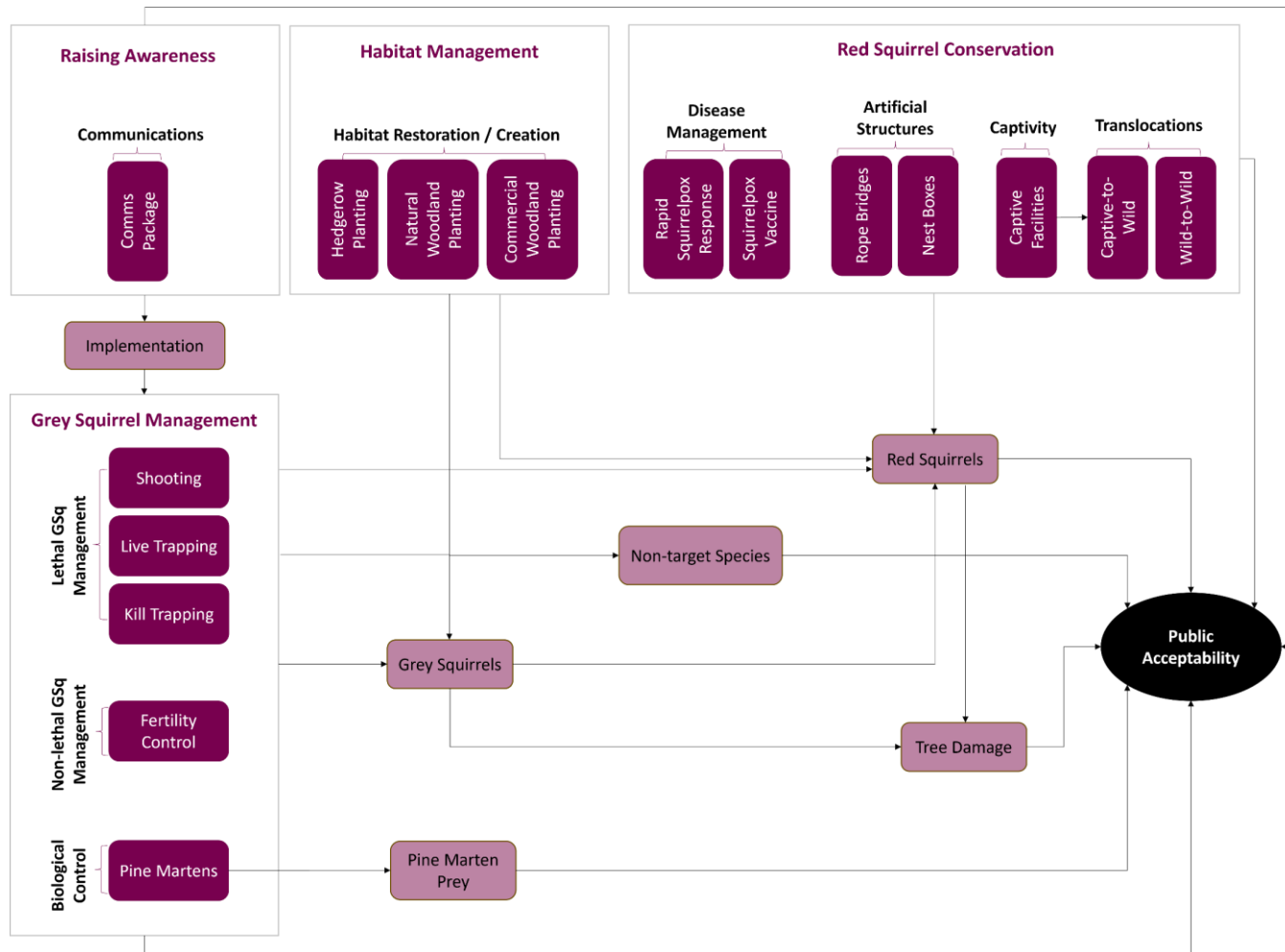


Figure 7. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of maximising public support.

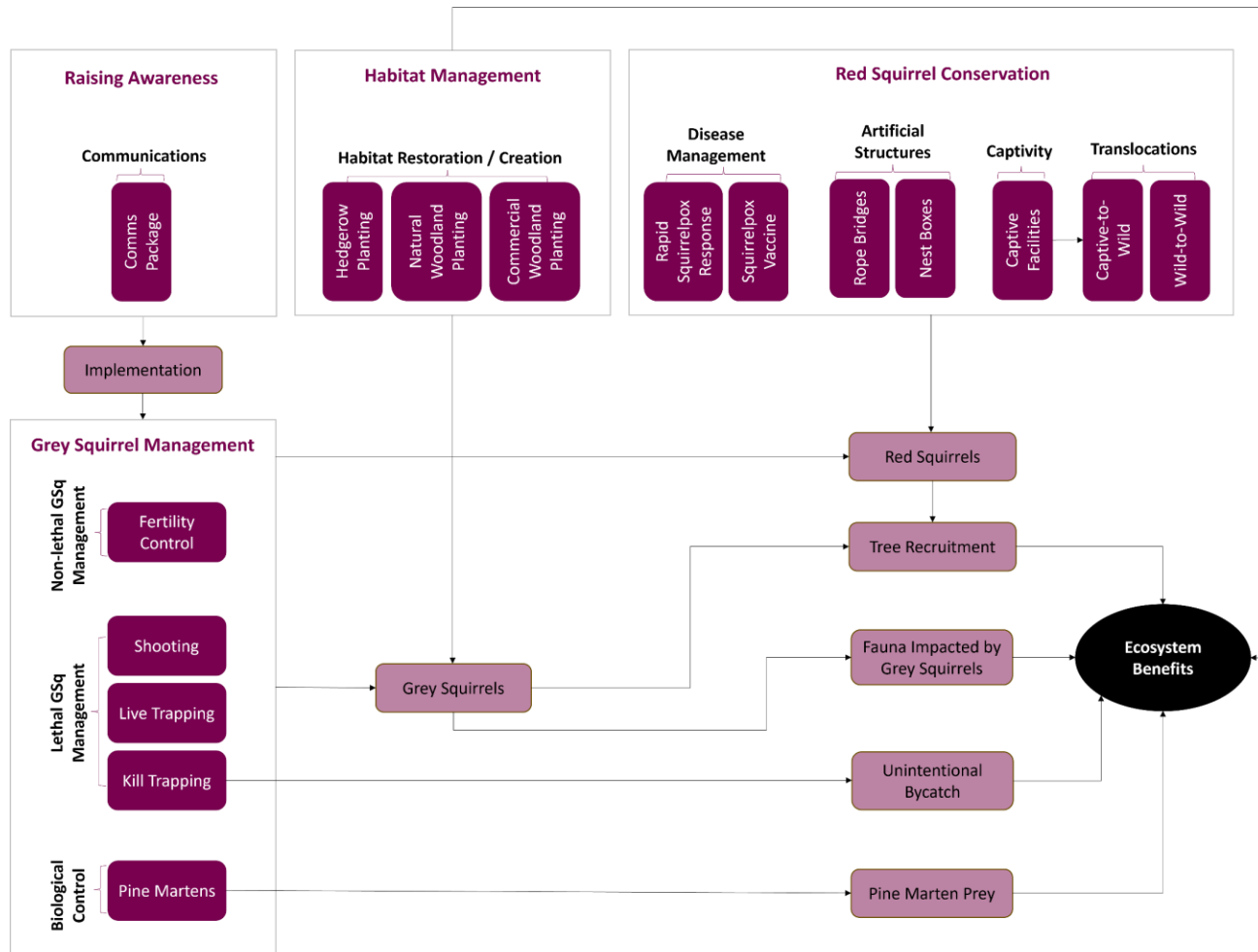


Figure 8. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of maximising wider ecosystem benefits.

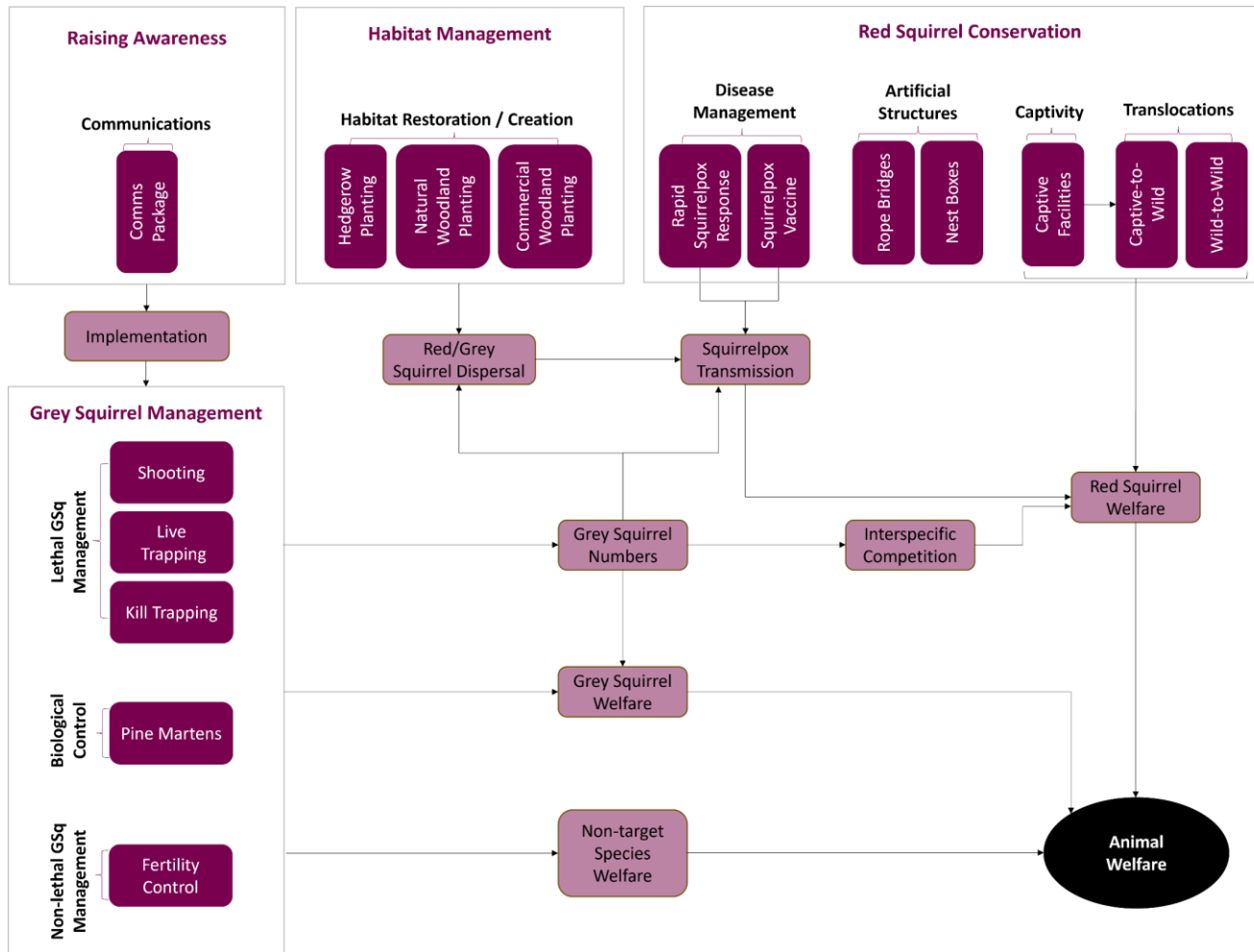


Figure 9. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of minimising negative welfare impacts on squirrels.

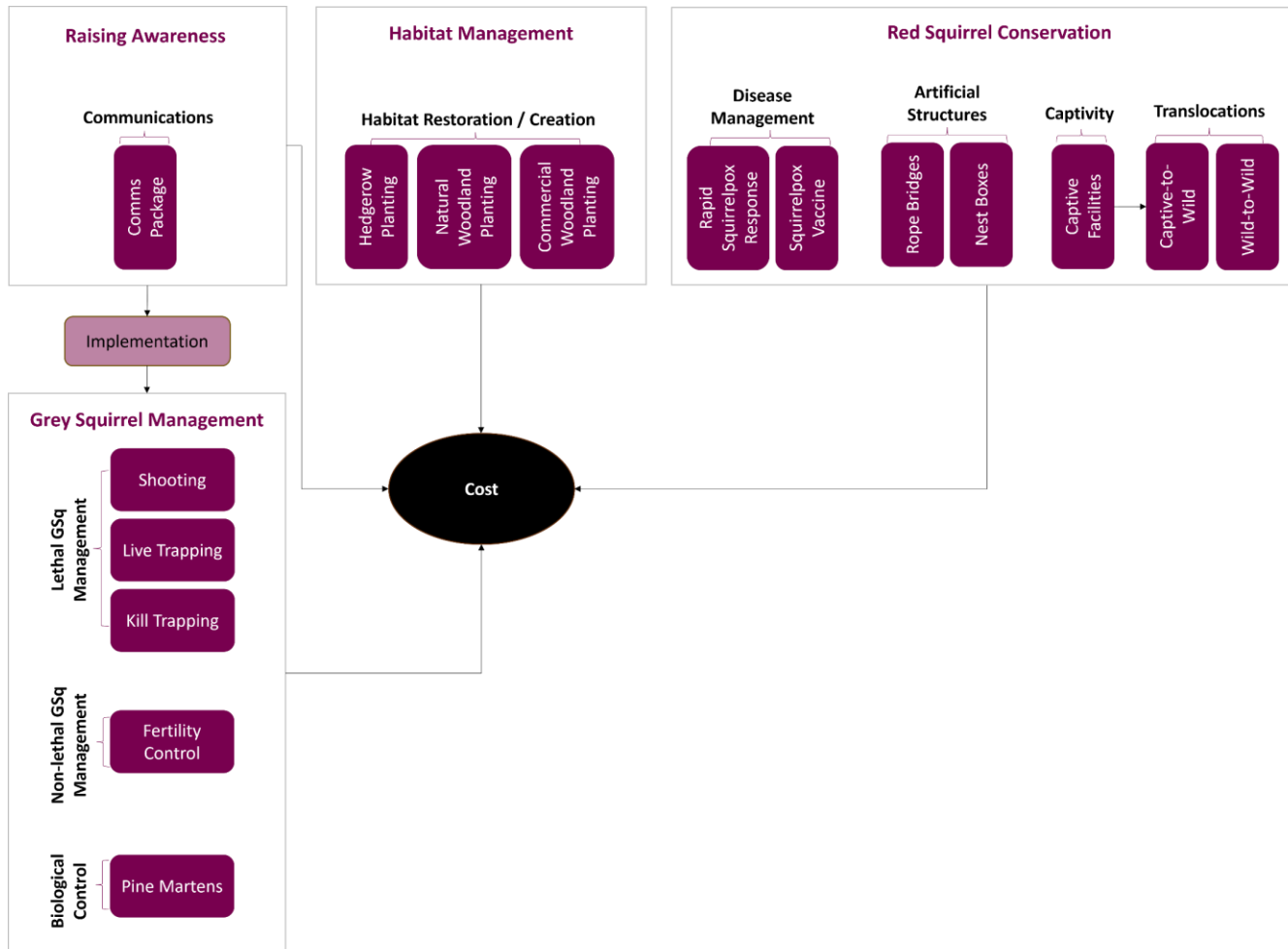


Figure 10. Causal map showing the key pathways (lighter rectangles) by which the actions (darker rectangles) can affect the fundamental objective (black oval) of minimising cost.

Building alternatives

Based on the discussions during the workshops and working group meetings, the Strategy Team started developing more complete alternatives. During this process, it became clear that some of the actions would not affect the outcomes at the intended scale of modelling or would need to be simplified to be included. Thus, some of the previously-established actions were removed (**Table 4**), leaving a shorter candidate action list split into four main themes: lethal grey squirrel management, non-lethal grey squirrel management, disease management, and red squirrel translocations (**Table 5**). We then built 18 strategies that spanned a range of options, whether these actions were included or not, and how they were implemented (e.g. at current effort levels or increased effort levels). These are the final 18 strategies, as shown in **Table 2**.

Table 4. Actions that were initially brainstormed but not included when building strategies alongside the justification for their exclusion.

Action	Reason for removal
Pine martens	<ul style="list-style-type: none"> • Unsure of effect on red and grey squirrels in England. • A species with its own long-term recovery strategy; will not be reintroduced as an action specific to red squirrel conservation. • Will be included in the models to interact with red and grey squirrels, just no direct action on pine martens for a red squirrel recovery strategy.
Rapid squirrelpox response	<ul style="list-style-type: none"> • It would be difficult to realistically estimate the detection process and the detection rate of squirrelpox. Also, the transmission is so quick between reds that spillover events are difficult to mitigate through euthanasia. As such, this action was also unlikely to influence transmission rates at the scale of the model.
Artificial structures	<ul style="list-style-type: none"> • Large-scale modelling at hectad level across the entirety of England so small-scale structures unlikely to contribute to any population changes in the models.
Wild-wild translocations	<ul style="list-style-type: none"> • No populations in England to act as a donor population. • Genetic provenance and disease risks need careful consideration before using a donor population from mainland Europe. • Post-release survival was estimated as slightly higher for captive individuals than wild in the expert elicitation, so we chose to use

Action	Reason for removal
	<p>captive-wild translocations in the strategies to capture the more optimistic outcomes.</p>
Captive populations	<ul style="list-style-type: none"> • Workshop participants proposed increasing the number of captive populations as an action to help with translocations and to help with raising awareness of red squirrel conservation through increased visitor engagement. • We group the increased visitor engagement into the raising awareness action (see below). • There are currently sufficient captive populations to meet the translocation strategies we propose in these overall strategies. If translocation appears to be a viable option after the model outputs, then increasing the captive populations and breeding effort could be considered in more detail.
Habitat management	<ul style="list-style-type: none"> • Any habitat modifications started now are unlikely to affect squirrel populations as time taken to reach maturity (approx. 30-40 years) is greater than the period of time we are modelling (25 years).
Raising awareness	<ul style="list-style-type: none"> • Any chosen strategy should include a communications package to raise awareness. This would not have changed between strategies and, therefore, would not have influenced the decision over which strategy to choose. However, it should be noted that this action requires costing and adding to the total cost of any chosen strategy.

Table 5. Actions that were included when building strategies and what the alternatives for each action can be.

Theme	Specific action	Alternatives
Lethal grey squirrel management	Live trapping	<ul style="list-style-type: none"> • Current effort levels. • Increased effort.
Lethal grey squirrel management	Kill trapping	<ul style="list-style-type: none"> • Current effort levels. • Increased effort. • Do not use in urban areas, or in areas with red squirrels, pine martens, or hazel dormice.
Lethal grey squirrel management	Shooting	<ul style="list-style-type: none"> • Use at current effort levels. • Increased effort. • Do not use in urban areas.
Non-lethal grey squirrel management	Fertility control	<ul style="list-style-type: none"> • Never becomes available. • Use when becomes available.
Disease Management	Squirrelpox vaccine	<ul style="list-style-type: none"> • Never becomes available. • Use when becomes available.
Red squirrel translocations	Captive-wild	<ul style="list-style-type: none"> • No translocations. • Reinforce existing populations in Northern England. • Reintroduce to form new populations: <ul style="list-style-type: none"> ○ At specified locations in the South West to complement ongoing pine marten reintroductions. ○ At opportunistic locations everywhere in England (including the South West) except the Northern England region.

Stage 4: Consequences

Background

The fundamental objectives represent the criteria against which choices between alternatives should be made, and ultimately, that success should be judged. As such, it is necessary to determine a way to measure the outcome (consequences) of the alternatives for each objective. We refer to these measurement criteria as performance attributes and use a range of techniques, including expert elicitation and population modelling, to predict the consequences of each alternative for each performance attribute.

Outcomes – Performance attributes

These were initially drafted during workshops and working group meetings and later refined by the Strategy Team. The detailed performance attributes are described in **Table 6**.

Table 6. The six fundamental objectives that stakeholders agreed upon with how each should be evaluated (performance attributes) when deciding between strategies.

Fundamental objectives	Performance attributes
<p>Maximise red squirrel recovery</p>	<p>Population size</p> <ul style="list-style-type: none"> • Average estimated national population size across England after 25 years. <p>Distribution</p> <ul style="list-style-type: none"> • Average number of occupied hectads after 25 years. • Average number of occupied counties after 25 years. <p>Population viability</p> <ul style="list-style-type: none"> • Probability of red squirrel persistence on mainland England over 25 years.
<p>Maximise socioeconomic benefits</p>	<p>Wellbeing / connection to nature</p> <ul style="list-style-type: none"> • Score comprised of the number of hectads occupied by grey squirrels only, red squirrels only, both species, and neither species at the end of 25 years. The scores are weighted by the type of species present, and number of people present then summed across England.

Fundamental objectives	Performance attributes
	<p>Forestry benefits</p> <ul style="list-style-type: none"> Total area of broadleaf woodland where grey squirrel density is lower than 90% of carrying capacity. This is a proxy measure of tree damage as bark stripping occurs when grey squirrel density gets closer to carrying capacity in broadleaf habitats. This was measured in the 25th year at the time when grey squirrel densities were highest that year.
<p>Minimise non-target bycatch in grey squirrel traps</p>	<ul style="list-style-type: none"> Average annual live trap days per hectad. Calculated as the average over 25 years of: the number of single capture live traps multiplied by the number of days used per year, divided by the number of hectads they are used in each year. This is a proxy measure of the potential for non-target species by-catch. Average annual kill trap days per hectad. Calculated as above but for the number of kill traps.
<p>Minimise opposition to grey squirrel management actions</p>	<ul style="list-style-type: none"> Percentage of the national population predicted to be opposed to the proposed grey squirrel management methods. Percentage of the local population (where grey squirrel management is taking place) predicted to be opposed to the proposed grey squirrel management methods.
<p>Minimise negative welfare impacts on squirrels</p>	<p>Grey squirrels</p> <ul style="list-style-type: none"> Individualised utility score based on assessment of relative welfare impacts of grey squirrel management methods. The assessment was done using a modified Sharp & Saunders (2011) approach with incorporation of the average number of grey squirrels being subject to each management method over the 25 years. <p>Red squirrels</p> <ul style="list-style-type: none"> Probability that red squirrel translocations take place as part of the strategy. Average total number of red squirrels that die from squirrelpox virus over 25 years.
<p>Minimise cost</p>	<ul style="list-style-type: none"> Average cost per year over 25 years (GBP).

Outcomes – Consequence tables

The results for each performance attribute across each alternative strategy are summarised in a consequence table (**Table 7**) followed by an additional consequence table highlighting the best and worst outcomes for each objective (**Table 8**).

Red squirrel numbers, hectads, counties, and persistence are natural measures of predicted red squirrel recovery (where higher values indicate better outcomes). A similar structure applies for the number of red squirrels dying from squirrelpox and the annual cost, but in these cases the higher numbers are worse outcomes for those objectives.

Live trap effort and kill trap effort are indices representing the potential for non-target species bycatch, where higher values again reflect poorer outcomes. The connection to nature score is another index, this time of people's connection to nature through having squirrels in their local area, but for this performance attribute higher scores are considered a better outcome. Tree damage is also presented so that the higher values are better outcomes, as the area of *undamaged* woodland is given in the table.

For public acceptability, the percentage of people predicted to oppose each strategy is given at the national and local level. Higher values represent lower acceptability and therefore poorer performance for this objective.

As well as the number of squirrels dying from squirrelpox, red squirrel welfare was also measured in relation to translocations. We assumed that translocations incur some negative welfare experiences for red squirrels. Therefore, the performance attribute is based on the probability that translocations go ahead in the strategies over the 1,000 model runs, where higher values indicate worse outcomes for red squirrel welfare.

We assessed grey squirrel welfare outcomes by grouping strategies that led to similar impacts — both in terms of the types of interventions used and the number of grey squirrels affected. These groups were then ranked, with the most favourable outcome (no intervention on any grey squirrels) placed first, and the least favourable (millions of grey squirrels subjected to all types of interventions) placed last. We then applied the rank order centroid method, giving higher-ranked groups proportionally more weight.

For more detail on what each performance attribute in the consequence table refers to and how it was calculated, please refer to **Table 6** above and to the **Process** section of the Consequences below.

Table 7. Predicted outcomes of each of the 18 strategies (left column) for the 14 performance attributes (second row) associated with the six fundamental objectives (top row). RSq = red squirrel; GSq = grey squirrel.

	Red squirrel recovery				Non-target bycatch		Socioeconomic factors		Public acceptability		Squirrel welfare			Cost
	RSq (#)	RSq hectads (#)	RSq counties (#)	RSq P ₍₂₅₎	Live trap effort	Kill trap effort	Connection to nature score	Undamaged broadleaf woodland (km ²)	National opposition (%)	Local opposition (%)	GSq score	RSq trans. prob	RSq dying from SQPV (# k)	Annual cost (£ mn)
1. Do nothing	1 (0-8)	2.5 (1.0-5.0)	1.1 (1.0-2.0)	0.078	0 (0-0)	0 (0-0)	56.1 (56.1-56.4)	7,181 (21-12,069)	0	0	0.340	0	16 (10-22)	0.00-0.00
2. Status quo	2 (0-16)	2.7 (1.0-6.0)	1.2 (1.0-3.0)	0.128	9 (5-5)	0 (0-0)	56.1 (55.9-56.4)	7,277 (53-12,069)	53.3	50.1 (3.4)	0.215	0	16 (9-22)	5.18-5.34
3. Status quo++	3 (0-16)	2.7 (1.0-6.0)	1.2 (1.0-3.0)	0.128	9 (5-5)	0 (0-0)	56.1 (55.9-56.4)	7,276 (53-12,069)	53.3	50.1 (3.4)	0.152	0	16 (9-22)	5.26-5.46
4. Non-lethal	1 (0-12)	2.6 (1.0-5.0)	1.1 (1.0-2.0)	0.104	6 (1-5)	0 (0-0)	56.1 (56.0-56.4)	7,202 (21-12,069)	14.4	13.4 (0.9)	0.215	0	16 (9-22)	2.98-3.13
5. NE supp	4,321 (0-23,477)	48.9 (1.0-219.0)	3.6 (1.0-7.0)	0.638	1,719 (245-4,351)	0 (0-0)	55.3 (52.4-56.8)	7,597 (1,184-12,069)	53.3	50.1 (3.4)	0.111	0	31 (9-116)	67.37-78.11
6. NE supp+	4,892 (0-26,889)	52.8 (1.0-236.7)	3.7 (1.0-7.2)	0.661	1,783 (245-4,158)	0 (0-0)	55.0 (52.4-56.7)	7,601 (1212-12069)	53.3	50.1 (3.4)	0.111	0	34 (9-122)	70.63-83.00
7. NE supp++	4,865 (0-26,889)	52.7 (1.0-236.7)	3.7 (1.0-7.2)	0.661	1,783 (245-4,158)	0 (0-0)	55.0 (52.4-56.7)	7,601 (1,212-12,069)	53.3	50.1 (3.4)	0.111	0	34 (9-122)	70.65-83.03
8. NE rf	4,098 (0-21,856)	47.9 (2.0-207.0)	4.0 (1.0-8.0)	0.731	1,709 (245-4,382)	0 (0-0)	55.4 (52.6-56.9)	7,606 (1,184-12,069)	53.3	50.1 (3.4)	0.111	0.88	32 (9-121)	67.37-78.11
9. NE rf+	5,422 (0-25,824)	58.9 (2.0-239.0)	4.5 (1.0-8.0)	0.757	1,959 (253-5,866)	0 (0-0)	55.4 (52.5-56.9)	7,472 (1216-12069)	53.3	50.1 (3.4)	0.111	0.93	37 (10-129)	70.63-83.01
10. NE rf++	4,754 (0-26,470)	53.0 (2.0-233.0)	4.3 (1.0-8.0)	0.756	1,784 (245-4,776)	0 (0-0)	55.2 (52.5-56.8)	7,610 (1,214-12,069)	53.3	50.1 (3.4)	0.111	0.94	35 (9-124)	70.65-83.03
11. SW rt	10,300 (0-75,178)	60.9 (2.0-268.2)	4.6 (1.0-10.0)	0.698	1,959 (253-5,866)	0 (0-0)	54.1 (48.6-56.6)	8,327 (3,146-12,069)	53.3	51.6 (7.1)	0.079	0.58	32 (9-118)	142.74-165.49
12. SW rt++	12,955 (0-83,993)	69.2 (2.0-300.2)	5.1 (1.0-10.0)	0.714	2,080 (253-5,963)	0 (0-0)	53.5 (48.6-56.4)	8,340 (3,211-12,069)	53.3	51.6 (7.1)	0.079	0.73	34 (9-127)	149.61-175.81
13. EN supp	43,527 (0-286,790)	120.4 (1.0-547.0)	6.6 (1.0-22.0)	0.67	1,615 (196-3,900)	1,359 (148-4,529)	31.8 (0.0-56.4)	11,950 (10,789-12,069)	55.7	55.3	0.054	0	22 (9-89)	486.92-567.59
14. EN supp+	52,468 (0-299,742)	132.7 (1.0-557.2)	6.9 (1.0-22.0)	0.692	1,855 (196-3,837)	1,559 (149-4,498)	24.2 (0.0-56.4)	11,979 (11,305-12,069)	55.7	55.3	0.054	0	21 (9-85)	494.57-582.14
15. EN supp++	52,463 (0-299,742)	132.7 (1.0-557.2)	6.9 (1.0-22.0)	0.691	1,881 (196-3,996)	1,559 (149-4,498)	24.2 (0.0-56.4)	11,979 (11,305-12,069)	55.7	55.3	0.054	0	21 (9-85)	494.62-582.22
16. EN rt (RoE)	53,664 (0-410,371)	139.8 (2.0-665.2)	9.4 (1.0-31.0)	0.739	1,526 (196-3,244)	1,308 (148-4,455)	33.6 (0.1-56.8)	11,950 (10,789-12,069)	55.7	55.3	0.054	0.80	24 (9-109)	486.93-567.60
17. EN rt++ (RoE)	66,125 (0-419,091)	157.7 (2.0-688.0)	10.3 (1.0-31.0)	0.758	1,855 (196-3,837)	1,542 (149-4,442)	26.9 (0.1-56.4)	11,979 (11,328-12,069)	55.7	55.3	0.054	0.90	24 (9-99)	494.67-582.28
18. EN rt+ (RoE + SW)	66,638 (0-419,281)	158.8 (2.0-698.7)	10.3 (1.0-31.0)	0.763	1,783 (245-4,158)	1,495 (149-4,468)	26.8 (0.1-56.4)	11,979 (11,301-12,069)	55.7	55.3	0.054	0.90	24 (9-100)	494.62-582.21

Table 8. Repeated consequence table with the best outcomes for each performance attribute in green and the worst outcomes in blue – a paler colour is used to show the next best or worst outcome if the first came from the ‘Do nothing’ strategy.

	Red squirrel recovery				Non-target bycatch		Socioeconomic factors		Public acceptability		Squirrel welfare			Cost
	RSq (#)	RSq hectads (#)	RSq counties (#)	RSq P ₍₂₅₎	Live trap effort	Kill trap effort	Connection to nature score	Undamaged broadleaf woodland (km ²)	National opposition (%)	Local opposition (%)	GSq score	RSq trans. prob	RSq dying from SQPV (# k)	Annual cost (£ mn)
1. Do nothing	1 (0-8)	2.5 (1.0-5.0)	1.1 (1.0-2.0)	0.078	0 (0-0)	0 (0-0)	56.1 (56.1-56.4)	7,181 (21-12,069)	0	0	0.340	0	16 (10-22)	0.00-0.00
2. Status quo	2 (0-16)	2.7 (1.0-6.0)	1.2 (1.0-3.0)	0.128	9 (5-5)	0 (0-0)	56.1 (55.9-56.4)	7,277 (53-12,069)	53.3	50.1 (3.4)	0.215	0	16 (9-22)	5.18-5.34
3. Status quo++	3 (0-16)	2.7 (1.0-6.0)	1.2 (1.0-3.0)	0.128	9 (5-5)	0 (0-0)	56.1 (55.9-56.4)	7,276 (53-12,069)	53.3	50.1 (3.4)	0.152	0	16 (9-22)	5.26-5.46
4. Non-lethal	1 (0-12)	2.6 (1.0-5.0)	1.1 (1.0-2.0)	0.104	6 (1-5)	0 (0-0)	56.1 (56.0-56.4)	7,202 (21-12,069)	14.4	13.4 (0.9)	0.215	0	16 (9-22)	2.98-3.13
5. NE supp	4,321 (0-23,477)	48.9 (1.0-219.0)	3.6 (1.0-7.0)	0.638	1,719 (245-4,351)	0 (0-0)	55.3 (52.4-56.8)	7,597 (1,184-12,069)	53.3	50.1 (3.4)	0.111	0	31 (9-116)	67.37-78.11
6. NE supp+	4,892 (0-26,889)	52.8 (1.0-236.7)	3.7 (1.0-7.2)	0.661	1,783 (245-4,158)	0 (0-0)	55.0 (52.4-56.7)	7601 (1212-12069)	53.3	50.1 (3.4)	0.111	0	34 (9-122)	70.63-83.00
7. NE supp++	4,865 (0-26,889)	52.7 (1.0-236.7)	3.7 (1.0-7.2)	0.661	1,783 (245-4,158)	0 (0-0)	55.0 (52.4-56.7)	7,601 (1,212-12,069)	53.3	50.1 (3.4)	0.111	0	34 (9-122)	70.65-83.03
8. NE rf	4,098 (0-21,856)	47.9 (2.0-207.0)	4.0 (1.0-8.0)	0.731	1,709 (245-4,382)	0 (0-0)	55.4 (52.6-56.9)	7,606 (1,184-12,069)	53.3	50.1 (3.4)	0.111	0.88	32 (9-121)	67.37-78.11
9. NE rf+	5,422 (0-25,824)	58.9 (2.0-239.0)	4.5 (1.0-8.0)	0.757	1,959 (253-5,866)	0 (0-0)	55.4 (52.5-56.9)	7,472 (1216-12069)	53.3	50.1 (3.4)	0.111	0.93	37 (10-129)	70.63-83.01
10. NE rf++	4,754 (0-26,470)	53.0 (2.0-233.0)	4.3 (1.0-8.0)	0.756	1,784 (245-4,776)	0 (0-0)	55.2 (52.5-56.8)	7,610 (1,214-12,069)	53.3	50.1 (3.4)	0.111	0.94	35 (9-124)	70.65-83.03
11. SW rt	10,300 (0-75,178)	60.9 (2.0-268.2)	4.6 (1.0-10.0)	0.698	1,959 (253-5,866)	0 (0-0)	54.1 (48.6-56.6)	8,327 (3,146-12,069)	53.3	51.6 (7.1)	0.079	0.58	32 (9-118)	142.74-165.49
12. SW rt++	12,955 (0-83,993)	69.2 (2.0-300.2)	5.1 (1.0-10.0)	0.714	2,080 (253-5,963)	0 (0-0)	53.5 (48.6-56.4)	8,340 (3,211-12,069)	53.3	51.6 (7.1)	0.079	0.73	34 (9-127)	149.61-175.81
13. EN supp	43,527 (0-286,790)	120.4 (1.0-547.0)	6.6 (1.0-22.0)	0.67	1,615 (196-3,900)	1,359 (148-4,529)	31.8 (0.0-56.4)	11,950 (10,789-12,069)	55.7	55.3	0.054	0	22 (9-89)	486.92-567.59
14. EN supp+	52,468 (0-299,742)	132.7 (1.0-557.2)	6.9 (1.0-22.0)	0.692	1,855 (196-3,837)	1,559 (149-4,498)	24.2 (0.0-56.4)	11,979 (11,305-12,069)	55.7	55.3	0.054	0	21 (9-85)	494.57-582.14
15. EN supp++	52,463 (0-299,742)	132.7 (1.0-557.2)	6.9 (1.0-22.0)	0.691	1,881 (196-3,996)	1,559 (149-4,498)	24.2 (0.0-56.4)	11,979 (11,305-12,069)	55.7	55.3	0.054	0	21 (9-85)	494.62-582.22
16. EN rt (RoE)	53,664 (0-410,371)	139.8 (2.0-665.2)	9.4 (1.0-31.0)	0.739	1,526 (196-3,244)	1,308 (148-4,455)	33.6 (0.1-56.8)	11,950 (10,789-12,069)	55.7	55.3	0.054	0.80	24 (9-109)	486.93-567.60
17. EN rt++ (RoE)	66,125 (0-419,091)	157.7 (2.0-688.0)	10.3 (1.0-31.0)	0.758	1,855 (196-3,837)	1,542 (149-4,442)	26.9 (0.1-56.4)	11,979 (11,328-12,069)	55.7	55.3	0.054	0.90	24 (9-99)	494.67-582.28
18. EN rt++ (RoE + SW)	66,638 (0-419,281)	158.8 (2.0-698.7)	10.3 (1.0-31.0)	0.763	1,783 (245-4,158)	1,495 (149-4,468)	26.8 (0.1-56.4)	11,979 (11,301-12,069)	55.7	55.3	0.054	0.90	24 (9-100)	494.62-582.21

For an accessible version of this table, please download the [supplementary document from the report page](#).

Outcomes – Consequences breakdown

A more detailed breakdown of the predicted consequences is given for each fundamental objective below.

Red squirrel recovery

For the red squirrel recovery objective, we first present the predicted population size of red squirrels over 25 years for each strategy (**Figure 11**), alongside maps showing the average abundance of red squirrels per hectad after 25 years (**Figure 12**), the probability of red squirrel presence per hectad after 25 years (**Figure 13**), and the probability of red squirrel presence per county after 25 years (**Figure 14**). Although not included as a performance attribute, we also present maps of the average abundance of grey squirrels per hectad after 25 years (**Figure 15**), and the probability of grey squirrel presence per hectad after 25 years (**Figure 16**). For the eight strategies that included translocations of red squirrels as a management action, we show the proportion of times from the 1,000 model runs that different hectads were chosen for reinforcement in Northern England (**Figure 17**), and reintroductions in the South West (**Figure 18**) and the Rest of England (**Figure 19**).

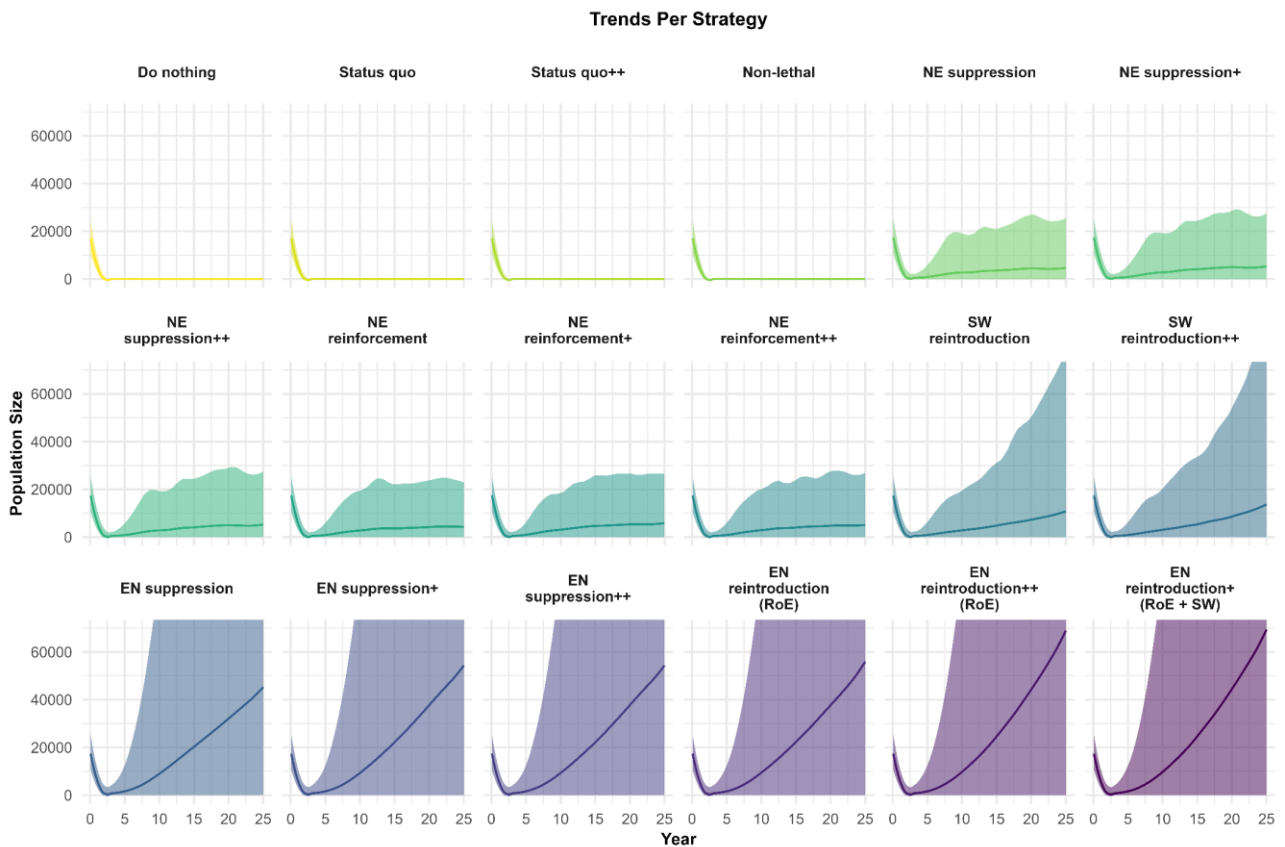


Figure 11. Predicted population size of red squirrels over 25 years for each strategy. Trend lines and 95% confidence intervals are shown, both smoothed using a LOESS fit – a method to reduce noise in non-linear trends. The initial reduction in population size during the first few years reflects the model’s burn-in period, which is required to account for an artificial overlap between red and grey squirrel populations. This should not be interpreted as a true population decline.

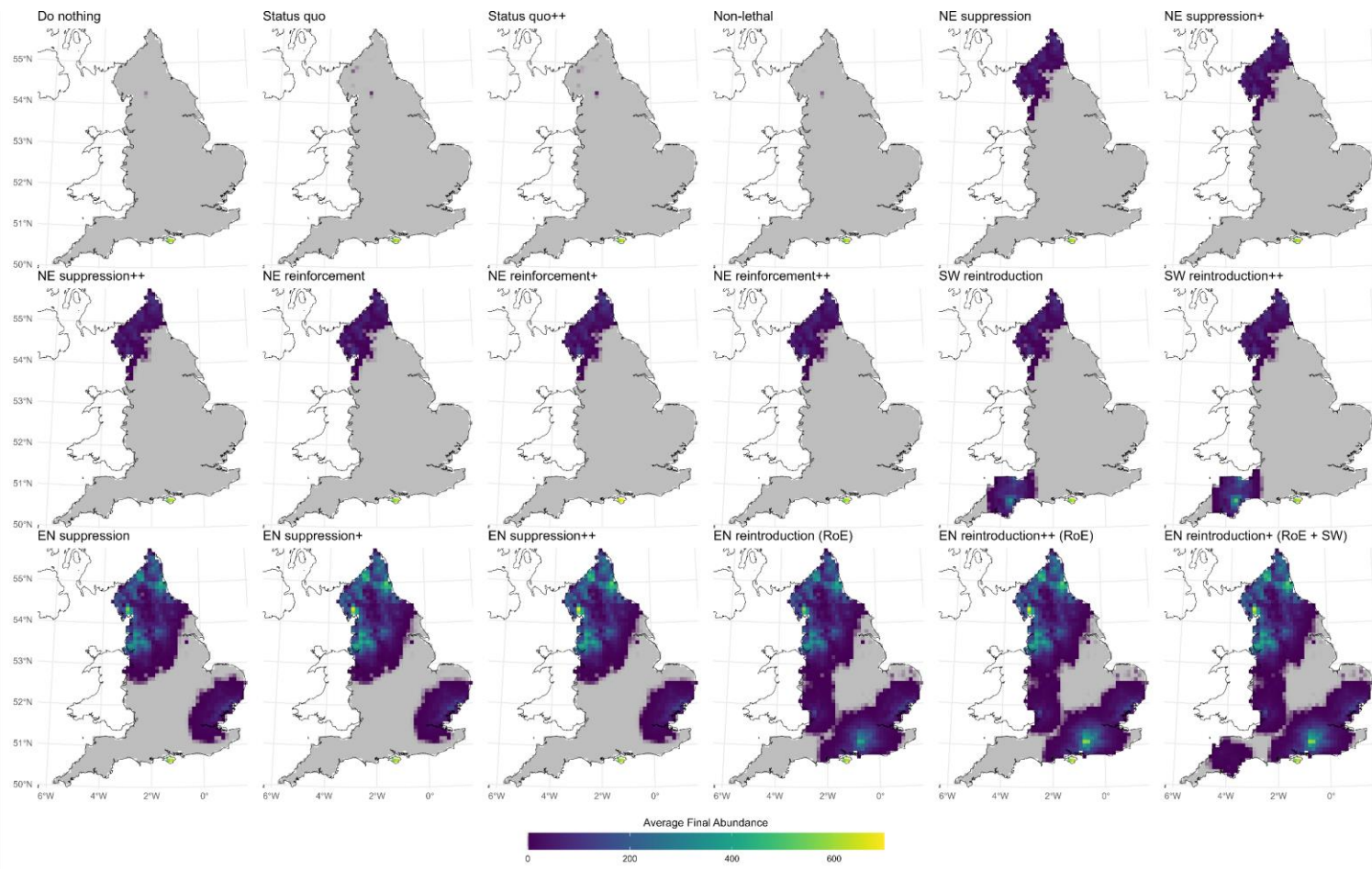


Figure 12. Average abundance of red squirrels in each hectad after 25 years for each of the 18 strategies over the 1,000 model runs. Note that for the England-wide strategies ('EN', bottom row), red squirrel translocations were restricted to the Rest of England (RoE) region, except for the final strategy (EN reintroduction+ (RoE + SW)) where translocations were also permitted opportunistically in the South West region.

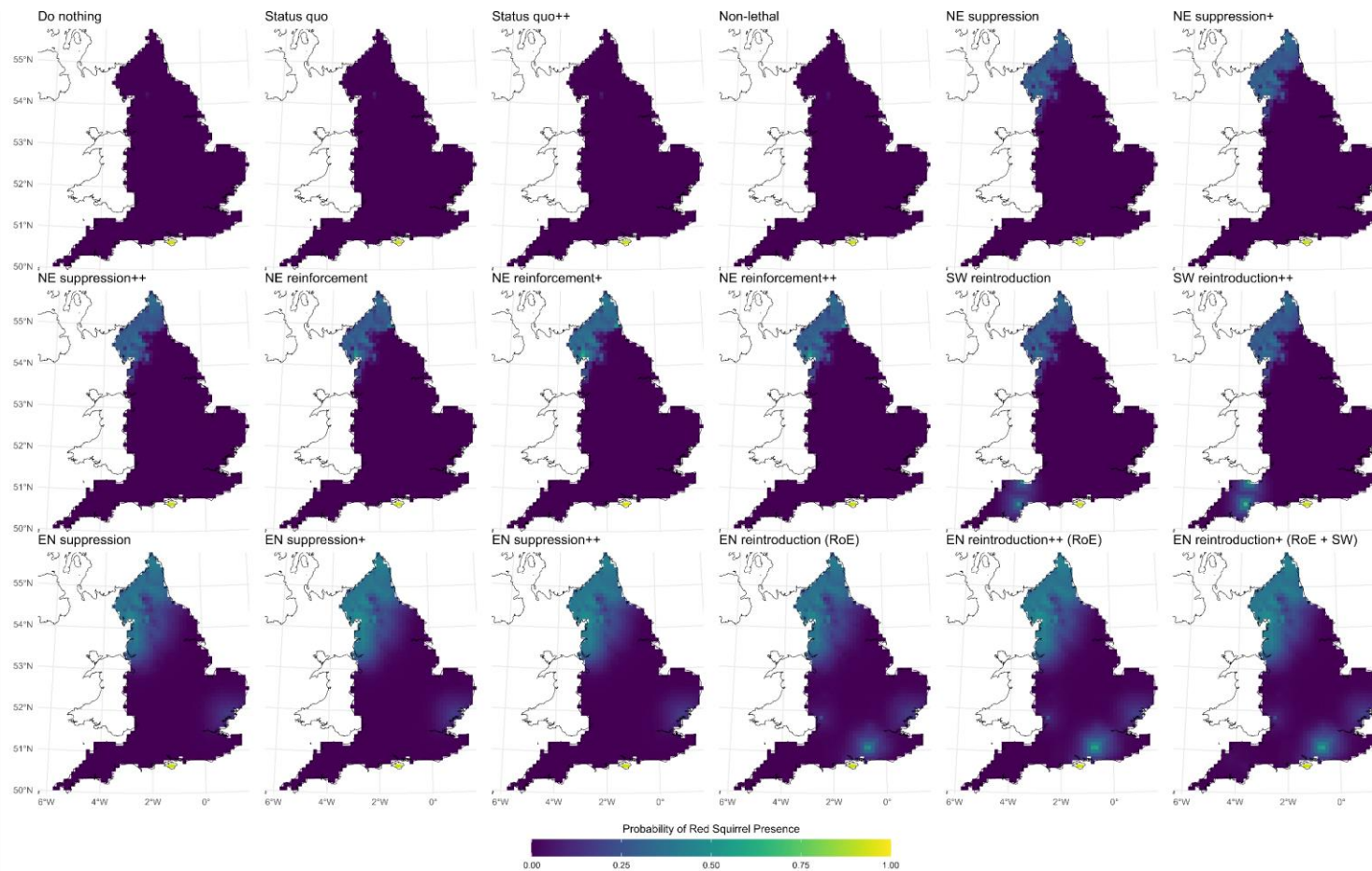


Figure 13. Probability of red squirrel presence in each hectad after 25 years for each of the 18 strategies. Note that for the England-wide strategies ('EN', bottom row), red squirrel translocations were restricted to the Rest of England (RoE) region, except for the final strategy (EN reintroduction+ (RoE + SW)) where translocations were also permitted opportunistically in the South West region.

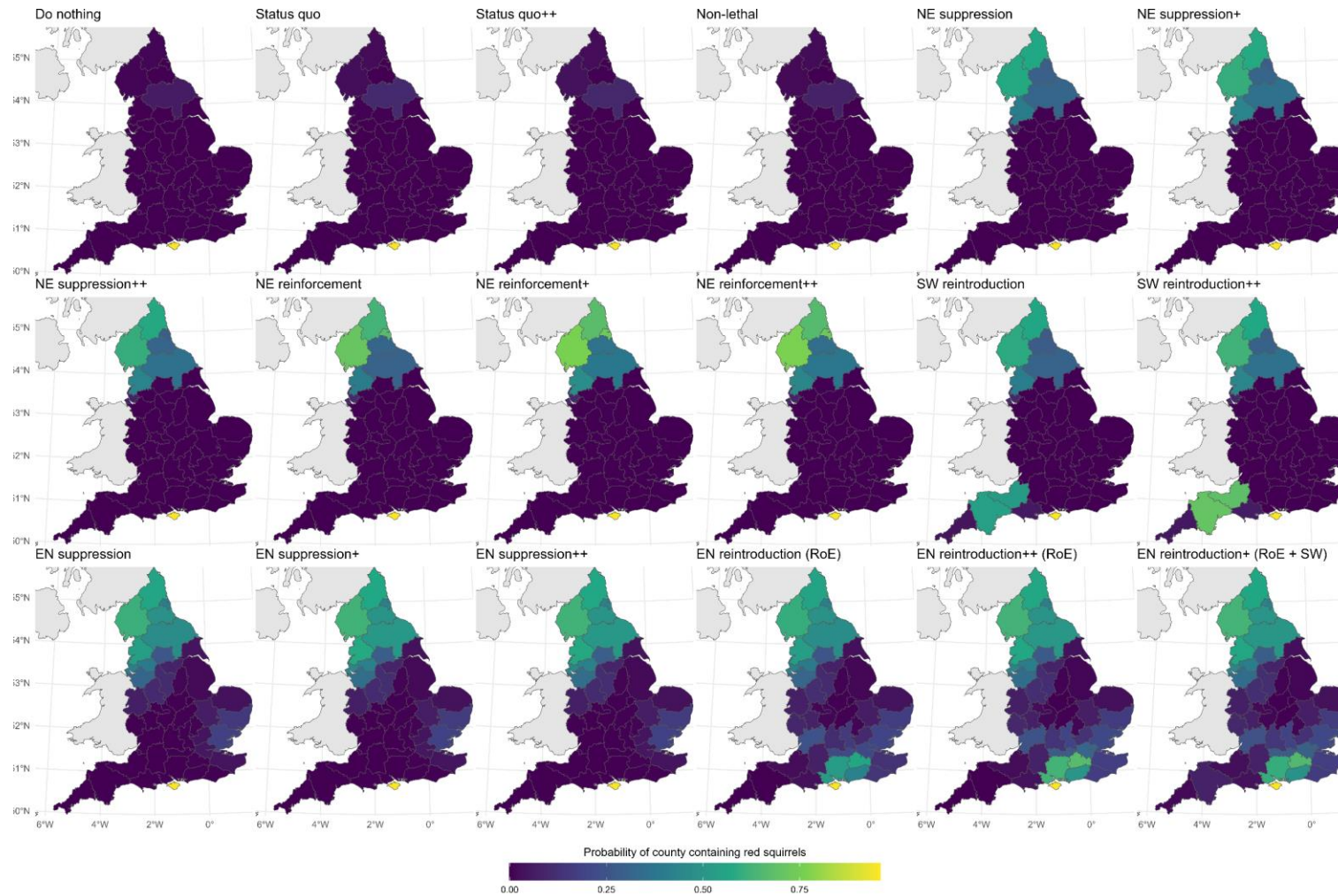


Figure 14. Probability of each county having red squirrels present after 25 years under the 18 strategies. Note that for the England-wide strategies ('EN', bottom row), red squirrel translocations were restricted to the Rest of England (RoE) region, except for the final strategy (EN reintroduction+ (RoE + SW)) where translocations were also permitted opportunistically in the South West region.

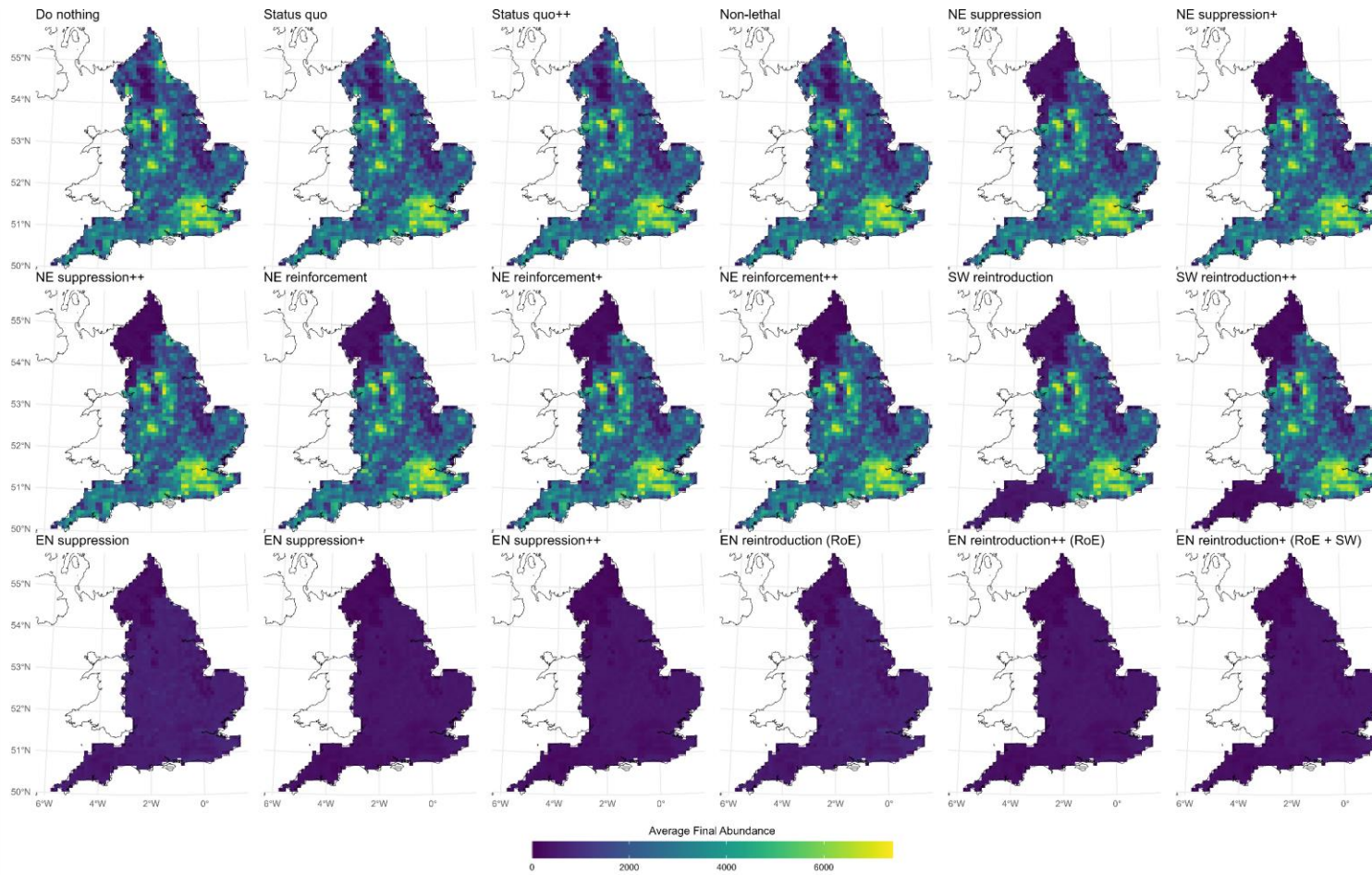


Figure 15. Average abundance of grey squirrels in each hectad after 25 years for each of the 18 strategies.

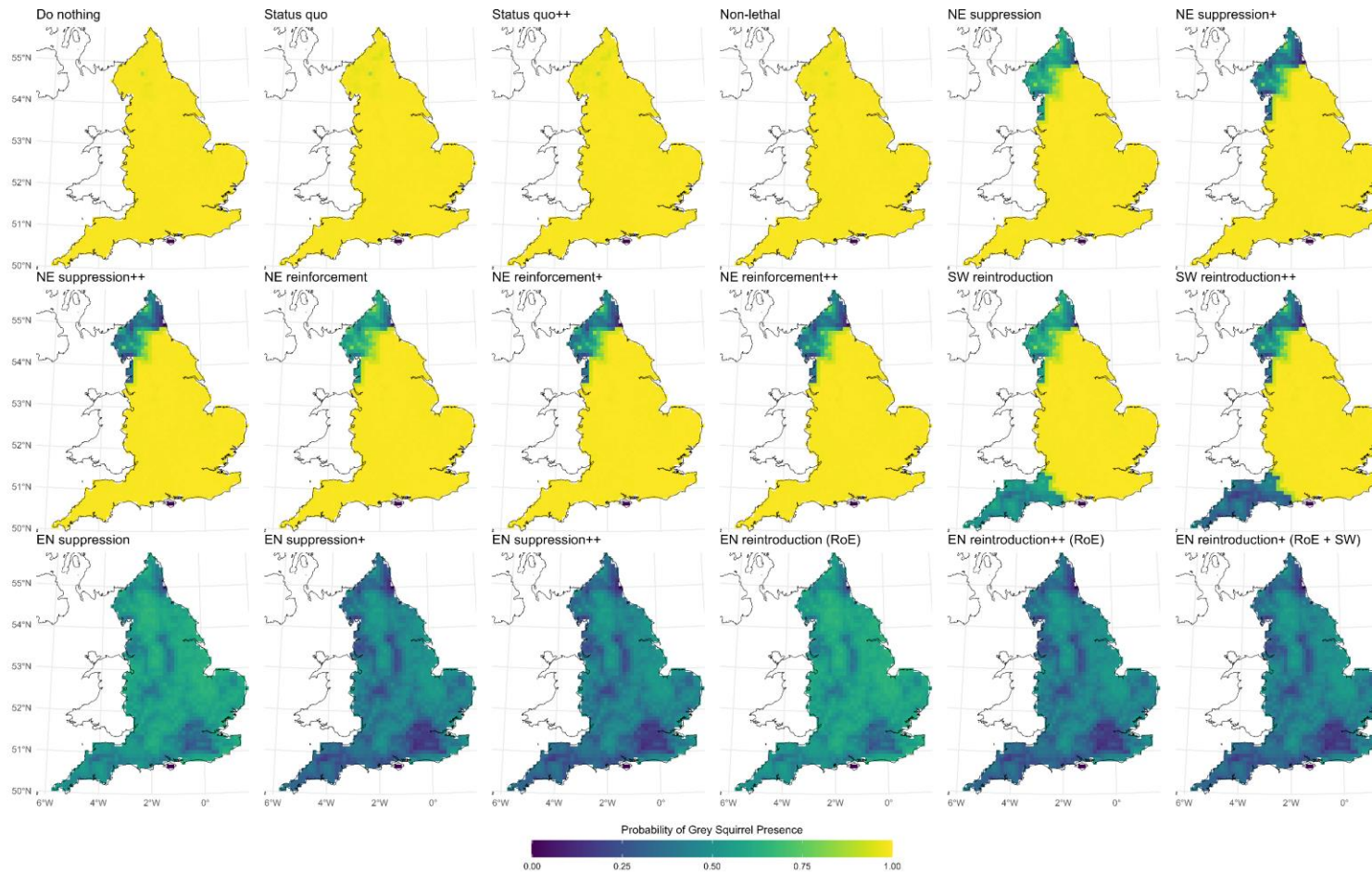


Figure 16. Probability of grey squirrel presence in each hectad after 25 years for each of the 18 strategies.

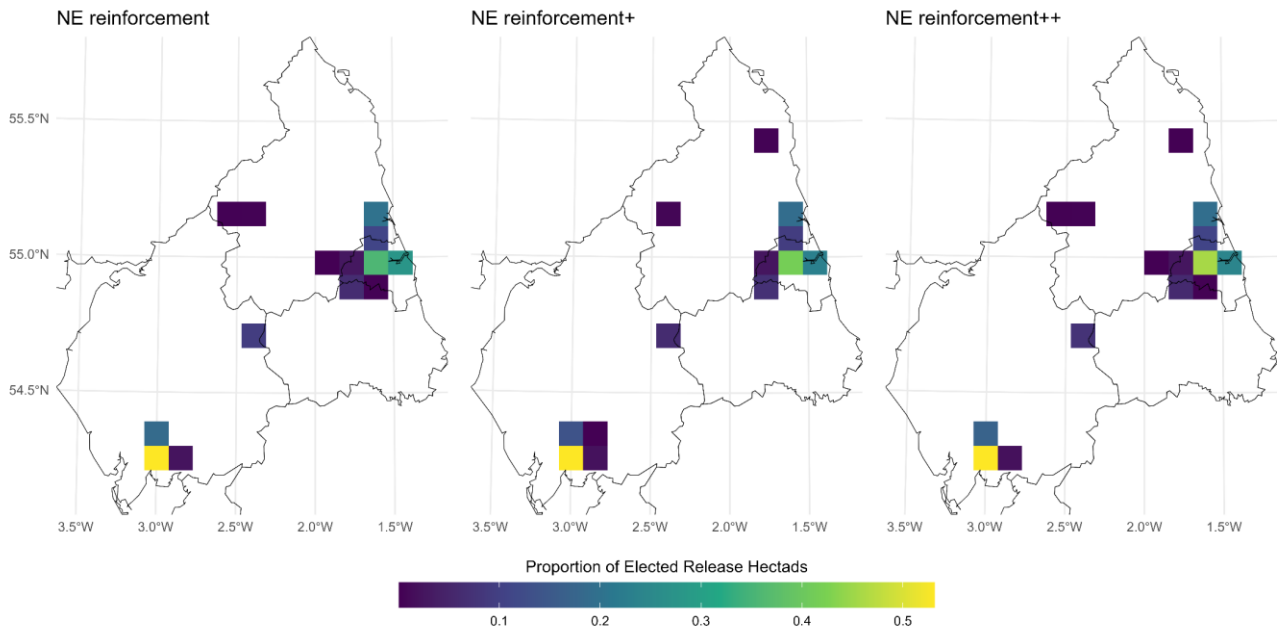


Figure 17. Proportion of times hectads were chosen for reinforcement in the Northern England strategies. These hectads were assigned opportunistically within the model runs given a set of criteria.

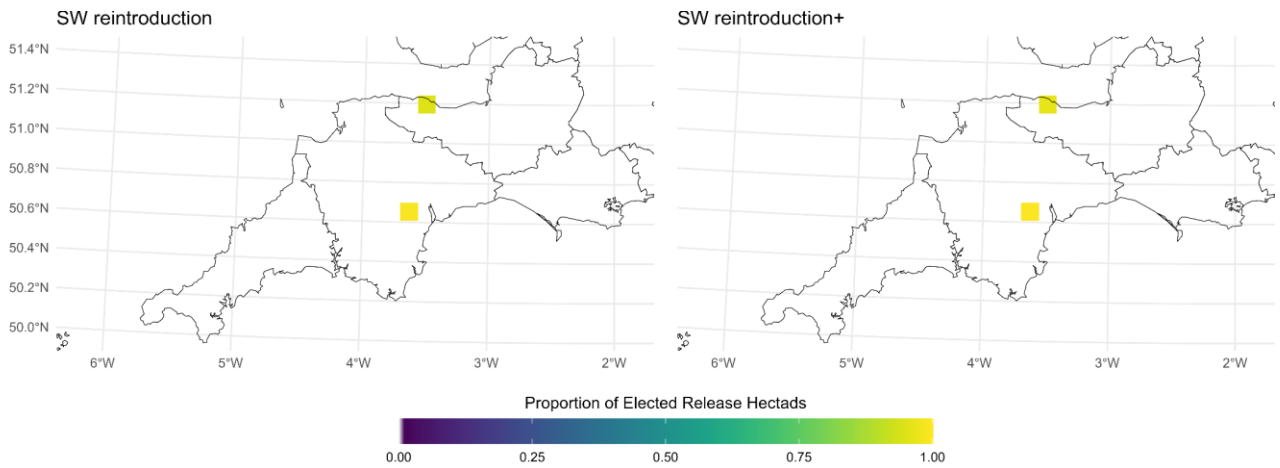


Figure 18. Proportion of times hectads were chosen for reintroduction of red squirrels in the South West specific strategies. The SW reintroductions were assigned to two specified hectads but could only take place if those hectads were cleared of grey squirrels for at least one year.

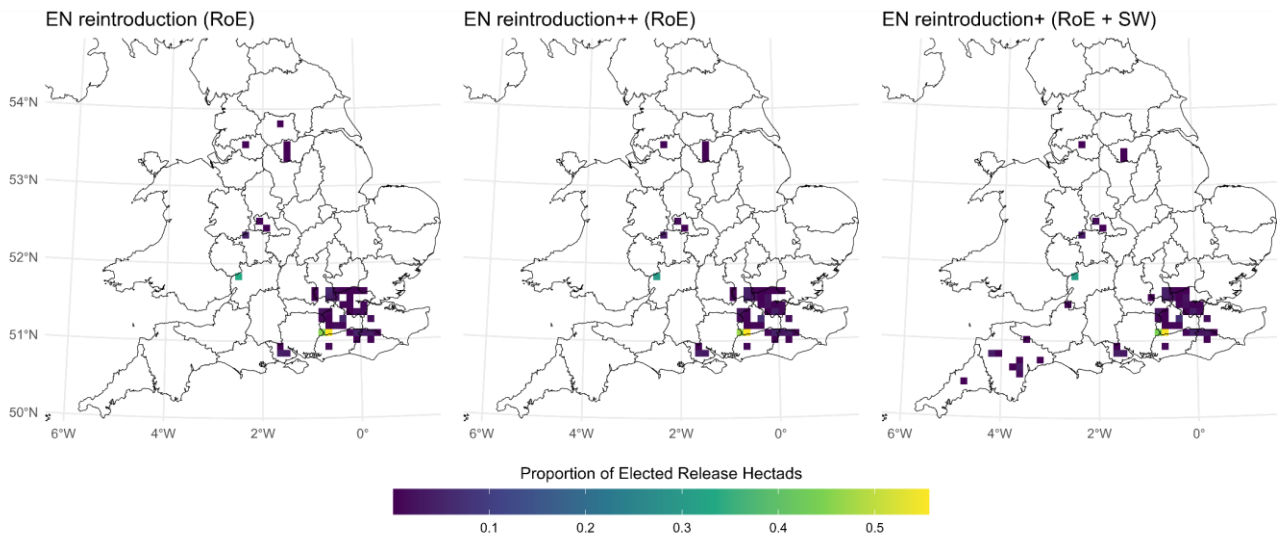


Figure 19. Proportion of times hectads are chosen for reintroduction in the England-wide strategies These hectads were assigned opportunistically within the model runs given a set of criteria. Note that for the England-wide strategies, red squirrel translocations were restricted to the Rest of England (RoE) region, except for the final strategy (EN reintroduction+ (RoE + SW)) where translocations were also permitted opportunistically in the South West region.

Non-target bycatch

There are no finer-detailed results for this objective than those presented in the consequence table (**Table 7**).

Socioeconomic benefits

For socioeconomic benefits, we first present a map of the probability of the presence of either red or grey squirrels per hectad after 25 years for each strategy (**Figure 20**). This aligns closely with the connection to nature score for wellbeing, i.e. people's connection to nature through potentially seeing squirrels, of either species, in their local area. We do not present the connection to nature score maps themselves, as they primarily reflect patterns of human population density, rather than providing meaningful insight into wellbeing from squirrel presence. For forestry benefits, we show maps of the area of broadleaf woodland (km²) per hectad predicted to have grey squirrels at densities greater than or equal to 90% of carrying capacity (**Figure 21**) and lower than 90% of carrying capacity (**Figure 22**). We use this as a proxy measure for the area of woodland expected to suffer, or not, from bark stripping damage from grey squirrels.

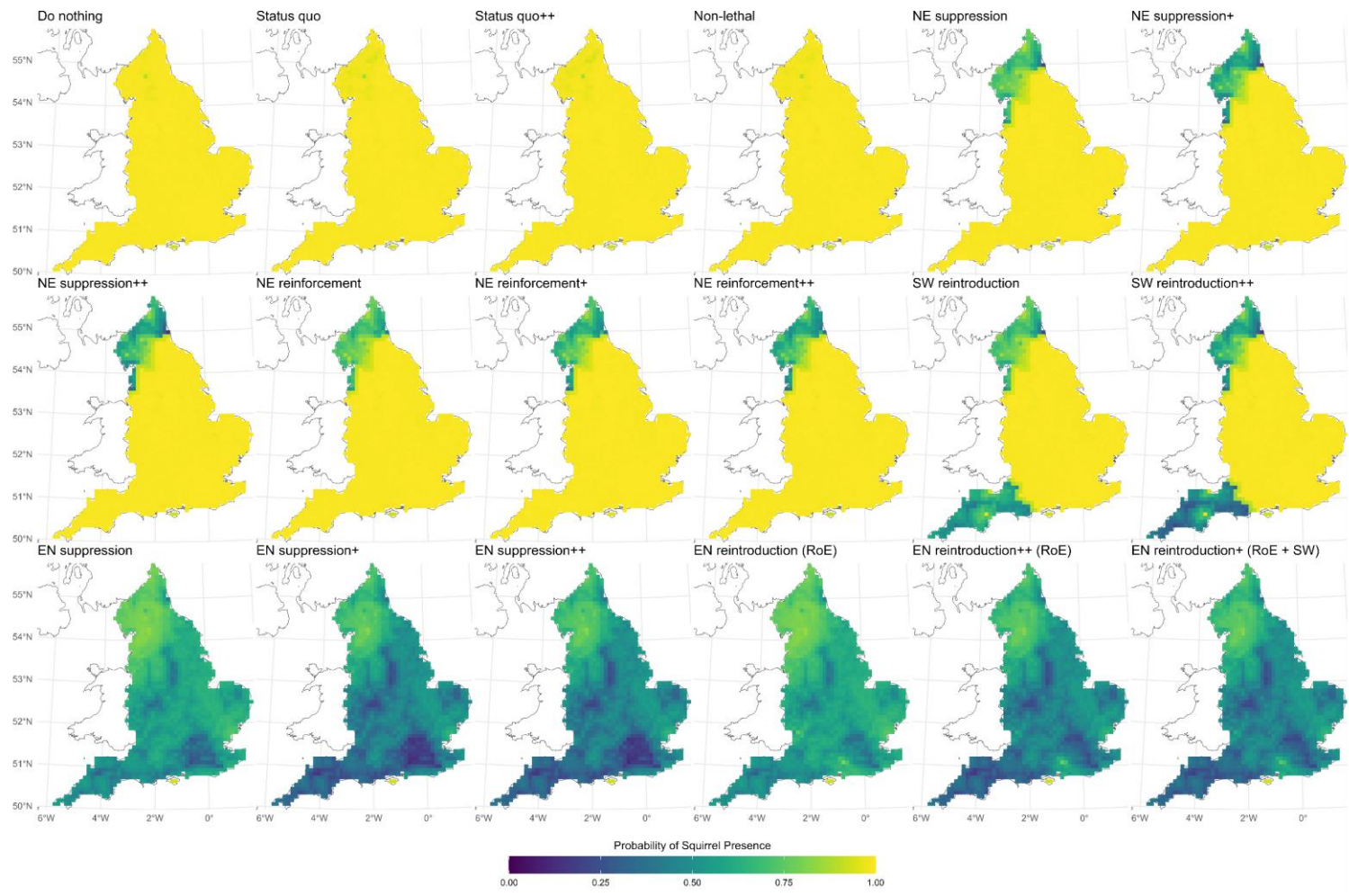


Figure 20. Probability of either red or grey squirrel presence per hectad after 25 years. Note that for the England-wide strategies ('EN', bottom row), red squirrel translocations were restricted to the Rest of England (RoE) region, except for the final strategy (EN reintroduction+ (RoE + SW)) where translocations were also permitted opportunistically in the South West region.

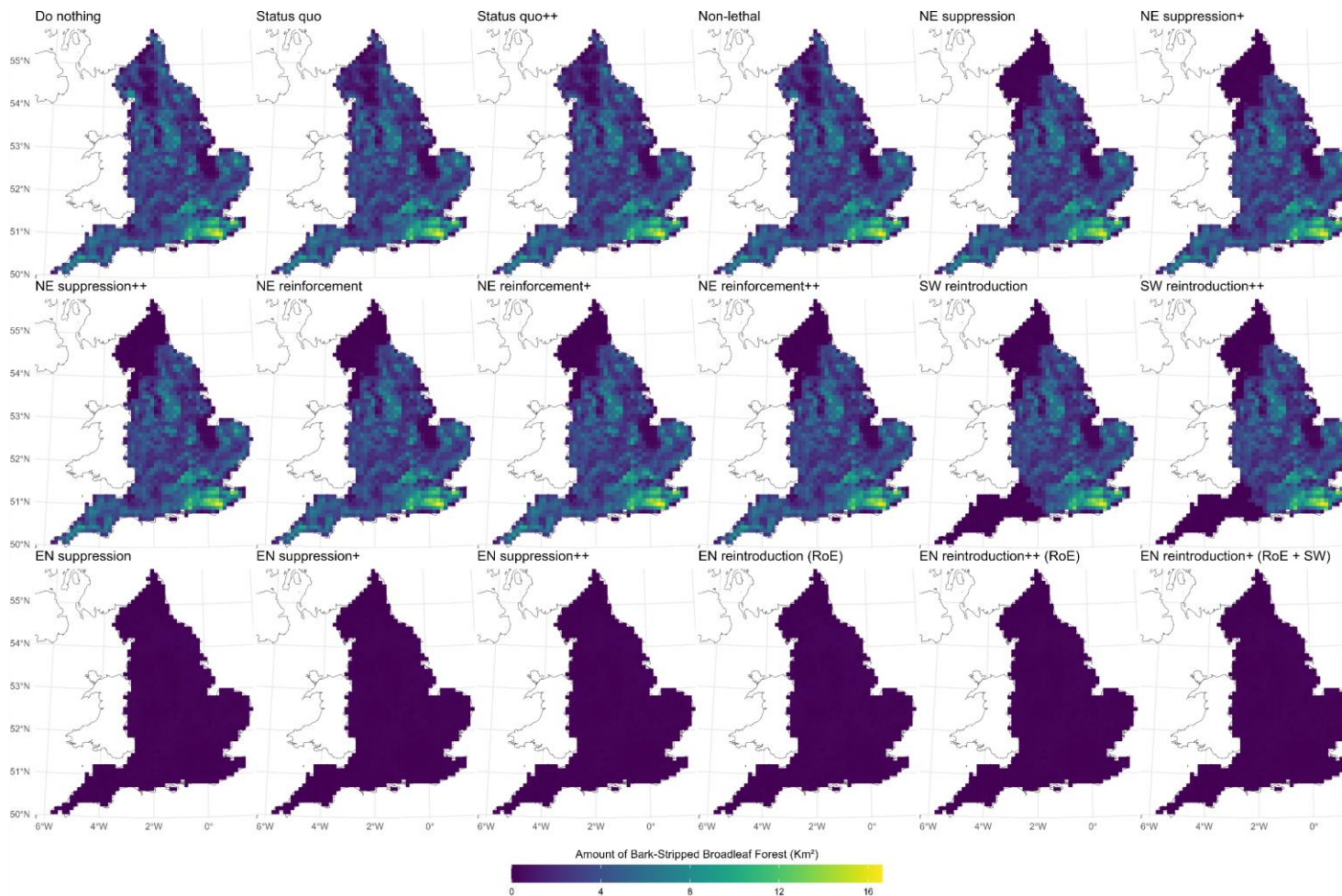


Figure 21. Area of broadleaf woodland (km²) per hectad predicted to have grey squirrels at densities greater than or equal to 90% of carrying capacity. This measure serves as a proxy for the amount of woodland expected to suffer bark stripping damage by grey squirrels. In these maps, the darker colours show areas with less tree damage.

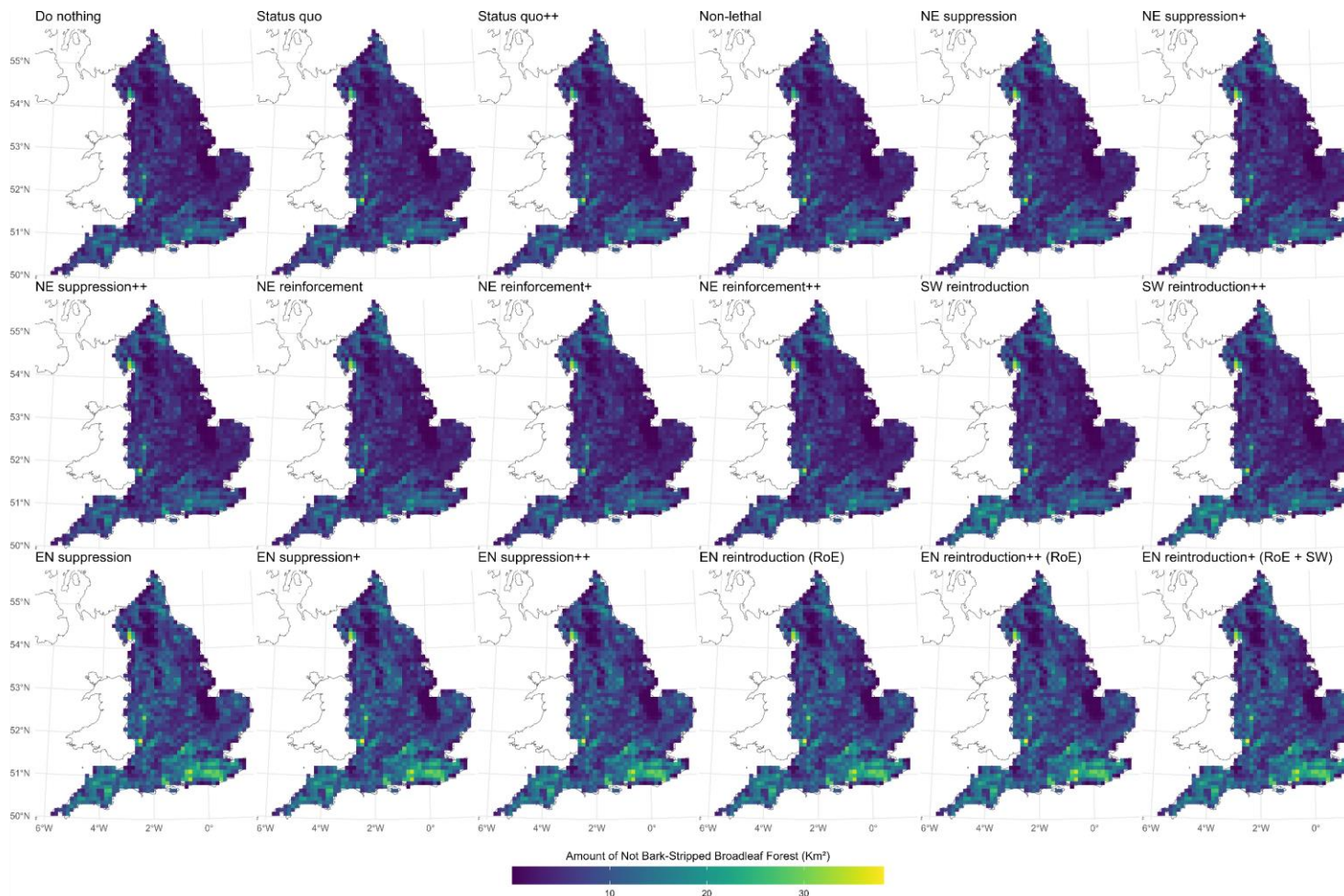


Figure 22. Area of broadleaf woodland (km²) per hectad predicted to have grey squirrels at densities lower than 90% of carrying capacity. This measure serves as a proxy for the amount of woodland not expected to suffer bark stripping damage by grey squirrels. In these maps, the lighter colours show areas with less tree damage.

Public acceptability

The predicted acceptability to the public of the four grey squirrel management methods included in the strategies is shown at a national (**Table 9**) and local (**Table 10**) level. Public opposition to the four methods, public support, and the ratio between the two are mapped across England in **Figure 23**, **Figure 24**, and **Figure 25**, respectively.

Table 9. Percentage of the population of England that is predicted to rate each grey squirrel management method as ‘highly unacceptable’ or ‘unacceptable’ (opposition), ‘highly acceptable’ or ‘acceptable’ (support), or ‘neither acceptable nor unacceptable’ (indifference). These new predictions were made using survey data originally collected by Forest Research (Dunn et al., 2018).

Method	Predicted national opposition (%)	Predicted national support (%)	Predicted national indifference (%)
Live traps and dispatch	44.82	33.09	22.08
Kill traps (snap/spring traps)	55.74	22.41	21.85
Shooting	53.28	25.27	21.45
Contraception	14.41	62.03	23.56

Table 10. Total number of local people opposed to the most unacceptable grey squirrel management method that takes place in that region in the different strategies. Predictions were made using survey data originally collected by Forest Research (Dunn et al., 2018).

Region	Most unacceptable method used in region	Number of people opposed to method	Total number of local people	Percentage of local people opposed to method (%)	Percentage of total national population (%)
NE	Shooting	1,515,118	3,024,439	50.1	3.4
NE	Contraception	405,885	3,024,439	13.4	0.9
SW	Shooting	1,663,425	3,140,597	53	3.7
EN	Kill Traps	21,489,140	38,445,076	55.9	48.2
NE+SW	Shooting	3,178,544	6,165,036	51.6	7.1
EN+NE+SW	Kill Traps + Shooting + Shooting	24,667,684	44,610,112	55.3	55.3

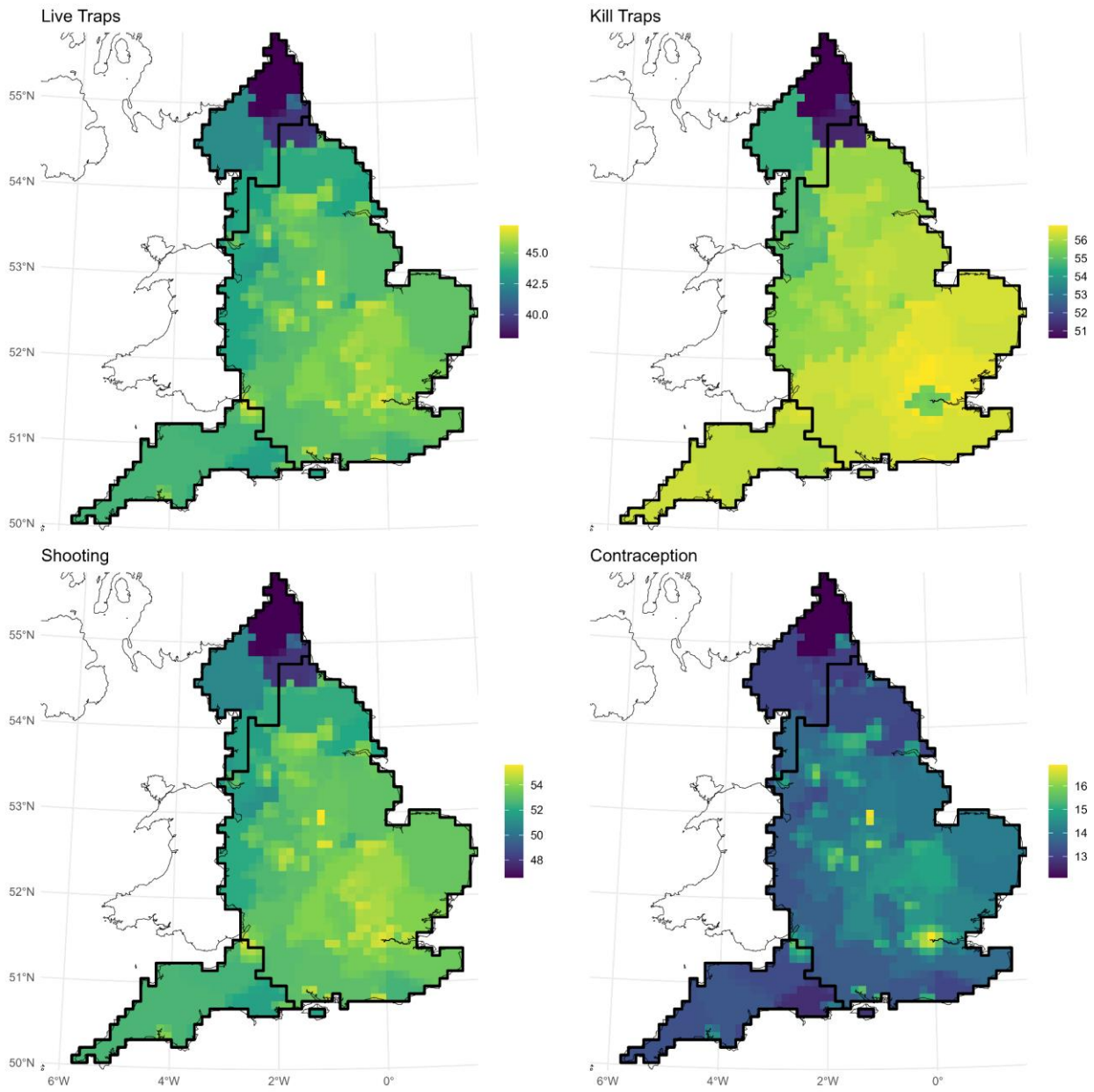


Figure 23. Percentage of people per hectad predicted to oppose each method (i.e. score the method as highly unacceptable or unacceptable on a five-point Likert scale).

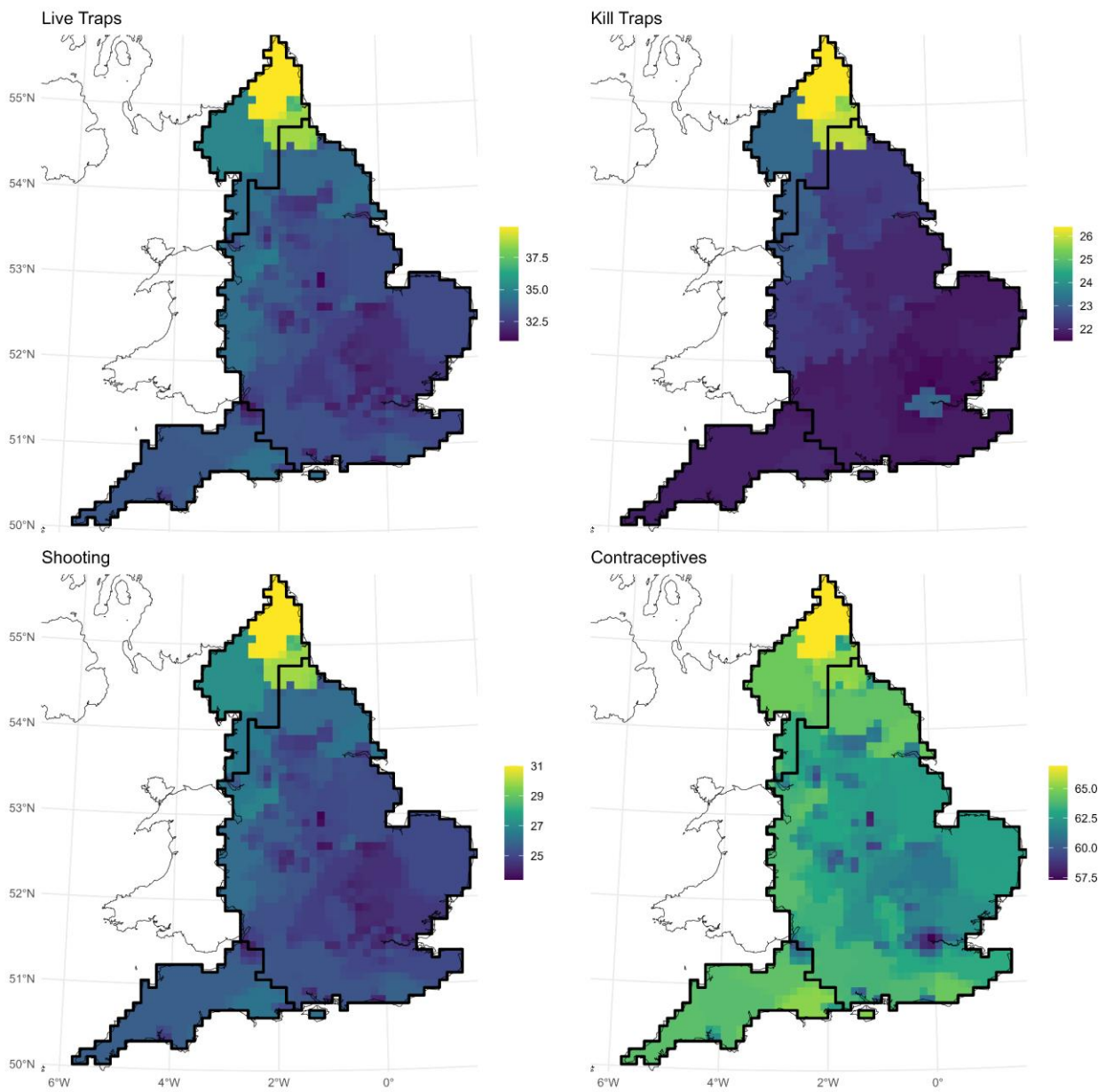


Figure 24. Percentage of people per hectad predicted to support each method (i.e. score the method as highly acceptable or acceptable on a five-point Likert scale).

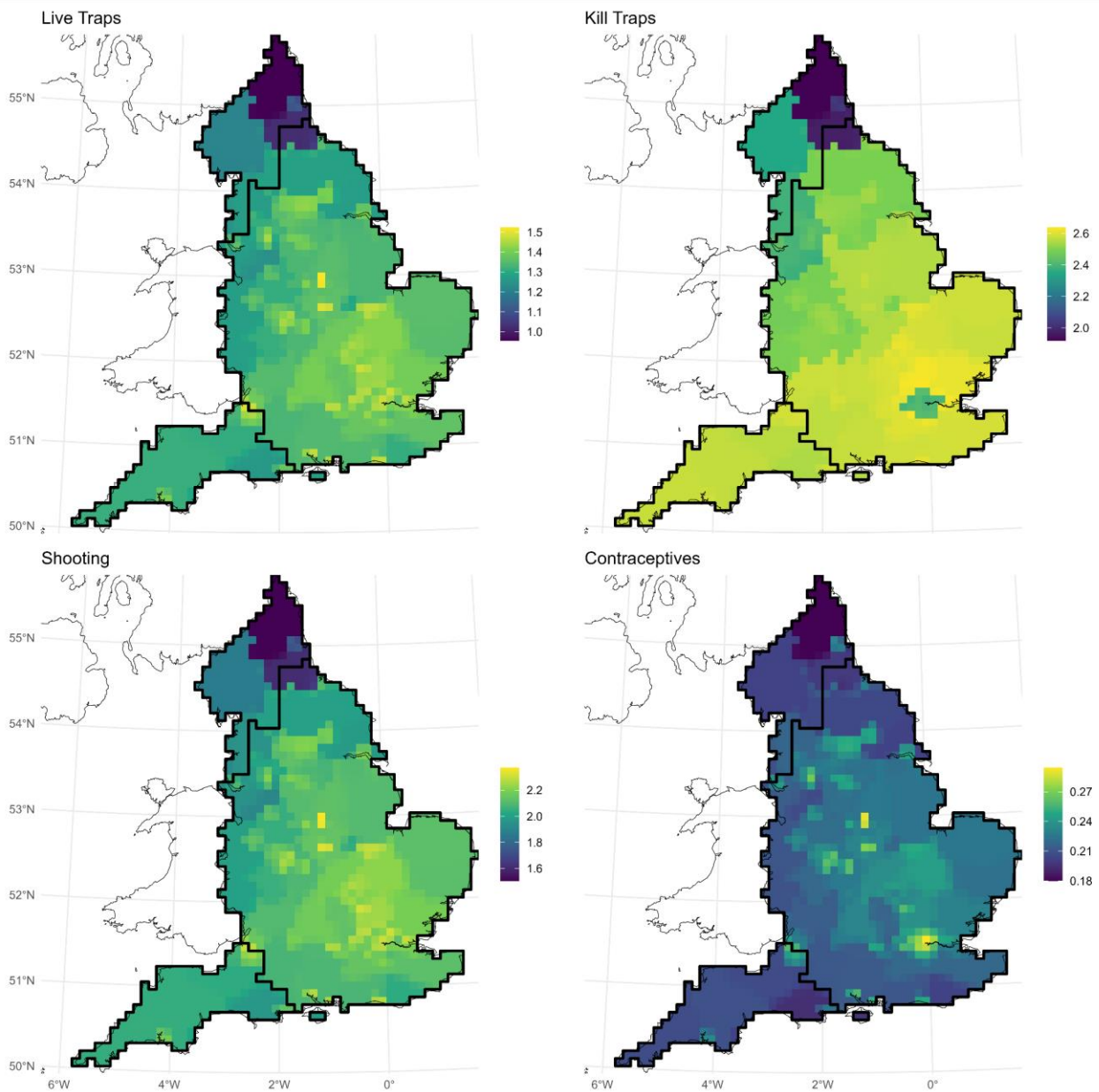


Figure 25. Ratio of people opposing to supporting each method, whereby opposing means they would rate the method as highly unacceptable or unacceptable on a five-point Likert scale compared to supporting as highly acceptable or acceptable. For example, a value of 2 means that for every 1 person supporting the method in that hectad, another 2 people oppose it.

Welfare

The breakdown of the scores for both Part A and Part B of the Sharp & Saunders model framework is provided for each of the four management methods in **Table 11**. Higher combined scores indicate greater negative welfare impacts. The number of squirrels being subjected to each of the management methods in each strategy is provided in **Table 12** alongside their rank score. The combined scores and the number of squirrels impacted by each method for each strategy are then shown combined together in **Figure 26**.

Table 11. Welfare impacts of the four broad grey squirrel management methods included in the strategies. Following the Sharp & Saunders (2011) model, Part A refers to the overall welfare impact of the method, and Part B refers to the level of suffering experienced from the onset of the mode of death until irreversible unconsciousness. As such, there is no Part B score for fertility control. *The strategies do not differentiate between the modes of dispatching a squirrel after live trapping, hence the score presented here is for cranial dispatch and shooting in the trap, as both were scored the same by the experts.

Method	Part A: Overall welfare impact	Part A: Time	Part A: Combined score	Part B: Mode of Death Impact	Part B: Time	Part B: Combined score
Single capture live trap then dispatch*	Mild – Severe	Hours	4 – 6	None – Moderate	Minutes	A, C – D
Free shooting / shooting at bait stations	None - Mild	Immediate to seconds – Minutes	1 - 3	None – Mild	Immediate to seconds	A – B
Snap/spring kill traps	None	Immediate to seconds – Minutes	1	None – Severe	Immediate to seconds – Minutes	A – E
Fertility control	None – Mild	Weeks	1, 6	NA	NA	NA

Table 12. Numbers (in thousands) of grey squirrels affected by each management type in each of the 18 strategies. The value in bold is the mean from the 1,000 runs of the model for each strategy, with the lower and upper confidence intervals provided in brackets. The final column shows the rank score for each strategy (see Page 90 for an explanation of how the rank scores were calculated).

Strategy	Live traps	Kill (snap) traps	Shooting	Fertility control	Rank score
1. Do nothing	0 (0-0)	0 (0-0)	0 (0-0)	0 (0-0)	0.340
2. Status quo	61 (6-95)	0 (0-0)	436 (24-1,492)	0 (0-0)	0.215
3. Status quo++	61 (6-95)	0 (0-0)	436 (24-1,492)	1 (0-4)	0.152
4. Non-lethal	38 (3-92)	0 (0-0)	261 (11-1,146)	0 (0-3)	0.215
5. NE suppression	935 (50-4,165)	0 (0-0)	563 (32-2,264)	0 (0-0)	0.111
6. NE suppression+	752 (50-3,455)	0 (0-0)	455 (31-1,779)	410 (0-2,898)	0.111
7. NE suppression++	751 (50-3,455)	0 (0-0)	455 (31-1,779)	410 (0-2,898)	0.111
8. NE reinforcement	935 (50-4,165)	0 (0-0)	563 (32-2,236)	0 (0-0)	0.111
9. NE reinforcement+	780 (51-3539)	0 (0-0)	471 (32-1,826)	430 (0-3,026)	0.111
10. NE reinforcement++	752 (50-3,455)	0 (0-0)	455 (31-1,774)	410 (0-2,897)	0.111
11. SW reintroduction	2,470 (118-10,813)	0 (0-0)	1,463 (79-6,212)	0 (0-0)	0.079
12. SW reintroduction++	1,973 (118-9,159)	0 (0-0)	1,174 (77-4,935)	983 (0-7,657)	0.079
13. EN suppression	9,203 (358-39,031)	1,332 (37-5,840)	6,315 (338-26,681)	0 (0-0)	0.054
14. EN suppression+	7,572 (358-36,376)	1,127 (37-5,308)	5,196 (334-23,296)	3,328 (0-25,459)	0.054
15. EN suppression++	7,569 (358-36,376)	1,127 (37-5,308)	5,196 (334-23,272)	3,327 (0-25,459)	0.054
16. EN reintroduction (RoE)	9,203 (358-39,031)	1,333 (37-5,840)	6,316 (339-26,681)	0 (0-0)	0.054
17. EN reintroduction++ (RoE)	7,569 (358-36,375)	1,127 (37-5,309)	5,196 (335-23,272)	3,328 (0-25,460)	0.054
18. EN reintroduction+ (RoE + SW)	7,569 (358-36,373)	1,127 (37-5,308)	5,196 (335-23,272)	3,328 (0-25,460)	0.054

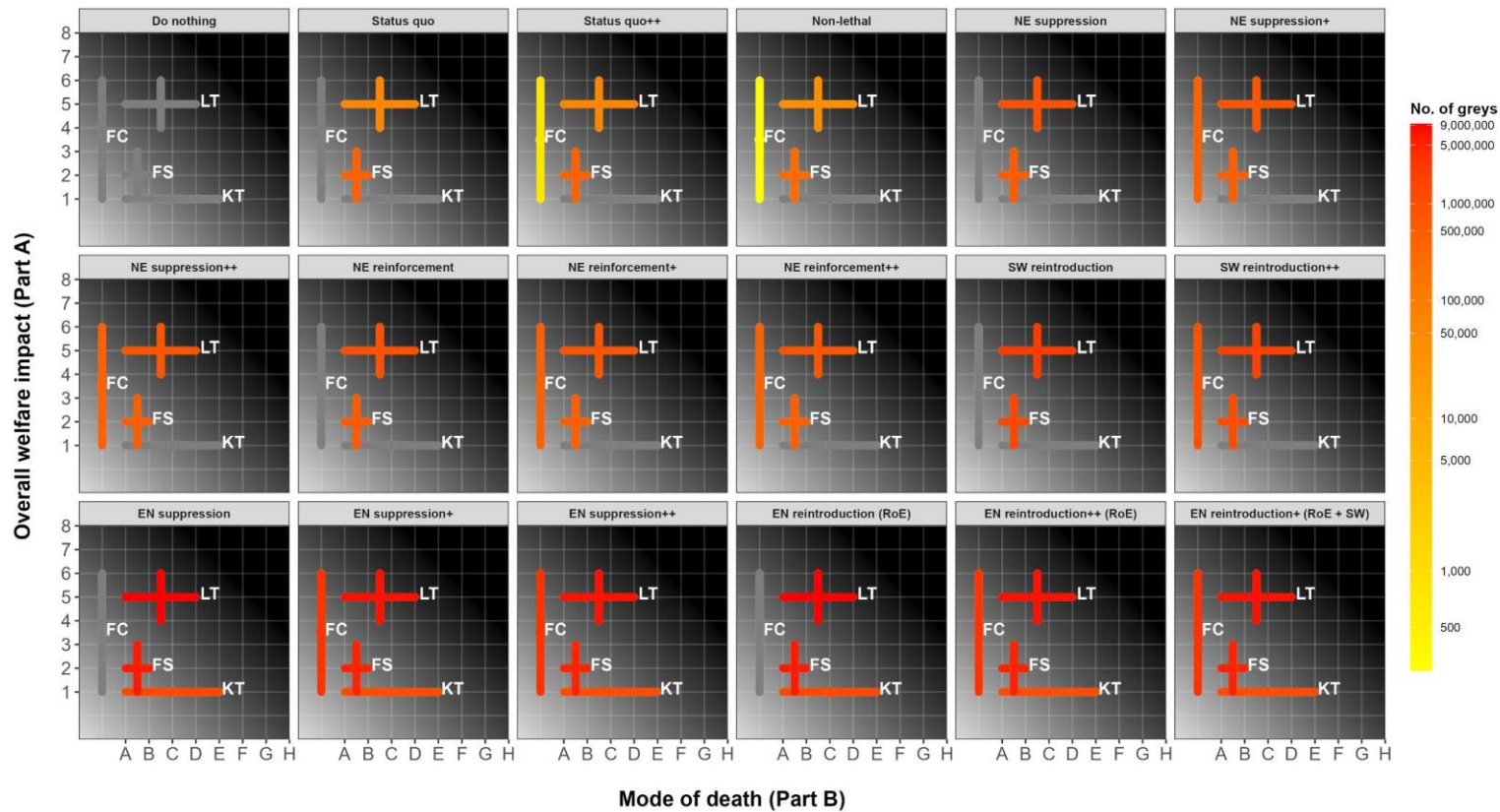


Figure 26. Welfare impacts on grey squirrels of grey squirrel management actions in each strategy. LT = single capture live traps then dispatch; FS = free shooting / shooting at bait stations; KT = snap/spring kill traps; FC = fertility control. The colour scale shows the mean total number of grey squirrels impacted over the 25 years by that method in each strategy. It is important to note that although the scores are represented as a continuum, for fertility control the Part A score was 1 or 6, and for single capture live traps then dispatch the Part B score was either A or C-D.

Cost

A more detailed breakdown of the costs for each method are provided in **Table 13**. Costs for grey squirrel management and vaccination are estimated based on the cost of paying full-time employees to carry out such work and are likely to be overestimates given that some of this work could be conducted by volunteers (as is currently the case).

Table 13. Breakdown of the costs in millions of GBP (£) for each method in the strategies alongside the total costs per strategy. The minimum and maximum costs are given for methods where a range of effort levels were incorporated into the costing.

Strategy	Live traps	Kill traps	Shooting	Fertility control	Vaccination	Translocation	Total	Total / year
1. Do nothing	0.0 - 0.0	0.0 - 0.0	0	0.0 - 0.0	0.0 - 0.0	0	0.0 - 0.0	0.0 - 0.0
2. Status quo	8.0 - 12.0	0.0 - 0.0	121.5	0.0 - 0.0	0.0 - 0.0	0	129.5 - 133.5	5.2 - 5.3
3. Status quo++	8.0 - 12.0	0.0 - 0.0	121.5	1.2 - 1.8	0.8 - 1.2	0	134.1 - 140.3	5.4 - 5.6
4. Non-lethal	4.4 - 6.6	0.0 - 0.0	67.1	1.2 - 1.8	1.9 - 2.8	0	80.1 - 86.6	3.2 - 3.5
5. NE suppression	537.0 - 805.5	0.0 - 0.0	1,147.10	0.0 - 0.0	0.0 - 0.0	0	1,684.1 - 1,952.7	67.4 - 78.1
6. NE suppression+	537.0 - 805.5	0.0 - 0.0	1,147.10	81.6 - 122.4	0.0 - 0.0	0	1,765.8 - 2,075.1	70.6 - 83.0
7. NE suppression++	537.0 - 805.5	0.0 - 0.0	1,147.10	81.6 - 122.4	0.4 - 0.6	0	1,767.5 - 2,077.7	70.7 - 83.1
8. NE reinforcement	537.0 - 805.5	0.0 - 0.0	1,147.10	0.0 - 0.0	0.0 - 0.0	0.1	1,684.5 - 1,953.0	67.4 - 78.1
9. NE reinforcement+	537.0 - 805.5	0.0 - 0.0	1,147.10	81.6 - 122.4	0.0 - 0.0	0.1	1,766.1 - 2,075.4	70.6 - 83.0
10. NE reinforcement++	537.0 - 805.5	0.0 - 0.0	1,147.10	81.6 - 122.4	0.4 - 0.6	0.1	1,767.8 - 2,078.0	70.7 - 83.1
11. SW reintroduction	1,137.9 - 1,706.8	0.0 - 0.0	2,430.50	0.0 - 0.0	0.0 - 0.0	0.1	3,568.6 - 4,137.5	142.7 - 165.5
12. SW reintroduction++	1,137.9 - 1,706.8	0.0 - 0.0	2,430.50	171.4 - 257.2	0.5 - 0.8	0.1	3,742.2 - 4,397.8	149.7 - 175.9
13. EN suppression	3,365.2 - 5,047.8	668.2 - 1,002.3	8,139.70	0.0 - 0.0	0.0 - 0.0	0	12,173.1 - 14,189.8	486.9 - 567.6
14. EN suppression+	3,293.1 - 4,939.6	668.2 - 1,002.3	7,985.70	417.3 - 625.9	0.0 - 0.0	0	12,364.3 - 14,553.6	494.6 - 582.1
15. EN suppression++	3,293.1 - 4,939.6	668.2 - 1,002.3	7,985.70	417.3 - 625.9	1.2 - 1.9	0	12,369.2 - 14,561.0	494.8 - 582.4
16. EN reintroduction (RoE)	3,365.2 - 5,047.8	668.2 - 1,002.3	8,139.70	0.0 - 0.0	0.0 - 0.0	0.1	12,173.4 - 14,190.1	486.9 - 567.6
17. EN reintroduction++ (RoE)	3,293.1 - 4,939.6	668.2 - 1,002.3	7,985.70	418.1 - 627.1	1.5 - 2.2	0.1	12,371.4 - 14,564.1	494.9 - 582.6
18. EN reintroduction+ (RoE + SW)	3,293.1 - 4,939.6	668.2 - 1,002.3	7,985.70	418.4 - 627.6	0.0 - 0.0	0.1	12,365.8 - 14,555.6	494.6 - 582.2

Process

Red squirrel recovery

Population model

We built a spatially explicit, stochastic, multi-species, female-only population model to assess red squirrel recovery in England. The model incorporates key ecological processes, including interspecific transmission of squirrelpox, interspecific competition, pine marten predation, and all the management actions outlined in the 18 recovery strategies. It operates at a hectad (10 × 10 km) scale across the entire country, with a temporal resolution of one-month time steps over a 25-year period. This model was adapted from several published models. Squirrelpox virus, competition and pine marten regulation dynamics were adapted from Slade et al. (2023), with further development in squirrelpox epidemiology following the discoveries in Howell et al. (2024). The relationships between management effort and grey squirrel population growth were adapted from Croft et al. (2021). For further details, see **Appendix 4**.

To incorporate parametric uncertainty and estimate unknown parameters, we conducted two expert elicitation workshops using the IDEA protocol (Hemming et al., 2018). During these workshops, experts provided estimates for various parameters related to squirrel ecology, conservation, and management (**Table 14**, **Table 15**). For each parameter, they were asked to specify: (a) the minimum plausible value, (b) the most likely value, and (c) the maximum plausible value. Additionally, they provided a fourth estimate—their confidence that the true value of the parameter fell within the specified range (a–c). These values were used to fit a beta-PERT (Clark, 1962) distribution for each combination of parameter and expert.

Table 14. Model population and disease parameters. RSq = red squirrel; GSq = grey squirrel.

Category	Species	Parameter	Estimate	Source
Mortality	RSq	Juvenile Mortality (Annual)	0.514 (0.377-0.828)	Elicited from experts (Adjusted from Odds-Ratio derived from elicitation)
Mortality	RSq	Adult Mortality (Annual)	0.6702	(Slade et al., 2023)
Mortality	GSq	Juvenile Mortality (Annual)	0.571 (0.457-0.851)	Elicited from experts (Adjusted from Odds-Ratio derived from elicitation)
Mortality	GSq	Adult Mortality (Annual)	0.6702	(Slade et al., 2023)
Mortality	PM	Juvenile Mortality	0.65	(Powell et al., 2012)
Mortality	PM	Subadult Mortality	0.25	(Powell et al., 2012)
Mortality	PM	Adult Mortality	0.12	(Powell et al., 2012)
Reproduction	RSq	Breeding Season Duration	7.798 (4.703-10.603)	Elicited from experts
Reproduction	Gsq	Breeding Season Duration	8.619 (4.536-11.735)	Elicited from experts
Reproduction	PM	Breeding Season Duration	8.514 (5.194-10.953)	Elicited from experts

Category	Species	Parameter	Estimate	Source
Reproduction	RSq	Litter Size	2.479 (0.590-5.039)	Elicited from experts
Reproduction	GSq	Litter Size	3.186 (0.755-7.674)	Elicited from experts
Reproduction	RSq	No of Litters	1.524 (0.069-2.556)	Elicited from experts
Reproduction	GSq	No of Litters	2.073 (0.504-3.672)	Elicited from experts
Reproduction	PM	Birth Rate	2.6	(Powell et al., 2012)
SQPV	RSq	SQPV Adult Days Until Mortality	12.377 (2.110-28.934)	Elicited from experts
SQPV	RSq	SQPV Juvenile Days Until Mortality	11.743 (3.125-27.392)	Elicited from experts
SQPV	RSq	SQPV Adult Mortality Rate	29.49 (12.62-173.00)	Back-calculated from "days until mortality"
SQPV	RSq	SQPV Juvenile Mortality Rate	31.08 (13.32-116.8)	Back-calculated from "days until mortality"
SQPV	GSq	SQPV Adult Mortality Rate	0	Grey squirrels do not die from SQPV
SQPV	GSq	SQPV Juvenile Mortality Rate	0	Grey squirrels do not die from SQPV
SQPV	RSq	SQPV Adult Recovery Rate	0	Red squirrels do not recover from SQPV

Category	Species	Parameter	Estimate	Source
SQPV	RSq	SQPV Juvenile Recovery Rate	0	Red squirrels do not recover from SQPV
SQPV	GSq	SQPV Adult Days Until Recovery	55.380 (0.639-340.454)	Elicited from experts
SQPV	GSq	SQPV Juvenile Days Until Recovery	74.893 (0.985-376.420)	Elicited from experts
SQPV	GSq	SQPV Adult Recovery Rate	6.59 (1.07-571.2)	Back-calculated from "days until recovery"
SQPV	GSq	SQPV Juvenile Recovery Rate	4.87 (0.96-370.56)	Back-calculated from "days until recovery"
SQPV	-	Transmission Reds to Reds	0.87	(Howell et al., 2024)
SQPV	-	Transmission Reds to Greys	0.22	(Howell et al., 2024)
SQPV	-	Transmission Greys to Greys	0.22	(Howell et al., 2024)
SQPV	-	Transmission Greys to Reds	0.22	(Howell et al., 2024)
SQPV	GSq	Partial Immunity	0.586 (0.289-0.893)	Elicited from experts

Category	Species	Parameter	Estimate	Source
SQPV	RSq	Partial Immunity	0	Red squirrels do not recover from SQPV
Competition	GSq	Competition Coefficient	1.65	(White et al., 2014)
Competition	RSq	Competition Coefficient	0.6	(White et al., 2014)
Predation Rate	GSq	Predation rate from Pine Martens	1.5 (0.7875-2.2125)	(Slade et al., 2023)
Predation Rate	RSq	Predation rate from Pine Martens	0.3 (0.1575-0.4425)	(Slade et al., 2023)

Table 15. Management parameters that were included in the biological model.

Category	Parameter	Estimate	Source
Lethal Management	Encounter Probability (Live traps)	0.05	(Croft et al., 2021)
Lethal Management	Encounter Probability (Kill traps)	0.017 (0.007-0.035)	Elicited from experts (Adjusted from Odds-Ratio derived from elicitation)
Lethal Management	Encounter Probability (Shooter)	0.11	Odds Ratio calculated from RSNE management data
Lethal Management	Shooting Coverage (Km2)	0.372 (0.040-1.260)	Elicited from experts
Fertility Control	Hopper Encounter Probability	0.05	(Croft et al., 2021)
Fertility Control	Hopper Competition Coefficient	0.775	(Croft et al., 2021)
Fertility Control	Contraceptive Duration (Months)	6.910 (2.000-17.000)	Elicited from experts
Fertility Control	Contraceptive Efficacy	0.685 (0.357-0.926)	Elicited from experts
Fertility Control	Time until Availability (Years)	10.63 (2.92-26.33)	Elicited from experts
Fertility Control	Probability of Successful Development	0.665 (0.261-0.940)	Elicited from experts
Squirrelpox Vaccine	Vaccine Efficacy	0.648 (0.186-0.942)	Elicited from experts
Squirrelpox Vaccine	Time until Availability (Years)	17.55 (3.33 - 48.33)	Elicited from experts
Squirrelpox Vaccine	Probability of Successful Development	0.341 (0.000-0.790)	Elicited from experts

Starting conditions

The starting population and distribution of grey squirrels, red squirrels, and pine martens that were used in the models are shown in **Figure 27**. These starting conditions were specified as follows:

Grey squirrels

We used a starting population ranging from 957,000 to 1,940,000 individuals, which corresponds to the lower confidence interval estimate to the mean estimate from the most recent population review in 2018 (Mathews et al., 2018). Each model run had a global population sampled from a uniform distribution using the range described. The population estimate numbers were halved when input into the model as it is a female-only model. Grey squirrels were assumed to be present across all of mainland England, with the only absence being the Isle of Wight. The grey squirrel population was spread across all hectads proportionally to carrying capacity (Table 16).

Red squirrels

We used a starting population ranging from 15,000 to 29,500 individuals. The lower limit is derived from government reports and red squirrel conservation groups (Wildwood Trust, n.d.). The upper limit corresponds to the lower confidence interval estimate from the 2018 population estimate (Mathews et al., 2018). The 2018 population estimate report indicated that the mean estimate was likely an overestimate, with the true population size being closer to the lower confidence interval. Given ongoing population declines and the seven-year difference from when the estimate was published, the lower confidence interval was deemed a more appropriate upper bound for the current estimate. Those values parameterised a uniform distribution that was sampled at every model run to determine the global population of red squirrels in England. The population estimate numbers were halved when input into the model as it is a female-only model.

The geographical distribution for the species was determined from the 2024 updated maps produced by the Mammal Society for the UK Squirrel Accord (per. comm.) using verified data collated between 2017 to 2022 and provided by CEDaR, Clocaenog Red Squirrels Trust, Colin Lawton, Mammal Society, Mid-Wales Red Squirrels Partnership, National Biodiversity Data Centre, National Parks and Wildlife Service, Red Squirrels Northern England, Saving Scotland's Red Squirrels, Trees for Life, Ulster Wildlife, University of Galway and Vincent Wildlife Trust. The allocation of individuals to hectads was stratified, with 3,500 individuals allocated to the Isle of Wight and the remainder allocated to the mainland hectads within the geographical distribution. Population size across all hectads within mainland England was allocated proportionally according to carrying capacity (Table 16). While Mersea Island was included in the geographic range of red squirrels due to its connection to the mainland, Brownsea Island was excluded from the analysis. At the hectad scale, the model artificially linked Brownsea to the mainland, misrepresenting its isolation and susceptibility to grey squirrel impacts. Given the small estimated population of approximately 250 red squirrels on Brownsea Island (Dorset Wildlife Trust, n.d.), we do

not expect this exclusion to affect any findings regarding the mainland population. However, we do acknowledge that Brownsea Island was not included in the model.

Pine martens

Although sporadic records of pine martens occur elsewhere in England, more established populations are known to be in Northumberland, North Yorkshire, Shropshire, the Forest of Dean, and the New Forest. Reintroductions also took place in 2024 in Devon (near Dartmoor National Park) and Cumbria (Grizedale Forest and Rusland Valley). Another reintroduction is planned for Somerset (near Exmoor National Park) for 2025/2026. The exact hectads that were assigned pine martens were selected by examining verified pine marten records from the NBN Atlas (NBN Trust, 2025) and maps provided by the Vincent Wildlife Trust (per. comms.). The planned locations of the Exmoor National Park releases were not known at the time, so were estimated by the Strategy Team according to pine marten carrying capacity in the hectads surrounding Exmoor National Park. The number of pine martens across England was stratified according to population estimates for each location (**Table 17**). Then, at each location that population was spread across those hectads proportionally to carrying capacity (**Table 16**). The population estimate numbers were halved when input into the model as it is a female-only model, except for the recent releases where the number of females was known.

Table 16. Carrying capacities for each species in each landcover habitat classification. All values are adapted from Slade et al., (2023) and republished under licence [CC-BY 4.0](https://creativecommons.org/licenses/by/4.0/).

Habitat	Red squirrels	Grey squirrels	Pine marten
Deciduous woodland	65	250	3.49
Coniferous woodland	35	15	1.15
Arable	0	0	0.05
Improve grassland	0	0	0.05
Neutral grassland	0	0	0.05
Calcareous grassland	0	0	0.05
Acid grassland	0	0	0.05
Fen	0	0	0.05
Heather	6	6	1.15
Heather grassland	0	0	0.05
Bog	0	0	0.05
Inland rock	0	0	0
Saltwater	0	0	0
Freshwater	0	0	0
Supralittoral rock	0	0	0
Supralittoral sediment	0	0	0
Littoral rock	0	0	0
Littoral sediment	0	0	0
Saltmarsh	0	0	0
Urban	32	95	0.05
Suburban	32	95	0.05

Table 17. Estimated pine marten populations across England that were used as the starting conditions in the model.

Location	Population estimate	Source
Cumbria	13 (8 females)	University of Cumbria: https://news.cumbria.ac.uk/news/pine-martens-thrown-a-lifeline-in-the-lake-district . [Accessed: 03/02/2025].
Dartmoor National Park	15 (8 females)	Devon Wildlife Trust / Two Moors Pine Marten Project: https://www.devonwildlifetrust.org/two-moors-pine-marten-project-timeline . [Accessed: 03/02/2025].
Exmoor National Park	15-20	Two Moors Pine Marten Project: https://www.devonwildlifetrust.org/two-moors-pine-marten-project-timeline . [Accessed: 03/02/2025]. This is an estimated number to be released in 2025/2026.
Forest of Dean	40-50	Gloucester Wildlife Trust: https://www.gloucestershirewildlifetrust.co.uk/project-pine-marten . [Accessed: 03/02/2025].
New Forest	20-60	New Wild Forest Pine Marten Project (per. comms.) – unofficial estimate from camera trap surveys and other activities conducted in this region.
Northumberland	20-50	Strategy Team estimate. Lowest mean pine marten density of 0.1/km ² for established populations (Stringer et al., 2018). Pine martens assigned to 12 hectads in this region, which comprise approximately 442km ² of woodland. At a density of 0.1km ² there would be 42 pine martens. This population is known to be a very low density, hence an estimate between 20-50 individuals was used. This is not an official estimate from any survey data.
North Yorkshire	0-10	Strategy Team estimate based on low number of records and comparisons of population sizes to other regions. This is not an official estimate from any survey data.
Shropshire Hills	20-30	Shropshire Wildlife Trust: https://www.shropshirewildlifetrust.org.uk/pinemartenproject [Accessed: 03/02/2025].

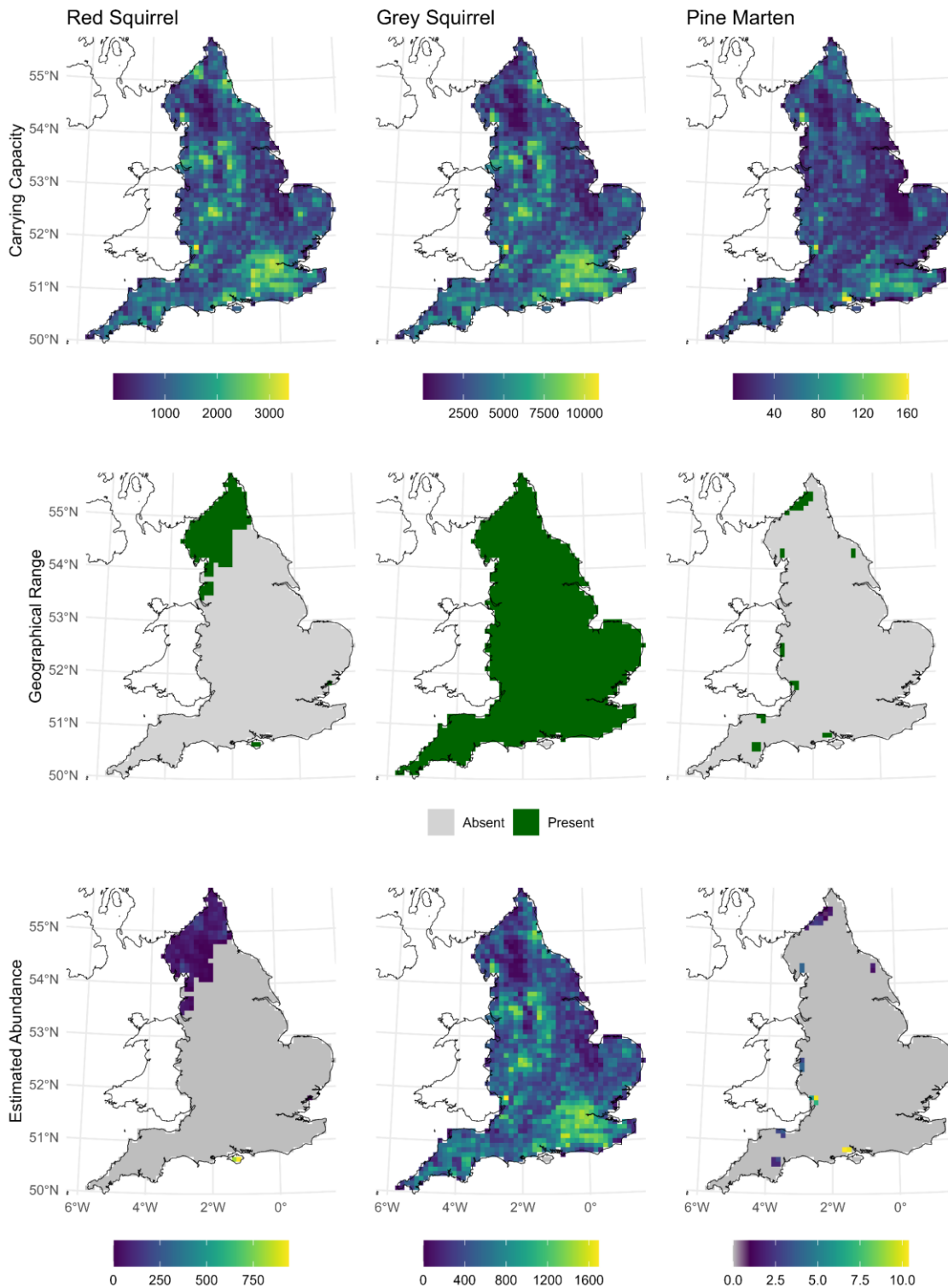


Figure 27. Model starting conditions for red squirrel, grey squirrel, and pine marten abundance and distribution. The population of each species were spread independently from each other across hectads according to their distribution and then proportionally to the predicted carrying capacity (top row) of each hectad within that distribution.

Management allocation

Lethal grey squirrel management

Current effort allocation for red squirrel-related activities (**Status quo** strategies) was calculated from data collated by Red Squirrels Northern England (RSNE) between 2021 and 2024. Much of this data was effort carried out and reported by local volunteer groups. We calculated the average yearly effort for shooting and trapping from this data and allocated it spatially, proportionally to the reported effort in each hectad.

For status quo, effort was kept at the same level and in the same locations for the full 25 years. In the other strategies with increased lethal management, effort was set at that reported in the literature for effective grey squirrel population suppression / eradication (Croft et al., 2021). Specifically, this was 5 live traps per ha for 45 days over 3 seasons of the year. As many volunteers report grey squirrel management activities through the whole year, we extrapolated this to get a total of 300 trap-days / ha per year. We calculated the amount of woodland in the areas undergoing grey squirrel management and allocated a total number of trap-days proportionally to woodland. We distributed some of the effort calculated for live traps to shooting and kill traps (where these activities are permitted), so that the expected ratio of squirrels removed through each method would be 5:5:1 (Shooting : Live-traps : Kill-traps). The effort for the other methods was defined according to the expected relative efficiency compared to live traps (where live traps are estimated to be roughly 3 times more efficient than kill traps, and 0.4 times less efficient than shooting).

Management effort was then allocated dynamically across hectads according to the carrying capacity of the hectad and whether grey squirrels were present. Kill traps were never used in hectads with red squirrels, pine martens or hazel dormice (*Muscardinus avellanarius*). Red squirrel and pine marten distribution changed through time as the model was running and this restriction was done dynamically. In contrast, as we are not including hazel dormice in the model itself, there is no changing population or distribution. Instead, hazel dormouse presence was assigned statically across years to hectads that fell within counties where dormice are said to be common (Morris, 2021). In addition, shooting effort was allocated proportionally to the amount of non-urban habitat in the hectad. Hectads with higher proportions of urban habitats were allocated less shooting effort, whereby a hectad with 100% urban/suburban cover would not be allocated any shooting. Once a hectad had been clear of grey squirrels for 1 year, the effort currently assigned to it was redistributed proportionally to carrying capacity across all the other hectads where greys were still present. We chose a relatively short timeframe of 1 year to trigger reallocation due to the model's stringent criteria for extirpation: not a single grey squirrel could be present in any timestep across the entire 100 km² hectad. Under these strict conditions, a hectad would only be considered eradicated if no individuals dispersed into it throughout the year, even it was then immediately removed. Starting conditions for the effort allocations are depicted for live traps (**Figure 28**), kill traps (**Figure 29**), and shooting (**Figure 30**).

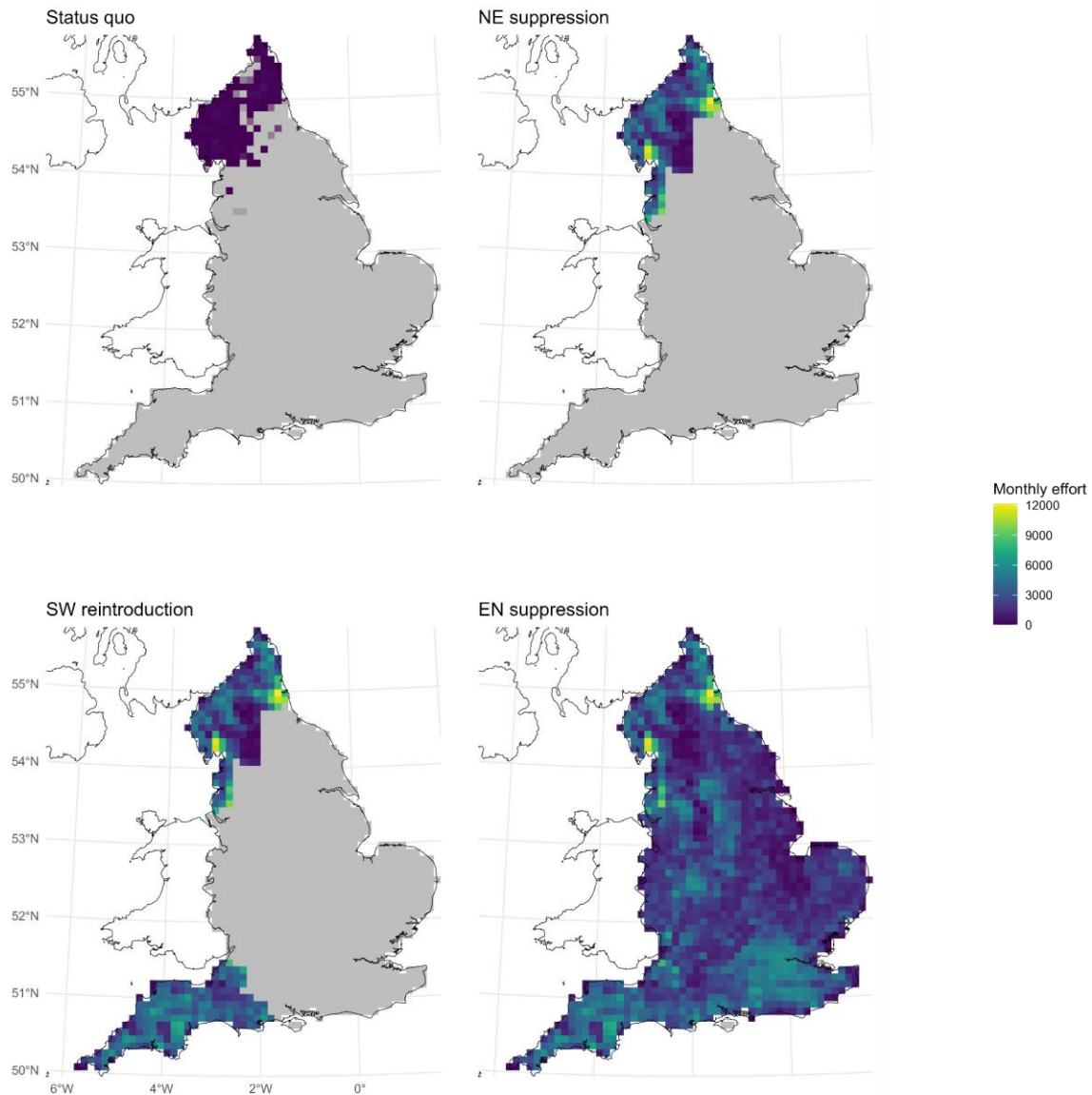


Figure 28. Effort allocation for live traps in the status quo strategy (current levels of grey squirrel management for red squirrel conservation) and when management effort is increased in the three major regions contained with the strategies: Northern England (top right), Northern England and the South West (bottom left) and the entire of England (bottom right).

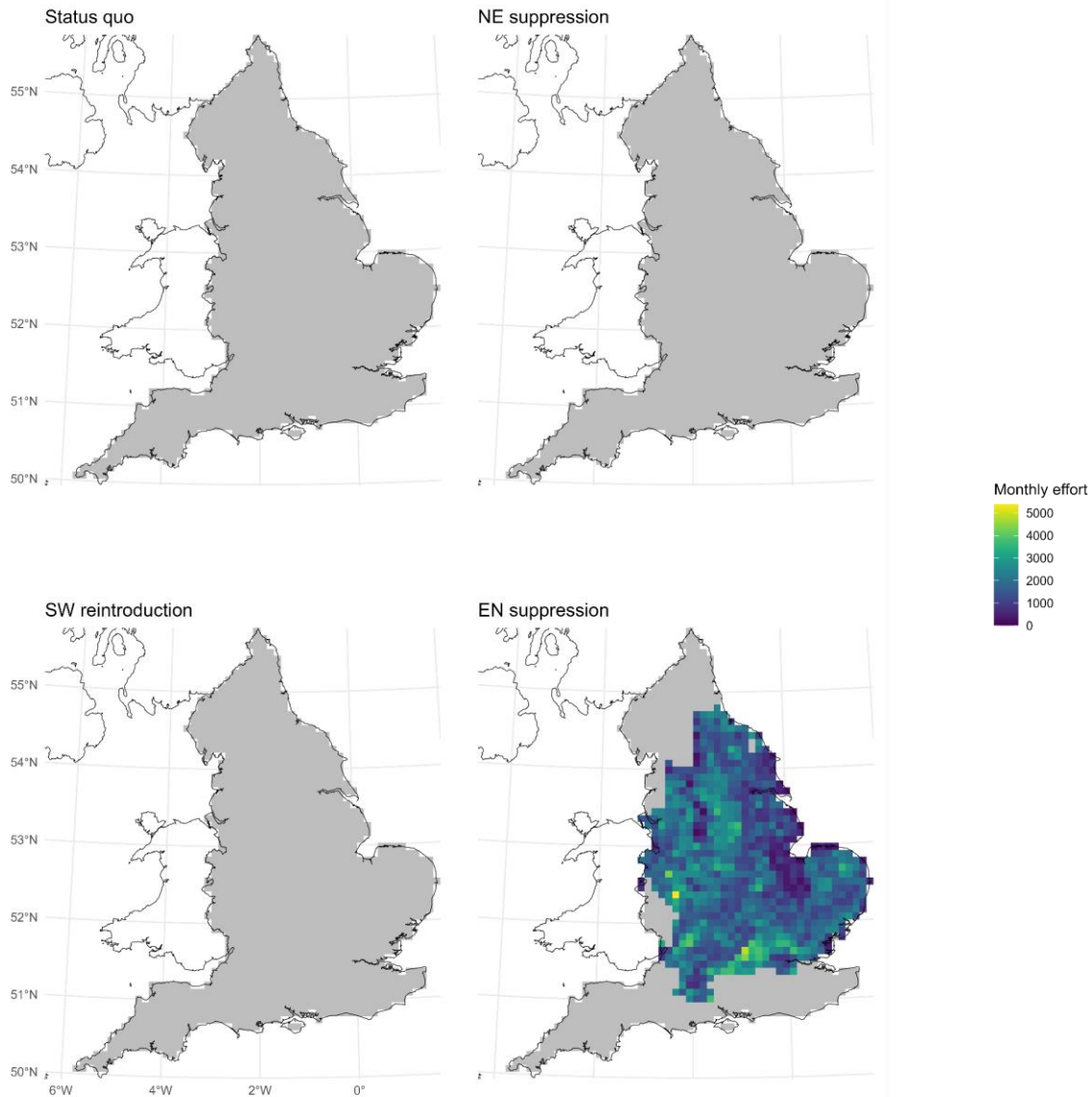


Figure 29. Effort allocation for kill traps in the status quo strategy (current levels of grey squirrel management for red squirrel conservation) and when management effort is increased in the three major regions contained with the strategies: Northern England (top right), Northern England and the South West (bottom left) and the entire of England (bottom right). Due to the presence of red squirrels in Northern England, and hazel dormice in the South West, kill traps were only assigned to hectads with the rest of England (bottom right).

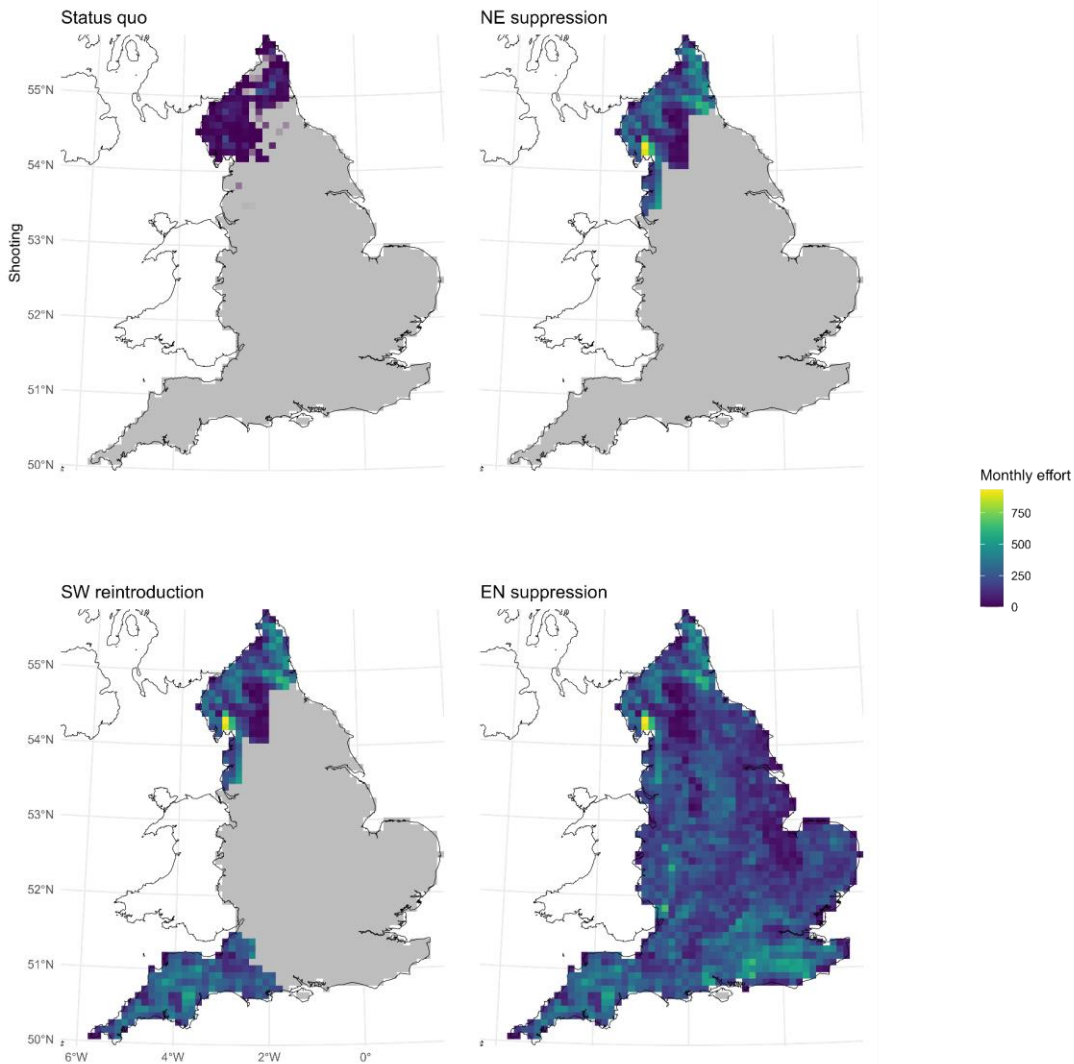


Figure 30. Effort allocation for shooting in the status quo strategy (current levels of grey squirrel management for red squirrel conservation) and when management effort is increased in the three major regions contained with the strategies: Northern England (top right), Northern England and the South West (bottom left) and the entire of England (bottom right).

Red squirrel translocation

All translocation strategies follow the same translocation pathway (see **Stage 3: Alternative strategies**), but in different locations, and were specified differently in the model. For the South West reintroduction strategy, releases were restricted to take place in either or both of OS Grid Reference SX88 and SS94, to complement ongoing pine marten reintroduction efforts (see **Stage 3: Alternative strategies**). For the Northern England reinforcement and the England reintroduction, hectads for releases of red squirrels were chosen dynamically. As such, the reinforcements in Northern England were not restricted to taking place only where pine martens are present, and we allowed a more organic selection to occur. The England reintroduction was restricted spatially so that releases could not occur in either the South West or Northern England regions. The translocations in the '**EN reintroduction+ (RoE + SW)**' strategy were allocated opportunistically across the South West region as well as the Rest of England region. This provided an opportunity to assess where reintroductions might take place in the South West if not restricted to the two hectads with pine martens that we dictated for the South West strategies.

In all three types of translocation strategy, the release hectads had to have been free of grey squirrels for at least one year. As the model was running, we programmed a check in June of each year that identified any hectads that met this criterion. If multiple hectads were available for release of red squirrels, we selected the hectad where red squirrel density was furthest away from the carrying capacity of the hectad. For the reintroduction strategies, this resulted in hectads with higher quality habitat for red squirrels being chosen (on the assumption that carrying capacity is a proxy for red squirrel habitat quality). For the reinforcement in Northern England, this resulted in hectads being chosen where red squirrel populations would most benefit from a population boost.

Fertility control

As fertility control is still under development, some model parameters and the uncertainty around them were estimated via the expert elicitation process. For the strategies that include fertility control, the probability that fertility control becomes available varies from 26.1% to 94% (95% confidence interval), with an average of 66.5%, and the time until it becomes available varies between 3 and 26 years (95% confidence interval) in the model (**Table 15**). When the time to availability is longer than the modelling timeframe, the model runs without fertility control. Given current research and advances by the APHA, we have assumed that a contraceptive would be delivered as an oral bait at grey-specific hoppers. Following Croft et al. (2021), we allocated the same number of trap days of hopper deployment as that of live traps. We also dynamically located them across hectads with grey squirrel presence (**Figure 31**).

Squirrelpox virus vaccine

The development of a squirrelpox virus vaccine is also uncertain, with parameters for the model having been estimated via expert elicitation. For strategies that include a vaccine, the probability that one becomes available varies from 0% to 79% (95% confidence

interval), with an average of 34.1%, and the time until it becomes available varies between 3 and 48 years (95% confidence interval) in the model (**Table 15**). When the time to availability is longer than the modelling timeframe, the model runs without vaccination. The exact mode of delivery of a vaccine is currently unknown, so we modelled vaccination as a static chance of a red squirrel being vaccinated at each time step of the model, as opposed to dynamically allocating a set amount of effort relating to delivery of the vaccine. To calculate this, we worked backwards from a target of 70% of the population being vaccinated 10 years after a vaccine becomes available. This gave a yearly vaccination rate of 0.12, i.e. each squirrel has a 1% chance of being vaccinated every month. The model randomly assigns this to individual red squirrels as it runs. Although a vaccine could also be administered to grey squirrels, we assumed that, at least in the time frame of this strategy, any vaccination efforts would be focused on red squirrels and so we only permitted vaccination of red squirrels and not grey squirrels in the models.

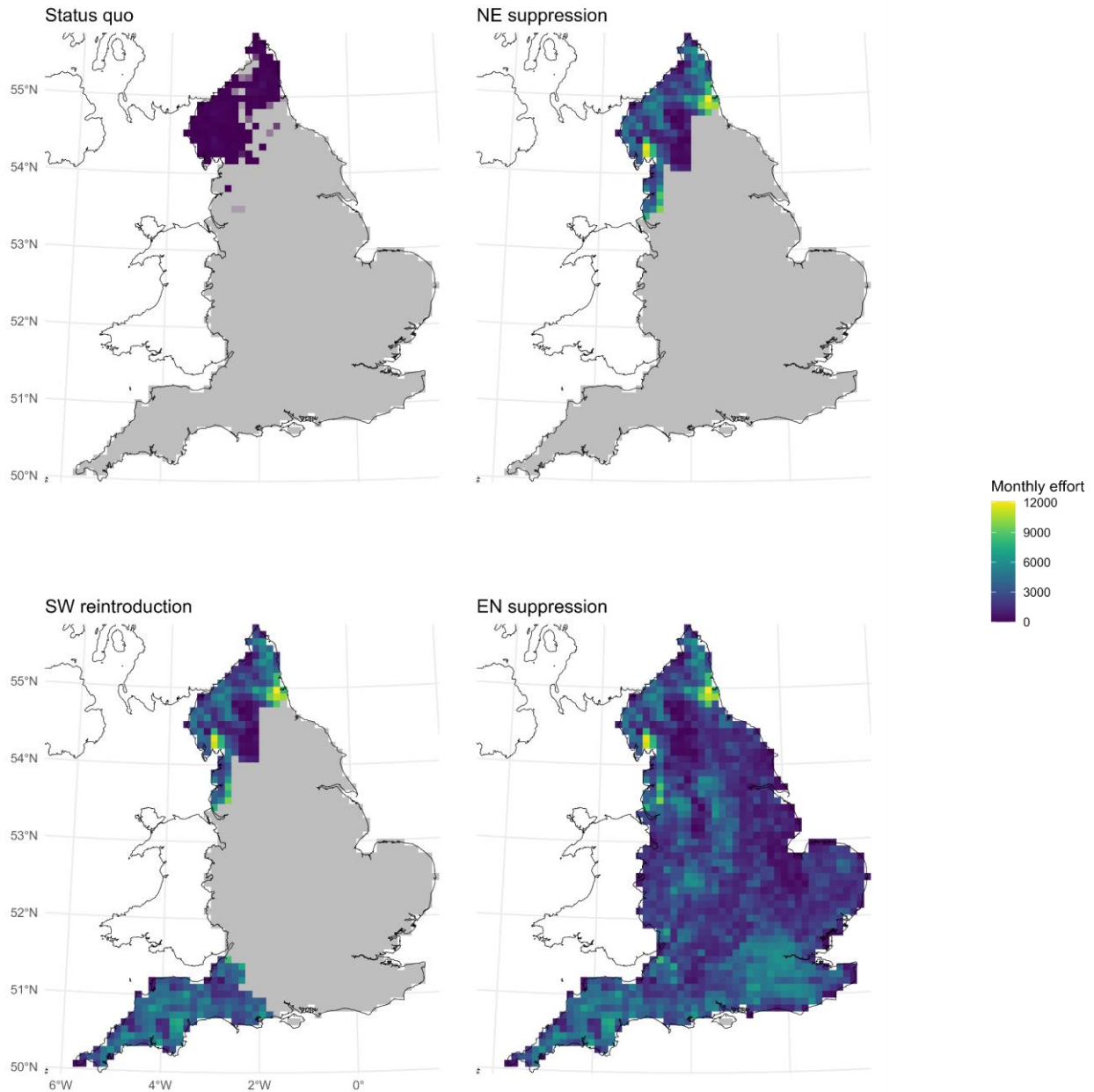


Figure 31. Effort allocation for fertility control in the status quo strategy (where lethal management of grey squirrels remains at current levels but fertility control becomes available) and when management effort is increased in the three major regions contained with the strategies: Northern England (top right), Northern England and the South West (bottom left) and the entire of England (bottom right).

Socioeconomic benefits

Wellbeing

The valuation of squirrel presence was based on the outputs from the biological model. Looking at the outcomes after 25 years, we assigned each hectad a value depending on which species of squirrel occupied it. Survey data from Dunn et al., (2018) indicated that respondents like to see both grey and red squirrels. While a significant portion of respondents expressed a desire to see grey squirrels in gardens (47%), local parks (57%), and the countryside (58%), red squirrels were consistently more desirable by 27–28% across these settings.

Thus, we assigned hectads with only grey squirrels a weight of 1, but those with either red squirrels only, or both red and grey squirrels, a weight of 1.3. Hectads cleared of grey squirrels without subsequent red squirrel replacement were given the lowest weight of 0. The hectad value was then adjusted according to the number of people per hectad, i.e. the number of people who would benefit from the presence of squirrels. The number of people per hectad was estimated using data from the latest census (Office for National Statistics (ONS), 2022). Specifically, the number of people in each upper tier local authority (UTLA) in the census data was distributed equally to 1 x 1 km cells within that UTLA. We then summed the number of people per hectad. The hectad scores (number of people x squirrel presence value) were then summed across England to give a total connection to nature score for each strategy.

Forestry benefits

The causal mechanisms underlying grey squirrel bark stripping behaviour are largely unknown. However, many consider bark stripping and subsequent tree damage to be a function of grey squirrel density with damage occurring as grey squirrels approach their carrying capacity in woodlands. Using outputs from the biological model, we estimated the total area of broadleaf forest where grey squirrel density was below 90% of carrying capacity at the end of the 25 years. This was determined by calculating the density of grey squirrels in broadleaf habitat for each hectad and then summing the total area of broadleaf woodland where grey squirrel density was below 2.25/ha.

Non-target species bycatch

We curated a list of non-target species that are sometimes caught in live traps and kill traps (**Table 18**). These species were gathered through informal discussions (such as during the workshops), from data collated by RSNE on the use of live traps and from a survey that was emailed to 21 of the workshop participants. Of these 21 stakeholders, seven responded with information on how different types of grey squirrel management, as well as how reductions in grey squirrel populations and increases in red squirrel populations, might affect other species either positively or negatively. We also asked for the source of this information, i.e. was it known from: personal experience; others' experiences; scientific literature/reports; news articles; social media, or other sources. The species listed were reported to be captured only rarely, and those caught in live traps were almost always said to be released alive.

Except for red squirrels and lesser spotted woodpeckers (*Dryobates minor*), all of the species listed have relatively uniform distributions across England, and very little density information exists for these species. This, coupled with a lack of detailed records and studies on bycatch rates under different levels of trapping effort, meant it was not possible to estimate or extrapolate what the potential impacts of the different strategies would be in terms of bycatch. Instead, we used a proxy measure based on the number of traps used and the geographical spread of traps as an indicator of relative potential for species to interact with traps and become bycatch. In other words, the higher the number of annual trap days per hectad, the higher the risk of bycatch. This was calculated directly from the model outputs as the mean across the 25 years of the annual effort per hectad (total trap days per year divided by the number of hectads in which trapping occurred).

Table 18. Table of species noted as occasionally caught in either live cage traps or kill traps (including GoodNature A18 traps) according to volunteer records and a survey distributed to stakeholders with experience of grey squirrel management methods. Individuals caught in live traps were mostly said to be released alive. This is not an exhaustive list of all species at risk of capture.

Taxa	Species	By-catch in live traps	By-catch in kill traps
Bird	“Small birds”	Not reported	Yes
Bird	Carrion crow (<i>Corvus corone</i>)	Yes	Not reported
Bird	Common blackbird (<i>Turdus merula</i>)	Yes	Not reported
Bird	Common pheasant (<i>Phasianus colchicus</i>)	Yes	Not reported
Bird	Eurasian jackdaw (<i>Coloeus monedula</i>)	Yes	Not reported
Bird	Eurasian jay (<i>Garrulus glandarius</i>)	Yes	Not reported
Bird	Eurasian magpie (<i>Pica pica</i>)	Yes	Not reported
Bird	Eurasian nuthatch (<i>Sitta europaea</i>)	Yes	Not reported
Bird	European robin (<i>Erithacus rubecula</i>)	Yes	Not reported
Bird	Great spotted woodpecker (<i>Dendrocopos major</i>)	Yes	Yes
Bird	Great tit (<i>Parus major</i>)	Yes	Not reported
Bird	Grey partridge (<i>Perdix perdix</i>)	Yes	Not reported
Bird	Lesser spotted woodpecker (<i>Dryobates minor</i>)	Yes	Yes
Mammal	“Small mammals”	Yes	Yes
Mammal	American mink (<i>Neovison vison</i>)	Yes	Not reported
Mammal	Brown rat (<i>Rattus norvegicus</i>)	Yes	Yes
Mammal	European hedgehog (<i>Erinaceus europaeus</i>)	Yes	Not reported
Mammal	European polecat (<i>Mustela putorius</i>)	Yes	Not reported
Mammal	Pine marten (<i>Martes martes</i>)	Yes	Yes
Mammal	Red squirrel (<i>Sciurus vulgaris</i>)	Yes	Not reported
Mammal	Stoat (<i>Mustela erminea</i>)	Yes	Not reported
Mammal	Wood mouse (<i>Apodemus sylvaticus</i>)	Not reported	Yes

Public acceptability

The acceptability to the public of the different grey squirrel management methods was predicted using data originally collected in a previous survey by Forest Research (Dunn et al., 2018). The published analyses of these data showed that support or opposition to different methods was significantly influenced by demographic factors (age and gender), as well as individuals' knowledge of the grey-red squirrel relationship, red squirrel conservation efforts in their local area, and grey squirrel management efforts in their local area (Dunn et al., 2018, 2021).

To determine the age and gender composition of each hectad in the model, demographic data from the 2021 census (Office for National Statistics (ONS), 2022) were used. We grouped ages from the census data to align with those used by Dunn et al. (2018): 18–24, 25–34, 35–44, 45–54, 55–64 and 65+, with individuals under 18 excluded to match the original sample. The population data were then evenly distributed across 1 km² grid cells within each upper tier local authority (UTLA) area of England and subsequently aggregated to hectads (10 km x 10 km cells). This provided an estimate of the number of people in each sex and age category per hectad. Whilst demographic parameters could be estimated from census data, the general knowledge base of the broader population remains unknown. To address this, we used the Dunn et al. survey data to estimate the percentage of people knowledgeable in the three squirrel topics (grey-red relationship, local red squirrel conservation, and local grey squirrel management) across the nine major regions of England (North East, North West, Yorkshire and the Humber, East Midlands, West Midlands, East of England, London, South East, South West). These broad regional knowledge estimates were then assigned to each hectad based on its regional location within England.

To model public opinion, the original dataset from Dunn et al. (filtered to include only responses from England) was used to run ordinal logistic regressions for each of the four squirrel management methods of interest. These regressions, which treated Likert scale responses as ordered factors, were conducted using the *polr()* function from the *MASS* package (Venables & Ripley, 2002) in R version 4.4.0 (R Core Team, 2024). The resulting models were used to predict Likert scores across England at the hectad level. Predictions accounted for all combinations of gender, age group, and knowledge levels, with probabilities weighted by the number of people in each category per hectad, along with the region-specific knowledge percentages.

The predicted number of individuals per Likert response category was then summed within each hectad. In the analysis, opposition was defined as Likert scores of 1 or 2 (i.e., "highly unacceptable" and "unacceptable"), while support was defined as scores of 4 or 5 ("acceptable" and "highly acceptable"). Neutral responses (score of 3) were excluded from summaries of support or opposition.

Due to the absence of data on public acceptability of combinations of management methods, the strategy-level assessment of opposition and support was based on the single most opposed method within each strategy. This approach assumes that public sentiment toward the least favoured method will shape the overall perception of the

strategy. Opposition was then reported at both national and local scales. At the national level, this refers to the percentage of the entire population that opposes the most controversial method in the strategy, regardless of its geographic implementation. At the local level, it refers to the percentage of the population within each hectad opposing the worst method in use in their area. Additionally, the number of local people opposed to the strategy was also expressed as a percentage of the national population.

Welfare

Grey squirrel management methods

We conducted a one-day in-person expert elicitation at the Zoological Society of London, with 18 participants - 16 attending in person and 2 joining online. Two participants could not contribute for the entire day, so we used responses from 16. Participants represented a range of expertise including wildlife veterinarians, conservation practitioners, and squirrel, rodent, and welfare researchers. We followed a modified version of the Sharp & Saunders (2011) method, which applies the Five Domains model to assess the negative welfare impacts of vertebrate pest management techniques. This approach has been used for several species, including another rodent species, the brown rat (*Rattus norvegicus*) (Baker et al., 2016, 2022).

Before the workshop, we provided each expert with an information booklet detailing the methods under assessment with previous studies on their welfare impacts, an explanation of the Sharp & Saunders framework, and the scoring criteria. We structured the elicitation using the IDEA protocol, where experts first submitted independent responses before reviewing summarised results for discussion (Hemming et al., 2018). We discouraged self-identification of scores but encouraged experts to share experiences and relevant studies that influenced their assessments. After discussion, they had the opportunity to adjust their scores. We collected all responses using an online Qualtrics survey.

The Sharp & Saunders approach divides the assessment into two parts. In Part A, experts evaluated overall welfare impacts (excluding death) for the average, individual grey squirrel by scoring the first four domains (Nutrition, Environment, Disease/Injury, and Behaviour) on a five-point categorical scale (No impact, Mild, Moderate, Severe, Extreme). If uncertain, they could select multiple categories. Scores for Domains 1-4 were used to inform the score for Domain 5, the overall Mental State, which is the final score for Part A. Experts scored Domain 5 using a probabilistic approach allocating 100 votes across the five categories based on their confidence in the true impact on an average grey squirrel being directly affected by the method in question. This differed from the traditional Sharp & Saunders approach that asks expert to pick an impact category and assign a confidence value. Part B of the Sharp & Saunders model focuses on assessing the intensity of suffering associated with the mode of death. Part B was assessed by the experts using the same voting method as for Domain 5 in Part A. Overall, eight methods were assessed for Part A impacts and ten for Part B impacts.

After experts distributed their 100 votes across categories, we assigned the final impact scores for Part B and Domain 5 in Part A by calculating the percentage of votes each category received. We first selected the category with the highest percentage of votes, and if any other categories were within 20% (absolute, not relative) of this, we included them to represent a range of likely impacts. We assigned combined scores using the matrices provided by Sharp & Saunders (2011) that combine the Part A score and the Part B score, with the duration that each is experienced (**Table 19**; **Table 20**). Higher scores indicate greater negative welfare impacts.

Table 19. Sharp & Saunders matrix for Part A scoring the overall welfare impact from None to Extreme against the length of time it occurs for.

	Immediate to seconds	Minutes	Hours	Days	Weeks
Extreme	5	6	7	8	8
Severe	4	5	6	7	8
Moderate	3	4	5	6	7
Mild	2	3	4	5	6
None	1	1	1	1	1

Table 20. Sharp & Saunders matrix for Part B scoring the level of suffering experienced (None-Extreme) from the onset of the mode of death to irreversible unconsciousness against the length of time it occurs for.

	Immediate to seconds	Minutes	Hours	Days	Weeks
Extreme	E	F	G	H	H
Severe	D	E	F	G	H
Moderate	C	D	E	F	G
Mild	B	C	D	E	F
None	A	A	A	A	A

The strategies modelled in this project only include a subset of the evaluated methods. Final scores for the four included methods are shown in **Table 11**. The strategies do not distinguish between modes of dispatch following live trapping, so the score applies to both cranial dispatch and shooting in the trap, which experts rated equally. Similarly, no distinction is made between shooting types, so we present the results for free shooting as they were comparable to shooting at bait stations. Drey poking was rated as having greater negative impacts but was excluded due to uncertainty about its prevalence. However, this should be considered in future iterations. Unlike the lethal methods, fertility control is not yet available and lacks research on its impact on grey squirrels. Scores for fertility control are therefore informed by welfare research in other species and the potential impacts of changing breeding behaviour. All results can be found in **Appendix 5**.

To account for the differences in the scale of the impacts from each strategy, we extracted the number of squirrels affected by each of the four methods over the 25 years from the biological model outputs. We plotted the Part A and Part B scores and colour-coded them by the number of squirrels impacted in each strategy **Figure 26**. We grouped strategies that resulted in similar welfare outcomes—based on both the type of interventions and the number of grey squirrels affected—and ranked these groups from most to least favourable. The best-ranked group involved no management intervention (i.e. no grey squirrels affected), while the worst involved all management methods applied at a large scale, affecting millions of individuals. We then used the rank order centroid method to assign weights to each group based on their rank, giving proportionally more weight to more favourable outcomes (**Table 12**).

Red squirrel translocations

Whilst assessing the negative welfare impacts of grey squirrel management methods, we also asked experts to assess the negative impacts of red squirrel translocations using the Sharp & Saunders method. As this is not a form of lethal management, only Part A was scored. Although we elicited these scores, we have not included them as an output in this process as the translocation pathway is the same in each strategy that includes translocations and involves a similar number of individuals. Instead, we simplified this to saying that any strategy with a translocation will have potential for negative welfare impacts on those individuals being translocated. Specifically, we use the probability that a translocation occurs over the 1,000 iterations of the model for each strategy to represent that some chosen strategies have a greater chance than others of negatively affecting red squirrels via translocations. The full results of the assessment can be found in **Appendix 5**.

Squirrelpox virus

Positive welfare impacts of the strategies for red squirrels are recorded in relation to the number of red squirrels dying from the squirrelpox virus over the 25 years. This value is output directly from the biological model and is averaged across the 1,000 model runs for each strategy.

Cost

Grey squirrel management

Most of the cost of each strategy is comprised of grey squirrel management actions. We calculated these costs in terms of effort (trap days and shooting days) in relation to the cost of paying full-time employees to carry out such work. Salary was costed at £94.50 per day per person to align with the National Living Wage and similar-priced job advertisements for grey squirrel management officers. This does not include costing of employment overheads. Variation in the total cost per year stems from variations in how many traps can be checked by a single person per day. After discussing this question with some of our stakeholder group who are familiar with *in-situ* grey squirrel management work, we estimated two costs, one where somebody can check 20 live traps per day and one where they can check 30 live traps per day. Kill trap effort and fertility control effort requirements were calculated relative to these values for live traps. Guidance on how many times a day traps should be checked varies, though consensus is that live traps should be checked at least twice per day and kill traps at least once per day. Thus, we assumed that double the number of kill traps than live traps can be checked by one person per day. Fertility control hoppers are stated to need checking five times less frequently than live traps as they do not capture individuals and just need the bait replenishing (Croft et al., 2021).

We would like to highlight that this method of costing the strategies provides what is likely to be an overestimation of the actual costs of the strategies given that it does not account for any economies of scale or free labour through volunteer effort. To prevent further inflating the costs, we did not include the costs of overheads for employers or equipment. Although the strategy costs are still likely to be overestimates, in terms of decision-making, our approach helps to set out the relative differences in labour requirements and cost for a comparison and trade-offs between strategies.

Squirrelpox vaccine

Although the delivery method of the vaccine is not yet established, for the purpose of estimating costs, we assumed that it would be delivered in the same way as an oral contraceptive at feeding hoppers. As such, we assumed that the cost of sterilising one individual grey squirrel is the same as the cost for vaccinating one individual red squirrel. To calculate the average number of red squirrels vaccinated per strategy we took the yearly average abundance of the global red squirrel population and multiplied it by the probability of vaccination each year (11.34%, derived from vaccination rates in the model – see **Table 15**). We then used the cost per individual sterilised (calculated above based on paid labour costs) and multiplied this by the average total number of individuals vaccinated across the 25 years of each strategy to get a cost for vaccination.

Translocations

As our strategies incorporated captive-to-wild translocations of red squirrels, the estimated annual cost of rearing one red squirrel (£500) was sought and provided by Wildwood

Trust. This value incorporates feed, supplement items and veterinary costs, and does not include housing, maintenance, or labour costs of those working to rear these animals. The cost of conducting a translocation was calculated using information provided by Natural Resources Wales (NRW) for the costs of the reinforcements in Clocaenog Forest, Wales and the average number of squirrels released across our 1,000 model runs for each strategy. For costing translocations, we used a hard release approach that doesn't require any holding infrastructure at the release site and included the costs of disease screening, nest boxes, hoppers and supplementary feed, VHF radio collars and associated equipment, camera traps for additional post-release monitoring, contingency planning (i.e. disease screening of carcasses), and appropriate labour time costed at £94.50 per day per person to match the National Living Wage.

Stage 5: Trade-offs & decision

Background

To decide on the best way forward, it is necessary to evaluate how each alternative performs across the full set of objectives. Because alternatives often involve trade-offs (performing better on some objectives and worse on others) an acceptable balance of outcomes must be identified. The decision process can be simplified by excluding dominated alternatives, which perform worse than others across all objectives. Importantly, trade-offs allow for the integration of both the “factual” consequences of each alternative, as estimated through methods such as modelling or expert elicitation, and the “subjective” importance placed on different objectives by stakeholders. Techniques such as multi-criteria decision analysis and facilitated deliberation are used to make these preferences explicit, ensuring that the final decision reflects both evidence and values.

Outcomes

We simplified the decision problem by first reducing the 14 performance attributes to nine attributes that mapped to nine independent fundamental objectives (see the Process section below for an explanation). In a one-day workshop with 29 stakeholders, we then elicited objective weights (how much each person valued each objective) using the SMARTER technique (Barron & Barrett, 1996) (**Figure 32; Figure 33**). This allowed us to calculate the overall ‘utility’ (satisfaction) of each strategy for each individual based on how they weighted the objectives. We then identified each individual’s top three ranking alternatives to determine which strategies, or groups of strategies, performed best for the group (**Figure 34**). Two of the stakeholders’ weights were not useable, so results are shown for 27 people

There was expected variation in how stakeholders valued each objective (**Figure 32**). While red squirrel persistence was most frequently ranked as the most important objective, others, such as red squirrel geographic range, tree damage, and grey squirrel welfare, were also ranked first by at least one participant. Overall, persistence, geographic range, and red squirrel welfare emerged as the highest-ranked objectives (**Figure 33**). In contrast, connection to nature and public opposition were consistently ranked lowest. This does not necessarily indicate that stakeholders dismissed their importance, but rather that these objectives had similar outcomes across all strategies and therefore had less influence on the decision.

England-wide reintroduction strategies were the most preferred, appearing in the top three for more than half the stakeholders. Specifically, ‘**EN Reintroduction+ (RoE + SW)**’ was the top choice for 12 individuals, and together with ‘**EN Reintroduction++ (RoE)**’, these strategies had the highest minimum utility scores across all strategies. Northern England reinforcement strategies were also highly rated, although not as much as England-wide strategies, in part due to the high penalisation the former suffer from tree damage outcomes. South West strategies had moderate utility scores but were rarely top-ranked,

likely due to costs to red squirrel welfare (a highly valued objective). The number of red squirrels predicted to die of squirrelpox was higher in the strategies that include translocations due to the maintenance of more contact regions between grey and red squirrels, thus increasing spillover between populations. Overall, reintroduction and reinforcement strategies outperformed suppression strategies, largely because they expanded red squirrel geographic range, the second highest-ranked objective. They also improved connection to nature, even though it was not a top-ranked priority, by partially compensating for the loss of grey squirrels in suppressed areas, increasing the areas where people see and interact with squirrels.

The '**Do nothing**' strategy ranked first for four stakeholders, despite failing to conserve red squirrels. These individuals placed high importance on red and grey squirrel welfare. In contrast, status quo strategies consistently scored among the lowest, with '**Status quo++**' having the lowest minimum utility score for any participants. The status quo strategies only ranked among the top ones for one stakeholder– in addition to failing to conserve red squirrels in the long-term, they still incur costs of conflicting objectives such as public opposition and grey squirrel welfare.

Overall, there are clear preferences expressed amongst the stakeholder group for England-wide reintroduction strategies or Northern England reinforcement strategies. Whilst there is some preference for doing nothing due to the high costs incurred for the other objectives, this strategy would lead to red squirrel extinction across mainland England.

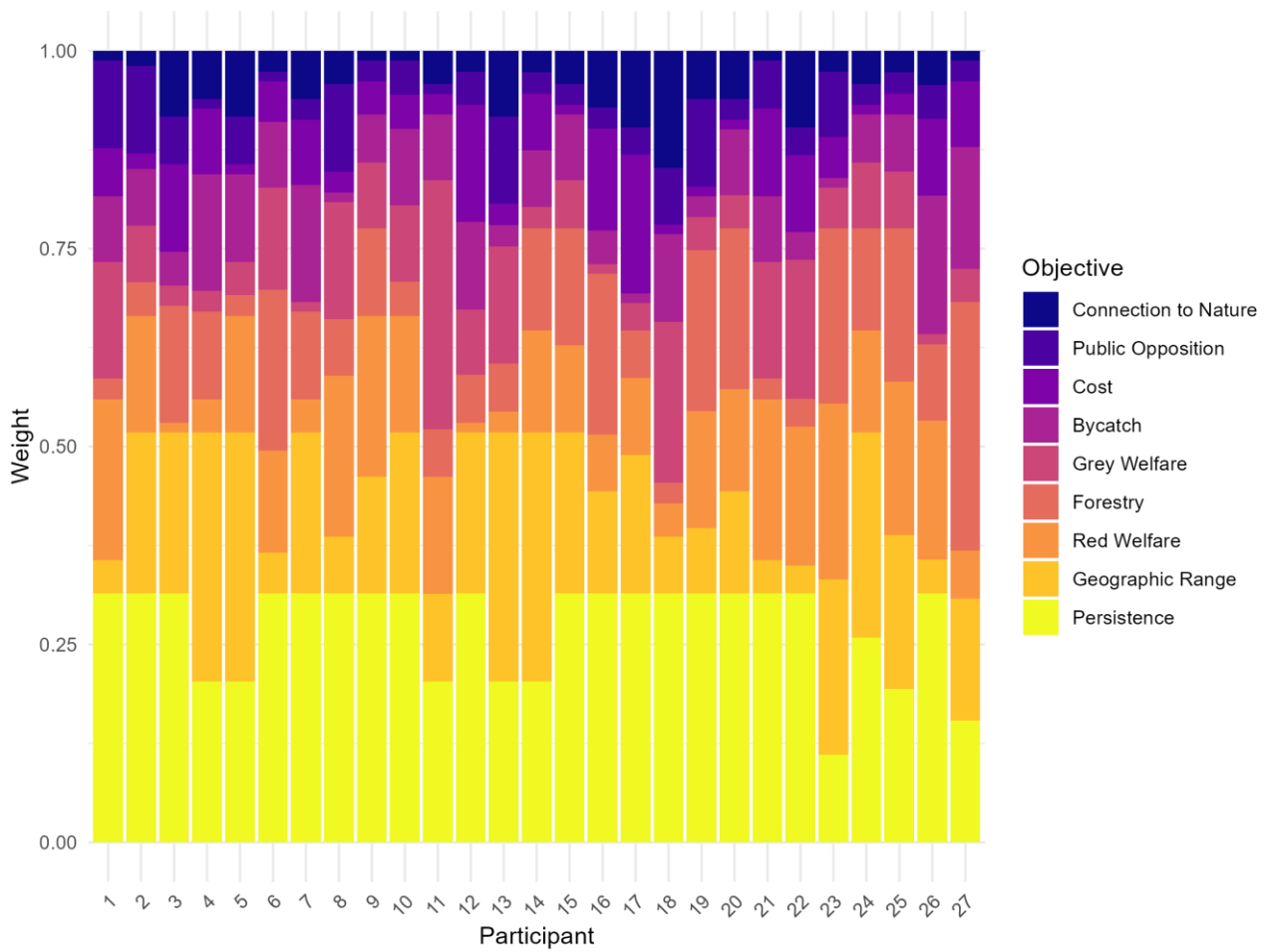


Figure 32. Expressed relative objective preferences (or weights) elicited from participants ranking the importance of the objectives relative to the outcomes of each objective. Results are randomised and anonymised.

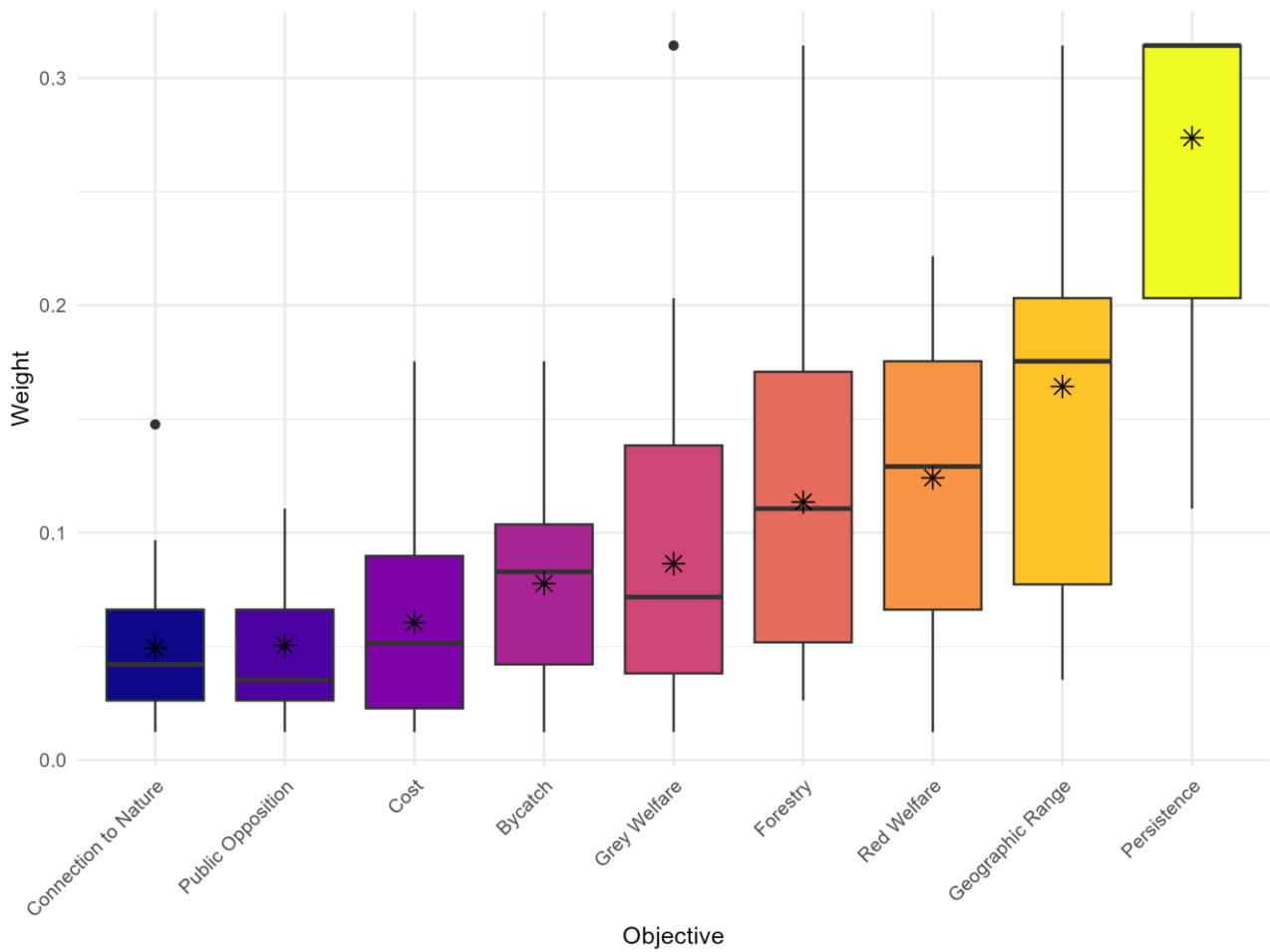


Figure 33. Summary of relative preferences (weights) for each objective across participants. The box area represents the interquartile range, the horizontal line represents the median value and the star represents the average value.

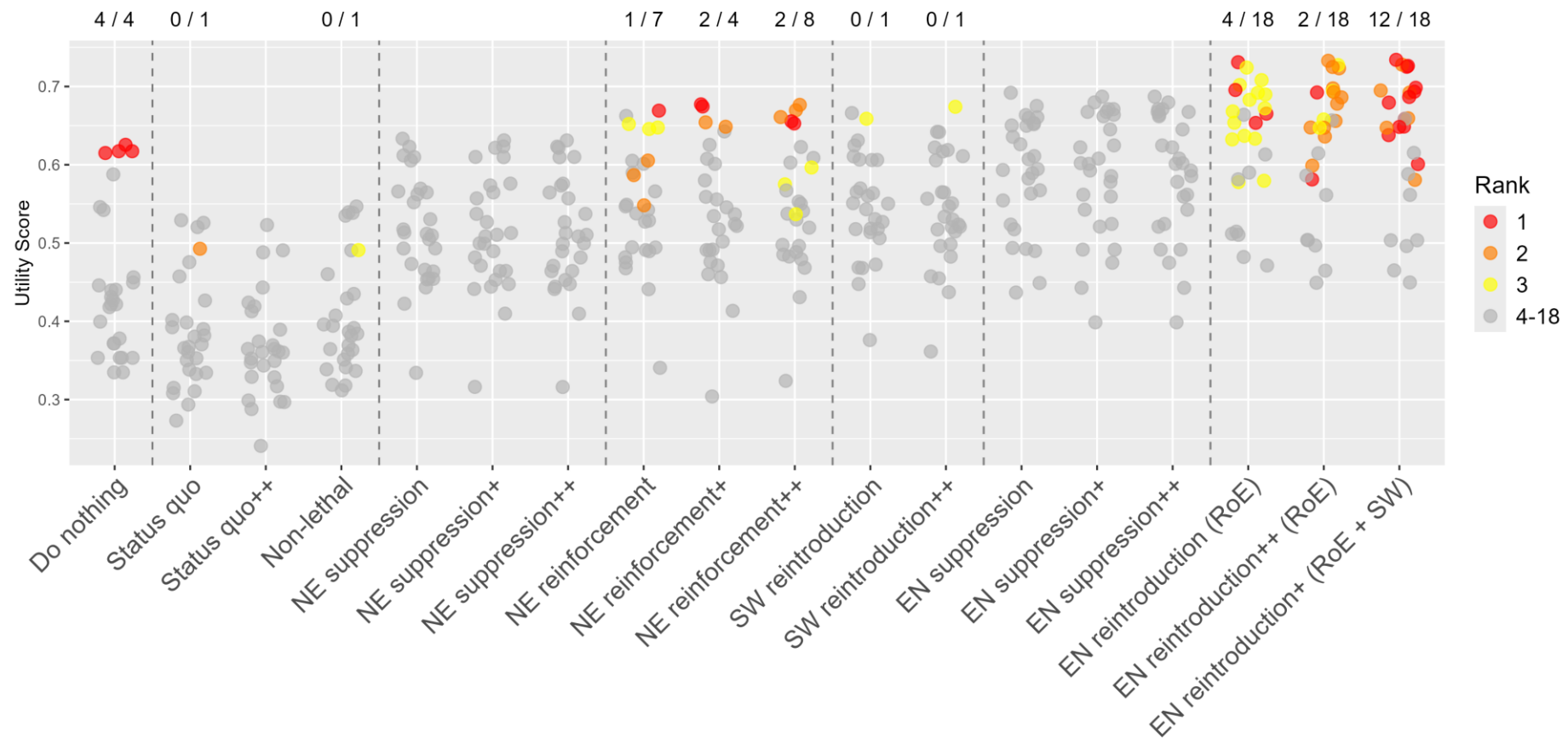


Figure 34. Individual stakeholders’ utility scores for each strategy. Higher utility scores represent better performance of the strategy for that individual. The three top-ranked strategies for each individual are coloured according to the legend. A count of the top three ranks is provided at the top of each strategy along with how many of those were a first rank, e.g. ‘NE reinforcement’ ranked in the top three for seven participants, for one of whom it was their top ranked objective (“1 / 7”).

Process

Decision simplification

First, we reduced the number of performance attributes assessed to avoid "double counting"—i.e. using multiple similar measures that count towards the same objective. For the "maximise red squirrel recovery" objective, we retained two performance attributes: the probability of red squirrel persistence on mainland England and the expected number of hectads occupied by red squirrels. For the "maximise socioeconomic benefits" objective, we also retained two attributes —connection to nature score and the 'total area of broadleaf woodland free of bark-stripping'—as they relate to fundamentally different aspects of the problem.

For the "minimise non-target bycatch in grey squirrel traps" objective, we used only the average annual kill trap days per hectad attribute, as stakeholders highlighted lethal bycatch in kill traps as the primary concern (as opposed to bycatch in live traps that is more commonly released alive). For the "minimise opposition to grey squirrel management actions" objective, we used the percentage of local opposition as the sole attribute. For the "minimise negative welfare impacts on squirrels" objective, we included two performance attributes: a Sharp & Saunders-based utility score for grey squirrels and the total number of red squirrel deaths due to squirrelpox virus. For "minimise cost" we used the maximum estimated annual cost rather than the minimum.

This left us with nine performance attributes, each representing a distinct feature of the decision problem. We interpret attributes within the same objective as pertaining to different "sub-objectives". For simplicity, we now refer to these nine performance attributes as "objectives" throughout this session. Particularly these are:

- maximise geographic range of red squirrels
- maximise red squirrel persistence on mainland England
- minimise non-target species bycatch in kill traps
- maximise connection to nature
- minimise forestry damage
- minimise local public opposition to grey squirrel management
- minimise negative impacts on grey squirrel welfare
- minimise the number of red squirrels dying from squirrelpox virus
- minimise cost.

Multi-criteria analysis

The SMARTER technique (Barron & Barrett, 1996) addresses multiple criteria decision problems by eliciting weights to express the relative subjective preferences for each objective and then applying these weights to normalised consequences for each objective.

This method enables the overall performance of an alternative to be calculated by weighing how well it performs for each objective j according to the subject's preference w_j and summing across objectives:

$$u_i = \sum_{j=1}^n w_j \cdot p_{i,j}$$

Higher values of u_i ('utility') indicate the alternative performs better across all objectives, accounting for the subjective's personal values and preferences (that are expressed by the quantity w_j).

To understand how the stakeholders involved in this project valued each objective, we held a one-day workshop in Penrith. We invited 43 people with 29 able to attend on the day. Participant expenses were paid for where required to ensure anyone invited who wanted to attend could do so. In this workshop, we presented the results of our modelling for each strategy and then asked participants to rank nine hypothetical scenarios. On each of these scenarios, all fundamental objectives were kept at their worst possible outcome among the strategies, except one objective, which was improved to its best outcome. This type of evaluation, called swing weighting, ensures that participants judged how much they value possible improvements on each objective among the alternatives based on the predicted model outcomes, and not just how much they care about each objective itself (See **Figure 35**). The rank that participants assigned each scenario determined the weight estimated by its corresponding objective (Barron & Barrett, 1996). In case of ties in a rank, the weight was distributed according to number of ties (for example, if two objectives were ranked first, the weights for both objectives would be the average between the first and second ranks). We were able then to calculate the utility u for all alternatives across participants.

These weights were then applied to normalised consequences rather than the raw consequences. Normalisation is conducted so that all consequences are on a scale of 0 (the worst possible outcome among the alternatives) and 1 (the best possible outcome among the alternatives). This allows for direct comparison between alternatives. The formula to conduct normalisation is

$$p_{i,j} = z - \frac{x_{i,j} - x_{j,\min}}{x_{j,\max} - x_{j,\min}}$$

where $p_{i,j}$ is the normalised score of consequence x of alternative i on objective j . $x_{j,\min}$ and $x_{j,\max}$ are the minimum and maximum values of the consequence across alternatives, respectively. z is a transformer variable that equals 0 when it is an objective to be maximised and 1 when the objective is to be minimised.

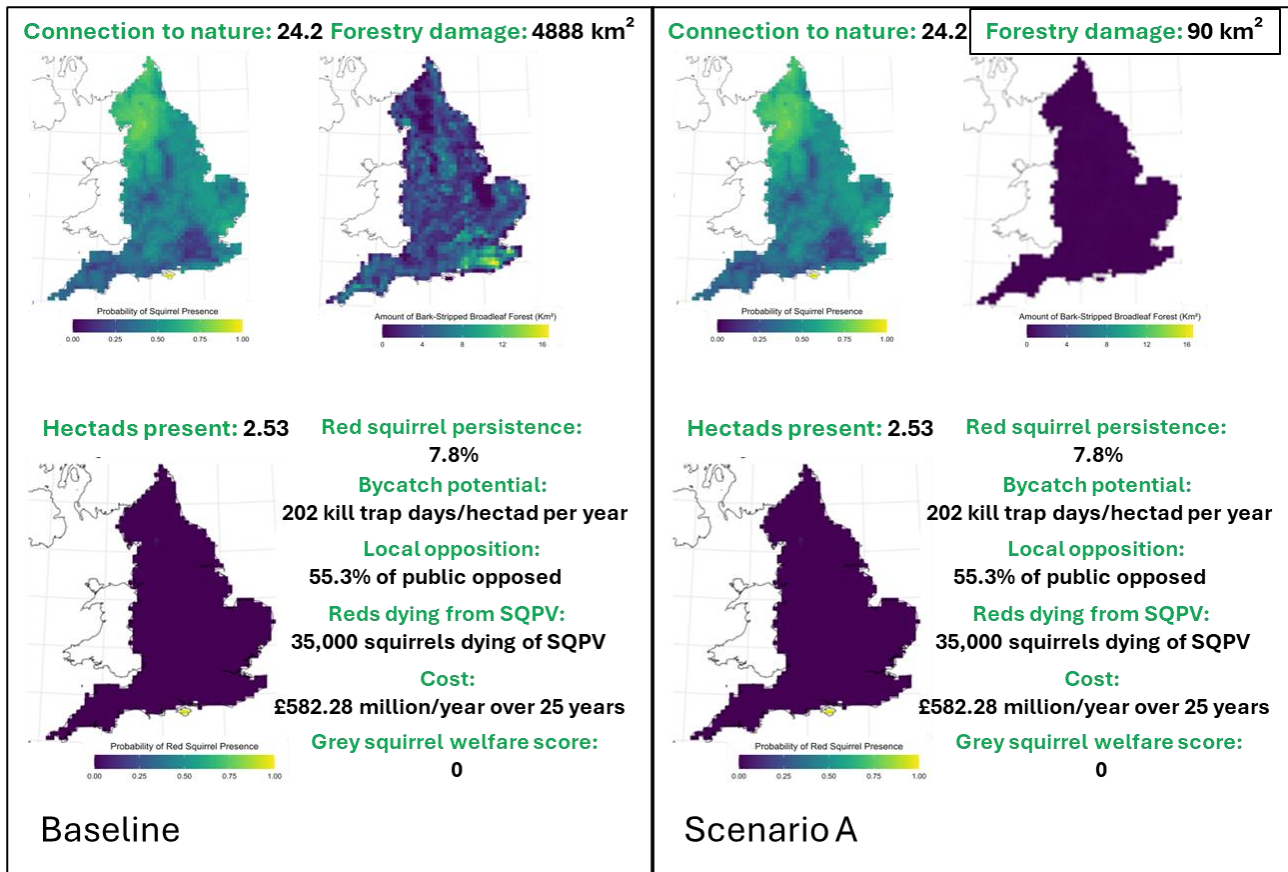


Figure 35. Example of scenario assessment through swing weighting. At the baseline scenario, all outcomes are the worst possible outcome for that objective across all alternatives. For scenario A, one single objective (Forestry damage) is changed to its best outcome among the alternatives. The participants ranked nine of those scenarios, one for each objective.

Discussion

Overall, our findings underscore that achieving the objectives for red squirrel recovery—namely, persistence and broader geographical distribution—requires high-intensity management strategies. Notably, strategies incorporating England-wide (**EN***) grey squirrel management demonstrate greater potential for red squirrel recovery, alongside reductions in tree damage from grey squirrel bark stripping. However, these benefits come with considerable trade-offs: strategies that perform best for red squirrels tend to perform poorly across several other objectives. Unsurprisingly, the England-wide strategies are the most expensive to implement and are associated with the highest potential for non-target species bycatch (due to the use of kill traps), the greatest predicted public opposition (due to the use of kill traps), the lowest connection to nature scores (due to large-scale grey squirrel removal), and the most significant welfare impacts on grey squirrels (**Table 7**).

These trade-offs are further highlighted when considering that the **‘Do nothing’** strategy performs worst for red squirrel recovery and tree damage objectives yet best, or joint best, for all the others (**Table 7**). Similarly, the **‘Status quo’** strategies consistently perform poorly for red squirrel recovery, while the **‘Non-lethal’** strategy (where lethal grey squirrel management is ceased if fertility control becomes available) performs similarly to **‘Do nothing’** across all objectives (**Table 7**). Although it is likely that the status quo levels of grey squirrel management are underestimated, it should be noted that even high-intensity suppression of grey squirrels does not guarantee red squirrel persistence. Consequently, doing nothing, continuing with the status quo, or switching from lethal to non-lethal grey squirrel management are not feasible strategies to achieve red squirrel recovery as all lead to high probabilities of red squirrel extinction across mainland England in the next 25 years.

Importantly, while an England-wide suppression strategy may be overly ambitious, more targeted regional approaches, such as those focused on Northern England and the South West, demonstrate comparable red squirrel persistence (**Table 7**). In particular, strategies incorporating the translocation of red squirrels for reinforcements in Northern England and reintroductions in the South West perform similarly, if not better, for red squirrel persistence than England-wide strategies. They also improve red squirrel distribution (in terms of occupied hectads) relative to regional strategies without translocations.

However, the benefits of the regional strategies that include red squirrel translocations come with increased red squirrel mortality from squirrelpox. This is because translocations lead to greater overlap between red and grey squirrel populations. This suggests that while regional strategies may be more feasible to implement, they also demand careful consideration of disease dynamics when widespread grey squirrel suppression is not taking place. While nearly all alternatives with both fertility control and a vaccine performed worse than the corresponding alternative with only fertility control, it should be noted that the delivery of a squirrelpox vaccine in the Northern England reinforcement strategy did reduce the number of red squirrel deaths from squirrelpox.

The consequences of the 18 strategies, therefore, present clear trade-offs between objectives. Understanding stakeholder values is critical to fully exploring the decision and

trade-off space. After asking stakeholders to rank the objective consequences in order of which they valued the most we found that England-wide strategies with red squirrel reintroductions were the highest scoring strategies as well as the highest-ranking strategies for over half of the stakeholders. Strategies focused on Northern England that include red squirrel reinforcements also scored highly and were highly ranked. In contrast, the South West reintroduction strategies, whilst highly scoring, were not as highly ranked as the Northern England reinforcement strategies. Aligning with the status quo strategies failing to deliver red squirrel recovery, these strategies were the lowest scoring across participants. However, the '**Do nothing**' strategy was the top-ranked strategy for four of the stakeholders, despite failing on red squirrel recovery. This result was driven by all four stakeholders ranking red and grey squirrel welfare alongside red squirrel persistence in their top three objectives.

This highlights an interesting area of the decision space, where for some people, red squirrel recovery comes at too high of a cost for the other objectives that they value. But, ultimately, doing nothing is not a feasible strategy for red squirrel recovery and either the England-wide or regional strategies provide greater satisfaction for a larger group of the stakeholders. Indeed, for two of the stakeholders for whom '**Do nothing**' ranked highest, '**NE reinforcement**' and '**NE reinforcement++**' ranked second and third, suggesting these regional strategies might also be acceptable to them. This is due to the regional strategies incurring fewer costs for other objectives than the England-wide strategies. As such, high intensity grey squirrel management at a regional level might be more feasible than the England-wide strategies.

In future iterations of this work, the most promising strategies can be refined to improve their feasibility and the models re-run. For example, non-target species bycatch and public opposition could be reduced by less reliance on using kill traps, or strategies could be implemented alongside a public communications campaign to help reduce public opposition to the strategy. Once more information is known about the welfare impacts of grey squirrel management, or if more welfare-friendly management methods are developed in the future, this new information could also be incorporated into the decision. In addition, the cost estimates are likely overestimates as they do not account for potential economies of scale or existing volunteer contributions. Factoring these in could substantially reduce the cost of implementation and make current costly strategies more economically viable.

Alongside the cost simplification, several other limitations of this work should be noted. First, our modelling was conducted at the hectad (10×10 km) scale, which may artificially inflate the number of red-grey contact points and potentially underestimate red squirrel persistence. While necessary for national-scale analysis, regional strategies could benefit from being refined and re-modelled at smaller spatial scales (e.g. tetrad or 1×1 km), supporting more locally nuanced decision-making. Furthermore, considerable uncertainty remains around the availability and effectiveness of emerging technologies such as fertility control, squirrelpox vaccination, and gene drive. As more evidence becomes available, our models can be updated to reflect improved estimates of feasibility and impact so that the decision over strategy implementation can be revisited through time.

The ability to revisit the decision and reiterate through the decision cycle is one of the many benefits of employing structured decision making (SDM) for complex conservation planning. Through this SDM approach, we engaged with over 60 stakeholders and experts from a wide range of sectors, thus capturing a broad and nuanced picture of views on red squirrel conservation. This inclusive engagement further highlights the strength and importance of the SDM approach: it ensures that people are meaningfully involved, their values are formally captured and considered, and decisions are made transparently using all available evidence. Through this process, we show that whichever conservation strategy is chosen for red squirrels, it should not sideline public welfare concerns or ethical considerations. Ultimately, a transparent, participatory and values-based approach is essential to ensuring both the legitimacy and the long-term support needed for successful red squirrel management.

Overall, despite the costs and trade-offs involved, our analyses suggest there is hope for red squirrel recovery—even if primarily at a local scale. However, achieving this requires significant investment, coordination, and buy-in from multiple actors across England. Along with careful consideration of the knock-on effects not just for the other social, economic and ecological objectives, but also for both red and grey squirrel populations in Scotland and Wales.

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Glossary

Action: A specific intervention or step that can be implemented towards one or several objectives. Actions are the building blocks of strategies.

Alternative: A given course of action considered in a decision-making process. In conservation, they might include various ways to manage a species or ecosystem.

Animal welfare: Many different definitions of animal welfare exist, though broadly it is referred to as the physical and mental state of an animal.

Conservation translocation: The intentional movement and release of a living organism where the primary objective is a conservation benefit.

Consequence: The outcome of a decision over a particular fundamental objective. The consequences are expressed through performance attributes.

Five Domains model: A framework for assessing animal welfare that encompasses nutrition, environment, health, behaviour, and the mental state of an animal.

Fundamental objective: Core value that represents what truly matters in the decision context. A decision can (and often does) include several fundamental objectives. They are ends in themselves, such as “maximise species viability” or “minimise negative animal welfare impacts”.

Invasive species: An invasive species is any animal or plant that can spread and cause damage to the environment, the economy, human health or how we live.

Non-native: Non-native refers to a species, subspecies or lower taxon, introduced outside its natural past or present distribution. It includes any part of the species that might survive and subsequently reproduce, including gametes, seeds, eggs and propagules. Non-native species include all fauna and flora except for genetically modified organisms, bacteria and viruses. The term 'non-native species' is the equivalent of 'alien species', as used by the Convention on Biological Diversity.

Performance attribute: A quantity used to describe the consequences of an alternative in relation to a fundamental objective.

Problem statement: A concise summary of the decision to be made, including its context, objectives, and key stakeholders. It defines the decision’s framing, scope, and scale, setting the foundation for structured decision making.

Reinforcement: Translocation of an organism into an existing population of the same species.

Reintroduction: Translocation of an organism inside its natural range from where it has disappeared.

Self-sustaining: A species or population of a species is self-sustaining if it can maintain itself without active and deliberate human intervention.

Sharp & Saunders model: A framework for assessing the relative negative welfare impacts of vertebrate wildlife management.

Structured decision making: A formal process for making complex decisions, especially under uncertainty. It involves decomposing a decision into its key components (objectives, alternatives, consequences, and trade-offs) and integrates scientific evidence and stakeholder values to support transparent and defensible decisions.

Strategy: Synonym for 'alternative' (see above) in the structured decision making framework (i.e. a combination of actions to be assessed).

Trade-offs: Situations in which improving one objective results in a reduction in another. Understanding trade-offs is key to selecting among alternatives in multiple objective scenarios.

Appendices

Appendix 1

Involvement of stakeholders

Table A1. Names and affiliations (at the time of involvement) of those who have been involved in the project through workshops, working groups (WG), expert elicitation sessions, or contributed data or other guidance. An asterisk (*) in the welfare expert elicitation column means this person contributed information in some way but was not involved in the workshop itself. Consent was obtained from all those listed to publish their names, affiliations, and contributions.

Name	Affiliation	2023 Initial Workshops	WG: Red squirrel recovery	WG: Ecosystem benefits	WG: Public acceptability	WG: Cost	WG: Socioeconomic benefits	Expert elicitation: Biological	Expert elicitation: Fertility control	Expert elicitation: Welfare	2025 Trade-offs Workshop	Data / Guidance Provider
Amy Wootton	Welsh Mountain Zoo											✓
Andrew Greenwood	Wildlife Vets International	✓	✓							✓	✓	
Cat McNicol	British Association for Shooting and Conservation							✓				
Charlotte Burn	Royal Veterinary College									✓		
Craig Shuttleworth	Bangor University							✓		✓		✓
David Adams	UK Squirrel Accord									✓	✓	
David Walter	UK Squirrel Accord; British Red Squirrel	✓	✓	✓	✓	✓	✓	✓			✓	
Ellie Scopes	Forest Research										✓	✓
Giovanna Massei	University of York								✓			
Harry Marshall	Forest Research											✓
Ian Danby	British Association for Shooting and Conservation			✓							✓	

Name	Affiliation	2023 Initial Workshops	WG: Red squirrel recovery	WG: Ecosystem benefits	WG: Public acceptability	WG: Cost	WG: Socioeconomic benefits	Expert elicitation: Biological	Expert elicitation: Fertility control	Expert elicitation: Welfare	2025 Trade-offs Workshop	Data / Guidance Provider
Ian Glendinning	Northern Red Squirrels	✓	✓	✓	✓			✓		✓	✓	
Jackie Foott	British Red Squirrel	✓	✓	✓				✓			✓	
Jenny MacPherson	Vincent Wildlife Trust											✓
John Gurnell	Queen Mary University of London							✓				
John Monaghan	Royal Forestry Society	✓										
Judi Dunn	BIAZA Red Squirrel Focus Group; Wildwood Trust	✓	✓					✓		✓		✓
Julian Chantrey	University of Liverpool		✓					✓				
Julie Bailey	Northern Red Squirrels; UK Squirrel Accord	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓
Justine Shotton	Royal Society for the Prevention of Cruelty to Animals									✓	✓	
Kat Hamill	Nottingham Trent University							✓			✓	
Kate Palphramand	Animal & Plant Health Agency								✓			
Katherine Walsh	Natural England	✓	✓		✓	✓	✓	✓			✓	✓
Katie Beckmann	University of Edinburgh							✓		✓		
Kay Haw	UK Squirrel Accord	✓	✓	✓	✓	✓	✓				✓	✓
Kristin Waeber	Institute of Chartered Foresters; National Trust	✓		✓		✓						

Name	Affiliation	2023 Initial Workshops	WG: Red squirrel recovery	WG: Ecosystem benefits	WG: Public acceptability	WG: Cost	WG: Socioeconomic benefits	Expert elicitation: Biological	Expert elicitation: Fertility control	Expert elicitation: Welfare	2025 Trade-offs Workshop	Data / Guidance Provider
Lauren Harrington	WildCRU, University of Oxford									✓		
Leon Savage	UK Squirrel Accord										✓	✓
Liam Wilson	The University of Edinburgh	✓						✓		✓	✓	
Lisa Leaver	University of Exeter									✓		
Luke Hemmings	Savills (UK) Forestry	✓					✓					
Manuel Berdoy	University of Oxford									✓		
María Diez-Leon	Royal Veterinary College									✓		
Mark Henderson	Red Squirrel Survival Trust	✓	✓		✓	✓					✓	
Martin Edwards	British Association for Shooting and Conservation	✓										
Matt Larsen-Daw	Mammal Society	✓									✓	
Melissa Marr	The University of Edinburgh	✓	✓								✓	
Mike Dunn	Forest Research	✓										✓
Mike Denbury	Red Squirrels Northern England	✓		✓		✓		✓			✓	✓
Mike Short	Game and Wildlife Conservation Trust									✓*		
Molly Frost	The Wildlife Trust for Lancashire, Manchester and North Merseyside;	✓	✓	✓							✓	

Name	Affiliation	2023 Initial Workshops	WG: Red squirrel recovery	WG: Ecosystem benefits	WG: Public acceptability	WG: Cost	WG: Socioeconomic benefits	Expert elicitation: Biological	Expert elicitation: Fertility control	Expert elicitation: Welfare	2025 Trade-offs Workshop	Data / Guidance Provider
	University of York											
Neil D'Cruze	World Animal Protection									✓		
Nick Leeming	Northern Red Squirrels Northumberland	✓	✓	✓								
Nick Reed-Beale	Woodland Trust	✓	✓	✓								
Nicole Still	Saving Scotland's Red Squirrels; Scottish Wildlife Trust	✓	✓									
Peter Garner	Independent	✓	✓		✓	✓		✓		✓	✓	
Peter Lurz	University of Edinburgh							✓				
Rebecca Clews-Roberts	Natural Resources Wales	✓	✓									✓
Rebecca Isted	Forestry Commission	✓									✓	✓
Rebecca Pinkham	Animal & Plant Health Agency								✓		✓	✓
Richard Kock	Royal Veterinary College	✓									✓	
Ross Clifton	Mammal Society											✓
Sarah Beatham	Animal & Plant Health Agency	✓	✓					✓	✓	✓	✓	✓
Sarah Woodfin	Trees for Life									✓		
Steve Belmain	University of Greenwich									✓*		
Tony Sainsbury	Zoological Society of London	✓									✓	
Trevor Cooper	Grasmere Red Squirrel Group	✓	✓		✓						✓	
Verity Burke	National Trust	✓										

Name	Affiliation	2023 Initial Workshops	WG: Red squirrel recovery	WG: Ecosystem benefits	WG: Public acceptability	WG: Cost	WG: Socioeconomic benefits	Expert elicitation: Biological	Expert elicitation: Fertility control	Expert elicitation: Welfare	2025 Trade-offs Workshop	Data / Guidance Provider
Wayne Penrose	Forestry England	✓									✓	
Anonymous	Wild New Forest Pine Marten Project											✓
Anonymous	Savills (UK) Forestry	✓		✓			✓					
Anonymous	Woodland Trust										✓	
Anonymous	Vincent Wildlife Trust											✓
Anonymous	Royal Society for the Prevention of Cruelty to Animals											✓

Appendix 2

Workshop discussion on objectives and performance attributes

It was clear that all participants want to see red squirrel populations recover and the prevention of their extinction in England. Several participants queried what 'recovery' means; a sentiment also captured by the range of performance attributes relating to the biological fundamental objective to 'maximise red squirrel recovery'. Discourse centred around whether recovery could be considered an increase in numbers in the current areas where red squirrels are present, or whether recovery also had to include a measure of distribution with red squirrels occupying parts, if not all, of their former range. To this end, performance attributes include numbers, distribution, and population viability so that all informative measures can be presented to the decision-makers.

Participants in both workshops raised that any conservation actions that also provided wider ecosystem benefits would be preferred. Exactly what these benefits would be and how they would be measured was slightly uncertain as ecosystem benefits are difficult to articulate and quantify. Commonly expressed performance attributes were assessments of critical species, existing government key performance indicators, and proxy measures of ecosystem functioning. This will be discussed in more detail and decided upon in the ecosystem working group moving forwards.

Concern was raised that including ecosystem benefits as a fundamental objective could overshadow the red squirrel fundamental objective with strategies favoured that perform less effectively for maximising red squirrel recovery due to their effectiveness at maximising ecosystem benefits. The workshop facilitators explained that not all fundamental objectives are valued equally and that different weights can be put on the objectives whilst trading off strategies and making decisions. Concerns were also voiced about including minimising cost as a fundamental objective due to the perception that this would mean spending the least amount of money possible. However, the facilitators explained that this formulation simply means that if two alternative strategies performed equally well against all objectives, but one was cheaper than the other, it would make sense to choose the cheaper option.

From both workshops, some participants expressed that whilst conservation actions (particularly grey squirrel lethal management) should go ahead regardless of public opinion, maximising public support should be strived towards. Participants felt that transparency to the public was needed to prevent backlash. It was hoped that with outreach and educational efforts, those opposed to grey squirrel management could be persuaded to understand its necessity for red squirrel conservation. Going forwards, the facilitators will work to understand public support for red squirrel conservation. This will feed into how effective each conservation strategy is likely to be (for example due to levels of compliance), as well as being a fundamental objective to ensure decision-makers can make a choice with the full awareness of the public response.

Separate to public support, and mostly only discussed in the second workshop, was the idea that stakeholders and local communities should benefit from red squirrel conservation

actions. Mostly this discussion centred around payments to landowners for conducting conservation work, commercial profits linked to reducing tree damage caused by grey squirrels and ensuring that local communities benefit (e.g. through job creation in conservation efforts or ecotourism or increase in physical and mental wellbeing through exposure to nature and native species).

Several process objectives were identified by the participants that describe how people would like the decision to be made and how the strategy should be implemented. Predominantly these centred around ensuring the strategy was feasible, including ensuring non-reliance on volunteers in the future. Participants also wanted to increase stakeholder engagement and agreement as well as ensuring future coordination between all actors and agencies. There was discussion over whether 'avoiding shying away from unpopular measures' should remain as an objective, as some felt that pushing forwards with unpopular measures could lead to a public backlash and to ineffective actions. However, most felt that lethal management of grey squirrels was critical and should take place regardless of public opinion to prevent red squirrels from going extinct in the short-term. It was suggested that actions should focus on education, outreach, and increasing public support for necessary actions, which can hopefully transition to more palatable non-lethal management such as contraceptives in the future.

Appendix 3

Workshop outputs

Table A2. Objectives taken from pre-workshop questionnaire and provided to participants along with where these objectives are captured in the objectives hierarchy in Figure 2. RSq = red squirrel; GSq = grey squirrel.

Workshop	Objectives	Captured in objectives hierarchy by:
June	Maximise RSq viability	Maximise RSq
June	Maximise RSq distribution	Maximise RSq
June	Maximise RSq numbers	Maximise RSq
June	Ensure captive stock of RSq	RSq captive breeding
June	Ensure natural expansion of RSq distribution	Maximise RSq
June	Conduct RSq translocation	Maximise RSq
June	Minimise RSq population fragmentation	Ensure genetic viability of RSq populations
June	Ensure RSq population health	Ensure healthy RSq populations
June	Protect RSq from disease	Protect RSq from disease
June	Reduce exposure of RSq to squirrelpox	Minimise RSq exposure to squirrelpox virus
June	Ensure RSq welfare	Ensure RSq welfare
June	Minimise interspecific competition between RSq & GSq	Minimise GSq competition with RSq
June	Maximise GSq-free areas	Reduce GSq numbers and distribution
June	Minimise GSq numbers	Reduce GSq numbers and distribution

Workshop	Objectives	Captured in objectives hierarchy by:
June	Minimise GSq control measures' impact on other wildlife	Minimise negative impacts of GSq on non-RSq species (including tree damage)
June	Minimise non-native invasive species	Beyond scope of project
June	Increase welfare consideration towards GSq	Ensure GSq welfare during GSq management
June	Maximise natural predators of GSq	Maximise native GSq predators
June	Avoid introduction of pine martens	Maximise landowner support
June	Maximise RSq habitat suitability	Maximise RSq habitat quantity and quality
June	Minimise habitat loss	Maximise RSq habitat quantity and quality
June	Minimise habitat degradation	Maximise RSq habitat quantity and quality
June	Increase connectivity	Increase connectivity between RSq populations
June	Avoid forestry management that makes things worse for RSq	Maximise RSq habitat quantity and quality
June	Minimise tree damage	Minimise negative impacts of GSq on non-RSq species (including tree damage)
June	Increase woodland functionality	Maximise ecosystem benefits
June	Increase public support for conservation activities	Maximise public support

Workshop	Objectives	Captured in objectives hierarchy by:
June	Maximise landowner acceptability	Maximise landowner support
June	Ensure non-reliance on volunteer GSq control	Ensure jobs for RSq conservation actions
June	Increase government & political support	Ensure government/political support for RSq conservation
June	Increase stakeholder agreement	Increase stakeholder engagement and agreement
June	Ensure financial resources for RSq recovery	Ensure financial resources for RSq conservation
June	Minimise cost	Minimise cost
June	Ensure coordination between actors	Ensure coordination between actors and agencies
June	Engage all relevant stakeholders	Increase stakeholder engagement and agreement
June	Address temporal scope of actions (short vs long term)	Address spatial and temporal scope of actions
June	Set achievable goals to break down the task	Ensure feasibility of conservation strategy and implementation
June	Address unrecognised hazards	Ensure feasibility of conservation strategy and implementation
June	Ensure actions are taken	Ensure feasibility of conservation strategy and implementation
June	Avoid unrealistic strategy	Ensure feasibility of conservation strategy and implementation
October	Increase RSq numbers	Maximise RSq

Workshop	Objectives	Captured in objectives hierarchy by:
October	Increase RSq distribution	Maximise RSq
October	Increase connectedness of RSq populations	Increase connectivity between RSq populations
October	Protect RSq from disease	Protect RSq from disease
October	Increase RSq genetic viability	Ensure genetic viability of RSq populations
October	Ensure protection of RSq strongholds	Maximise RSq
October	Ensure natural recolonisation of RSq	Maximise RSq
October	Increase RSq sustainability	Maximise RSq
October	Avoid GSq competition	Minimise GSq competition with RSq
October	Decrease numbers of GSq	Reduce GSq numbers and distribution
October	Decrease GSq geographical range	Reduce GSq numbers and distribution
October	Improve GSq control methods	Improve GSq control methods
October	Ensure broad invasive non-native species control	Beyond scope of project
October	Ensure landowners carry out GSq control	Reduce GSq numbers and distribution
October	Avoid reliance on extensive GSq culling	Improve GSq control methods
October	Increase presence of GSq predators	Maximise native GSq predators

Workshop	Objectives	Captured in objectives hierarchy by:
October	Support pine marten conservation	Maximise native GSq predators
October	Increase wider biodiversity	Maximise ecosystem benefits
October	Address effects of climate change on habitat	Maximise RSq habitat quantity and quality
October	Improve RSq habitat quality	Maximise RSq habitat quantity and quality
October	Preserve current conifer forests	Maximise RSq habitat quantity and quality
October	Avoid reliance on non-native conifer strongholds	Maximise RSq habitat quantity and quality
October	Increase planting of large-seeded broadleaves	Maximise RSq habitat quantity and quality
October	Increase public support towards conifers	Maximise RSq habitat quantity and quality
October	Increase inspiration towards wider biodiversity conservation	Beyond scope of project
October	Ensure government support	Ensure government/political support for RSq conservation
October	Ensure stakeholder / landowner engagement	Maximise landowner support
October	Ensure long-term support for actions	Ensure long-term support
October	Increase public support for GSq control	Maximise public support
October	Increase public support for RSq	Maximise public support

Workshop	Objectives	Captured in objectives hierarchy by:
October	Ensure funding	Ensure financial resources for RSq conservation
October	Ensure jobs for conservation of RSq	Ensure jobs for RSq conservation actions
October	Avoid reliance on volunteer groups for implementation	Ensure jobs for RSq conservation actions
October	Ensure local solutions	Address spatial and temporal scope of actions
October	Ensure coordination between actors and agencies	Ensure coordination between actors and agencies
October	Ensure feasibility of conservation strategy	Ensure feasibility of conservation strategy and implementation
October	Avoid shying away from unpopular measures	Avoid shying away from unpopular measures

Table A3. Summary of preferred action themes among workshop participants. 'Support' is the number of people (out of 32 participants) across both workshops that chose at least one action on that theme as their preferred strategy. 'Impact' is the average assessed impact of all evaluated actions on the red squirrel objective across each theme (where a value of -2 means "High negative impact", -1 means "Low negative impact", 0 means "No impact", 1 means "Low positive impact" and 2 means "High positive impact"). 'Confidence' is the average assessed confidence of all evaluated actions across each theme (where a value of -1 means "Not very confident", 0 means "Somewhat confident" and 1 means "Very confident"). The column "Popular actions" shows the three most supported actions within each theme, where the action in bold is the most popular action. If less than three actions were suggested, then all are shown. RSq = red squirrel; GSq = grey squirrel.

Theme	Support	Impact	Confidence	Popular actions
Awareness & Communication	26	1.47	0.34	<ul style="list-style-type: none"> • RSq in national curriculum • Raise RSq awareness in community • Raise awareness about GSq management
Ensure Implementation	26	1.43	0.23	<ul style="list-style-type: none"> • Recruitment and training for GSq management • Key landowner engagement • Incorporate GSq management in other conservation roles
Geographically Explicit Grey Squirrel Management	25	1.47	0.34	<ul style="list-style-type: none"> • Management in GSq/RSq interface areas • Management in GSq incursion routes • Maintenance of a buffer zone through GSq management
Fertility Management	24	1.54	-0.28	<ul style="list-style-type: none"> • GSq fertility management
Grey Squirrel Trapping	22	1.15	0.35	<ul style="list-style-type: none"> • Cranial dispatch • Smart traps (distinguish RSq and GSq) • Auto-reset kill traps
Policy	22	1.23	0.10	<ul style="list-style-type: none"> • Facilitate WS3 applications

Theme	Support	Impact	Confidence	Popular actions
				<ul style="list-style-type: none"> Adapt land management subsidies to RSq objectives Vocal honesty from big organisations
Connectivity	21	1.35	0.26	<ul style="list-style-type: none"> Increase population connectivity Habitat corridors / stepping stones RSq bridges
Habitat Creation & Improvement	20	0.79	0.06	<ul style="list-style-type: none"> Mixed planting scheme for RSq benefit Expand woodland cover Include conifers in woodland creation
Disease Management	18	1.51	0.26	<ul style="list-style-type: none"> Rapid SQPV response Correct cleaning of feeders SQPV vaccine
Habitat Protection	18	1.30	0.39	<ul style="list-style-type: none"> Selective felling instead of clear felling Support habitats in commercial woodland Support long term forest retention
Native Predators	15	0.76	0.08	<ul style="list-style-type: none"> Pine marten recovery Raptor recovery
Other GS Actions	14	0.58	-0.23	<ul style="list-style-type: none"> Training in lethal techniques Better infrared scopes Discourage feeding of GSq
Gene Drive	13	1.58	-0.32	<ul style="list-style-type: none"> GSq gene drive
Grey Squirrel Eradication	13	1.88	0.20	<ul style="list-style-type: none"> GSq full eradication

Theme	Support	Impact	Confidence	Popular actions
Translocation	13	1.25	-0.17	<ul style="list-style-type: none"> • Captive-to-wild translocation • RSq translocation • New isolated populations
Grey Squirrel Shooting	11	0.72	0.04	<ul style="list-style-type: none"> • Shooting over bait points • Drey poking • Shooting on Crown land
Red Squirrel Tourism	7	0.79	0.22	<ul style="list-style-type: none"> • RSq tourism
Other Habitat Management	5	1.86	0.71	<ul style="list-style-type: none"> • GSq management in created woodlands • Prioritise GSq management where carbon sequestration is most likely
Other RS Conservation Actions	5	0.65	0.00	<ul style="list-style-type: none"> • Artificial RSq nests • Not feeding incorrect foods to RSq • Management of pets (e.g., cats)
Captivity	4	0.44	-0.33	<ul style="list-style-type: none"> • Increase captive populations
Climate Change	1	1.50	0.00	<ul style="list-style-type: none"> • Prioritise climate-change resilient habitat

Appendix 4

Biological model

The underlying biological model is such that the instantaneous change of a population of red squirrels, H_R is

$$\frac{dH_R}{dt} = A_R - bH_R - \mu_R H_R P$$

where b is the annual death rate μ_R is the predation coefficient of pine martens under red squirrels, P is the density of pine martens, and A_R is the realized birth rate given density-dependence due to intra- and inter-specific competition:

$$A_R = (a_R - q_R(H_R + c_G H_G))H_R$$

where a_R is the intrinsic birth rate, q_R is the susceptibility to crowding and c_G is the competitive effect of grey squirrels. The equations for growth of grey squirrels are the same, with the R and G subscripts swapped. This model does not include the effects of squirrelpox virus (SQPV) in the population. This is done by modelling the different epidemiological classes separately:

$$\frac{dS_{1,R}}{dt} = A_R H_R - J_R(S_1) - bS_{1,R} - \mu_R S_{1,R} P$$

$$\frac{dI_{1,R}}{dt} = J_R(S_1) - \alpha_R I_{1,R} - \gamma_R I_{1,R} - bI_{1,R} - \mu_R I_{1,R} P$$

$$\frac{dS_{2,R}}{dt} = \gamma_R I_{1,R} - bS_{2,R} - \mu_R S_{2,R} P - J_R(S_2)$$

$$\frac{dI_{A,R}}{dt} = J_R(S_2) + \sigma J_R(R) - \alpha_R I_{A,R} - \gamma_R I_{A,R} - bI_{A,R} - \mu_R I_{A,R} P$$

$$\frac{dR_R}{dt} = \gamma_R R_R - \sigma J_R(R) - bI_{A,R} - \mu_R I_{A,R} P$$

where J is a function that describes the infection processes for any given class epidemiological class C

$$J_R(C) = C_R(\beta_{RR} I_R^* + \beta_{GR} I_G^*)$$

and I_R^* is the effective number of infectious red squirrel individuals ($I_{1,R} + I_{A,R}$). β_{GR} is the transmission rate from grey squirrels to red squirrels. γ represents the recovery rate from SQPV, and α the mortality rate. σ is a coefficient that regulates partial immunity of recovered individuals; when $\sigma = 0$ recovered individuals have complete immunity, and when $\sigma = 1$ they are as susceptible as individuals in the susceptible class. The use of five epidemiological age classes instead of the usual three on a SIR (Susceptible-Infected-Recovered) model follows the finding of Howell et al 2024, that showed a model including

two infection occasions before development of partial immunity better describes the dynamics of SQPV in grey squirrel populations. It is important to note that we assume no grey squirrels die from SQPV and red squirrels never recover from it, therefore α_G and γ_R are always zero. We still display the corresponding terms in the equations for the sake of generalizability. Because $\gamma_R = 0$, the only epidemiological classes that do exist in red squirrel populations are S_1 and I_1 , collapsing the more complex SQPV model into a SI model for red squirrels. This set of equations describes most of the biological processes underlying red and grey squirrel dynamics. Because we need a spatially explicit model to predict country-wide squirrel dynamics, we decided to model each hectad in the UK as an independent population, and incorporate two further processes: dispersal and inter-hectad transmission of SQPV.

The rate at which individuals on any class disperse from their hectad at a rate

$$m = C_R(H_R + c_G H_G)/K_R$$

where $m = \frac{2b}{10}$. This assumes that at carrying capacity, each squirrel would disperse on average twice in its lifetime between 1km² cells (as assumed by Slade 2023). The division by 10 accounts for the dimensional increase in the cell size. Dispersing individuals were randomly assigned a neighbouring hectad to disperse to. The probability of choosing each neighbouring hectad was weighted by its habitat quality (expressed as its carrying capacity).

We incorporated between-hectad transmission of SQPV by changing how we calculate the effective number of infectious individuals, I^* :

$$I_R^* = I_{1,R} + I_{A,R} + \theta \sum_{Adjacent} (I_{1,R} + I_{A,R}) + \theta^2 \sum_{Corner} (I_{1,R} + I_{A,R})$$

where θ is the average daily movement of a squirrel, as a proportion of the cell side length.

These equations describe the expected dynamics of both species in a continuous time-frame. We decided to use a step-wise model, therefore converted all component transition rates of the population into probabilities, using the formula

$$p(x) = 1 - e^{-\frac{x}{\Delta t}}$$

where x is the underlying transition rate and Δt is the size of time-step being modeled, in years. For example, the term describing pine marten predation $\mu_R C_R P$ would then be converted as $1 - e^{-\frac{\mu_R P}{\Delta t}}$ (the term C_R is dropped because the probability applies to a single individual, therefore $C_R = 1$).

We incorporated age structure in the model by keeping track of the age class of all individuals, and only allowing the individuals over 6 months old to reproduce. There was also differential natural mortality, SQPV mortality and SQPV recovery rate between age classes, for both species.

Management actions

Vaccination

We modelled vaccination of red squirrels by adding an additional term to all epidemiological classes C_R , except R_R

$$\frac{dC_R}{dt} = \dots - \omega C_R$$

where w is the yearly vaccination rate. Individuals vaccinated are removed to class C_R and added to R_R , therefore $\frac{dR_R}{dt}$ is adjusted to

$$\frac{dR_R}{dt} = \dots + \omega(S_{1,R} + S_{2,R} + I_{1,R} + I_{A,R})$$

Grey squirrel management

The probability that a given squirrel is caught in a trap was adapted from Croft et al 2021. We model the probability from the perspective of the trap - the probability of a trap catching a squirrel in a given day is modelled as

$$p(\text{trapping}) = 1 - (1 - e_t)^n$$

where e_t is the baseline chance of a squirrel being caught in a trap given it finds it, and n is the number of squirrels available for a given trap. This is calculated by multiplying the number of squirrels in a hectad (H_G) by the average home range of a squirrel as a proportion of the hectad area. For each trap-day deployment, the number of squirrels removed was sampled as a binomial process using $p(\text{trapping})$. This approach was used to both live traps and kill traps, using different baseline encounter rates e_t (derived from Croft et al 2021 and through elicitation).

Similarly, we calculated the probability of a shooter culling *at least one squirrel* using the formula

$$p(\text{shooting}) = 1 - (1 - e_s)^n$$

However, because a shooter can cull more than one squirrel over a shooting day, the probability of culling was adjusted to a rate s

$$s = -\log(1 - p(\text{shooting}))$$

The number of squirrels removed by a shooter on a given day were sampled using a Poisson distribution.

We also modelled the probability of a given squirrel being sterilised through contraceptives deployed through feeding hoopers. Because a hooper can be used by many squirrels, we modelled the probability of contraception through the perspective of the squirrel.

The probability that a squirrel is sterilised was calculated as

$$p(\text{sterilisation}) = (1 - (1 - e_h)^h) \times (1 - q)^k \times w$$

Where the first term $((1 - (1 - e_h)^h))$ is the probability that a squirrel will feed on the contraceptive hopper. e_h is the baseline hopper encounter probability, and h is the number of hopper days available within a squirrel home range. The second term $((1 - q)^k)$ describes the probability that a squirrel will be able to access the hopper (i.e., it will not be prevented from using it by co-specifics). q denotes the probability that a squirrel being denied access to all hoppers at a squirrel:hopper density ratio of 1:1, k is the squirrel:hopper ratio in a given hectad, and w is the efficacy of the contraceptive (i.e. the probability the squirrel will indeed be sterilised given oral consumption). The number of squirrels sterilised this way on each timestep and each hectad was sampled from a binomial distribution. Individuals that were sterilised remained so for a given number of time steps - after this number passed, they reverted to being fertile individuals and bred normally.

Pine martens

Pine martens were modelled using a simple demographic model where

$$\frac{dP}{dt} = aP - bP$$

where a is the intrinsic birth rate and b is the intrinsic death rate. Pine marten dispersal was modelled in two different ways, short and long distance dispersal. Short dispersal happened when population births occurred that would put the population above carrying capacity. The number of individuals above carrying capacity were forced to disperse into neighbouring hectads. Long dispersal was modelled with a rate $d_p = 0.05$. Individuals conducting long distance dispersal moved to any hectad within a radius of 50km of their source hectad. For both types of dispersal, the destination hectad for each dispersing individual was defined at random, with each candidate hectad weighed according to its carrying capacity for pine martens. We incorporated age structure in a similar way we did for squirrels, where juveniles, sub-adults and adults have differential birth and death rates. Similarly, only adults and sub-adults were allowed to disperse.

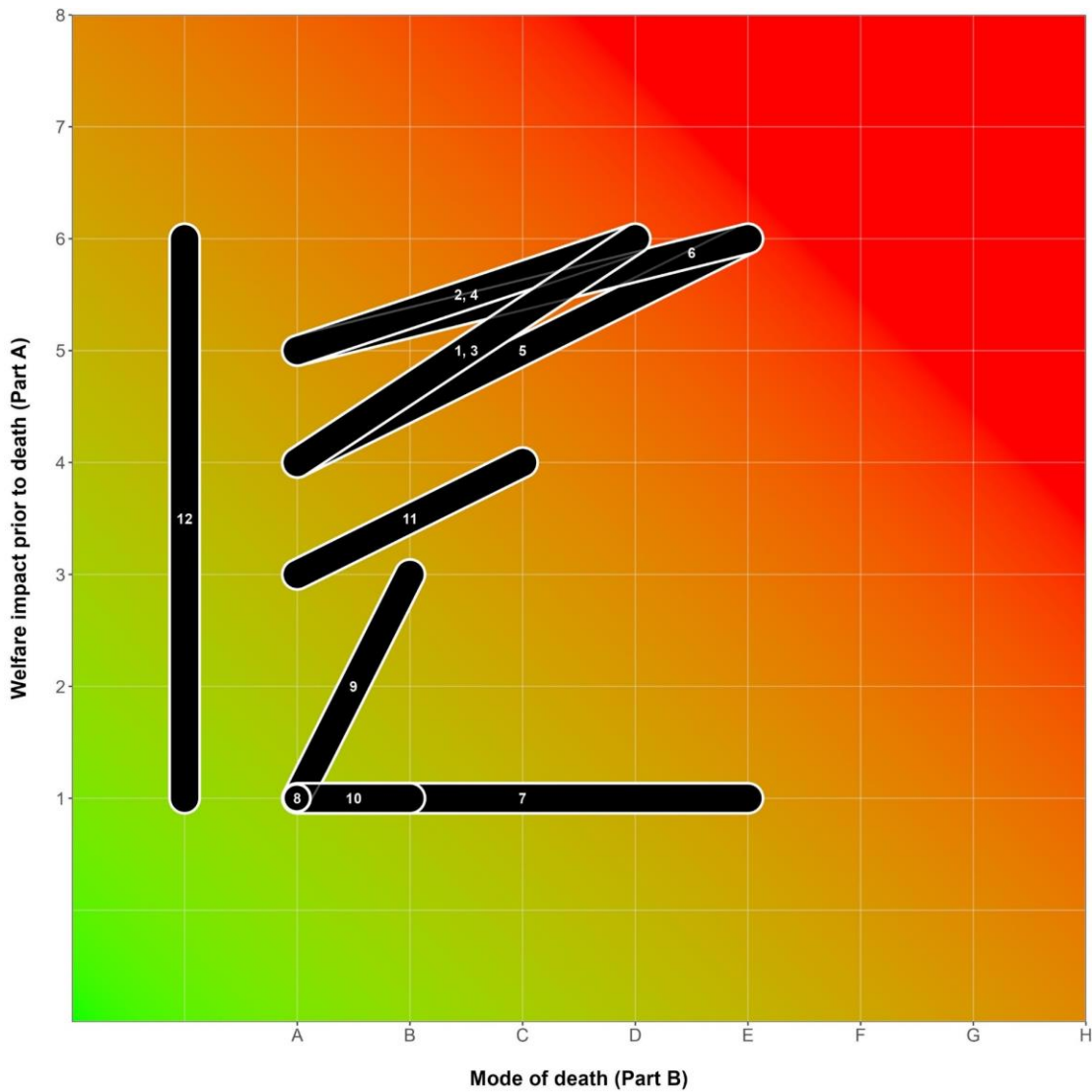
Appendix 5

Welfare

Table A4. Selected impact categories for all methods of grey squirrel management that were assessed. The impact and the time that it is experienced combine to give the score(s) (following Sharp & Saunders, 2011).

Part	Method	Impact	Time	Score
A	Single capture: <4 hours	Mild – Moderate	Hours	4 – 5
A	Single capture: 4-12 hours	Mild – Severe	Hours	4 – 6
A	Single capture: 12-24 hours	Severe – Extreme	Hours	6 – 7
A	Multi-capture (2-3 squirrels): <4 hours	Mild – Moderate	Hours	4 – 5
A	Multi-capture (2-3 squirrels): 4-12 hours	Moderate – Severe	Hours	5 – 6
A	Multi-capture (2-3 squirrels): 12-24 hours	Severe – Extreme	Hours	6 – 7
A	Multi-capture (4-7 squirrels): <4 hours	Mild – Severe	Hours	4 – 6
A	Multi-capture (4-7 squirrels): 4-12 hours	Moderate – Severe	Hours	5 – 6
A	Multi-capture (4-7 squirrels) - 12-24 hours	Severe – Extreme	Hours	6 – 7
A	Snap/spring traps	None	Immediate to seconds - Minutes	1
A	GoodNature traps	None	Immediate to seconds - Minutes	1
A	Free shooting	None – Mild	Immediate to seconds - Minutes	1 – 3

Part	Method	Impact	Time	Score
A	Shooting at bait stations	None	Minutes	1
A	Drey poking	Moderate	Immediate to seconds - Minutes	3 – 4
A	Immunocontraceptives	None – Mild	Weeks	1, 6
B	Cranial dispatch	None – Moderate	Minutes	A, C – D
B	Shoot in the trap	None – Moderate	Minutes	A, C – D
B	Kill trap in the trap	None – Severe	Minutes	A, C – E
B	Stun gun in the trap	None – Moderate	Minutes	A, C – D
B	Drowning	Extreme	Minutes	F
B	Snap/spring traps	None – Severe	Immediate to seconds - Minutes	A – E
B	GoodNature traps	None	Immediate to seconds - Minutes	A
B	Free shooting	None – Mild	Immediate to seconds	A – B
B	Shooting at bait stations	None – Mild	Immediate to seconds	A – B
B	Drey poking	None – Moderate	Immediate to seconds	A – C



Key:

- | | |
|---|------------------------------|
| 1 Single capture live trap + cranial dispatch | 7 Snap/spring kill traps |
| 2 Multi-capture live trap + cranial dispatch | 8 Goodnature A18 kill traps |
| 3 Single capture live trap + shooting | 9 Free shooting |
| 4 Multi-capture live trap + shooting | 10 Shooting at bait stations |
| 5 Single capture live trap + kill trap | 11 Drey poking |
| 6 Multi-capture live trap + kill trap | 12 Immunocontraceptives |

Figure A1. Sharp & Saunders welfare assessment scores for common methods of grey squirrel management. For live traps, the scores refer to the most common case of squirrels being in a trap for 4-12 hours, and multi-capture traps refer to when 2-3 squirrels are in the same trap. It is important to note that although the full range is shown, some of these scores are binomial with two separate groupings. For example, the score for immunocontraceptives is either a 1 or a 6. The full scores are given above in Table A4.

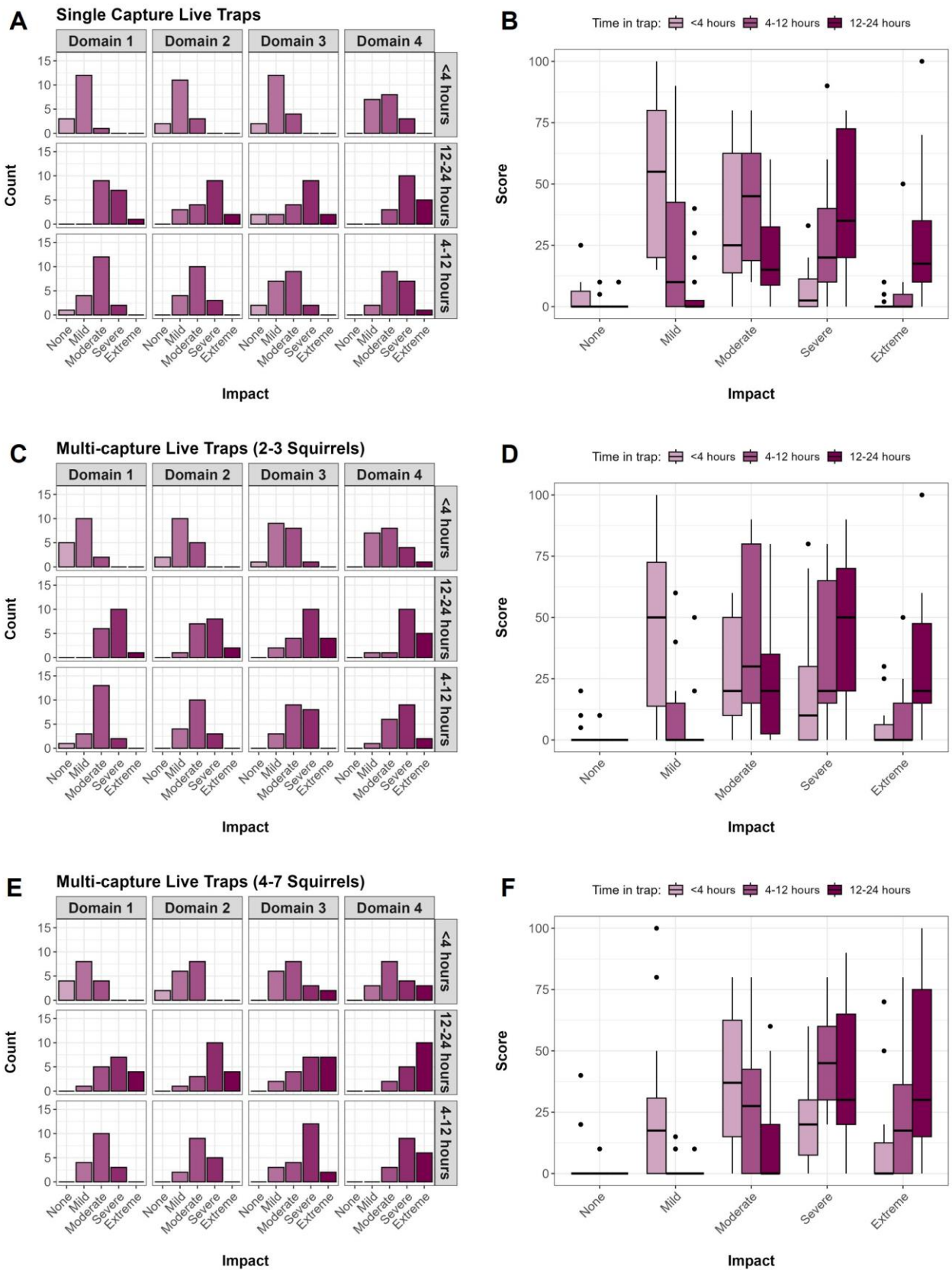


Figure A2. Number of experts who selected each impact category for each of Domains 1 - 4 for different types of live traps (left) alongside the spread of the votes for each category for Domain 5 for each corresponding trapping context (right).

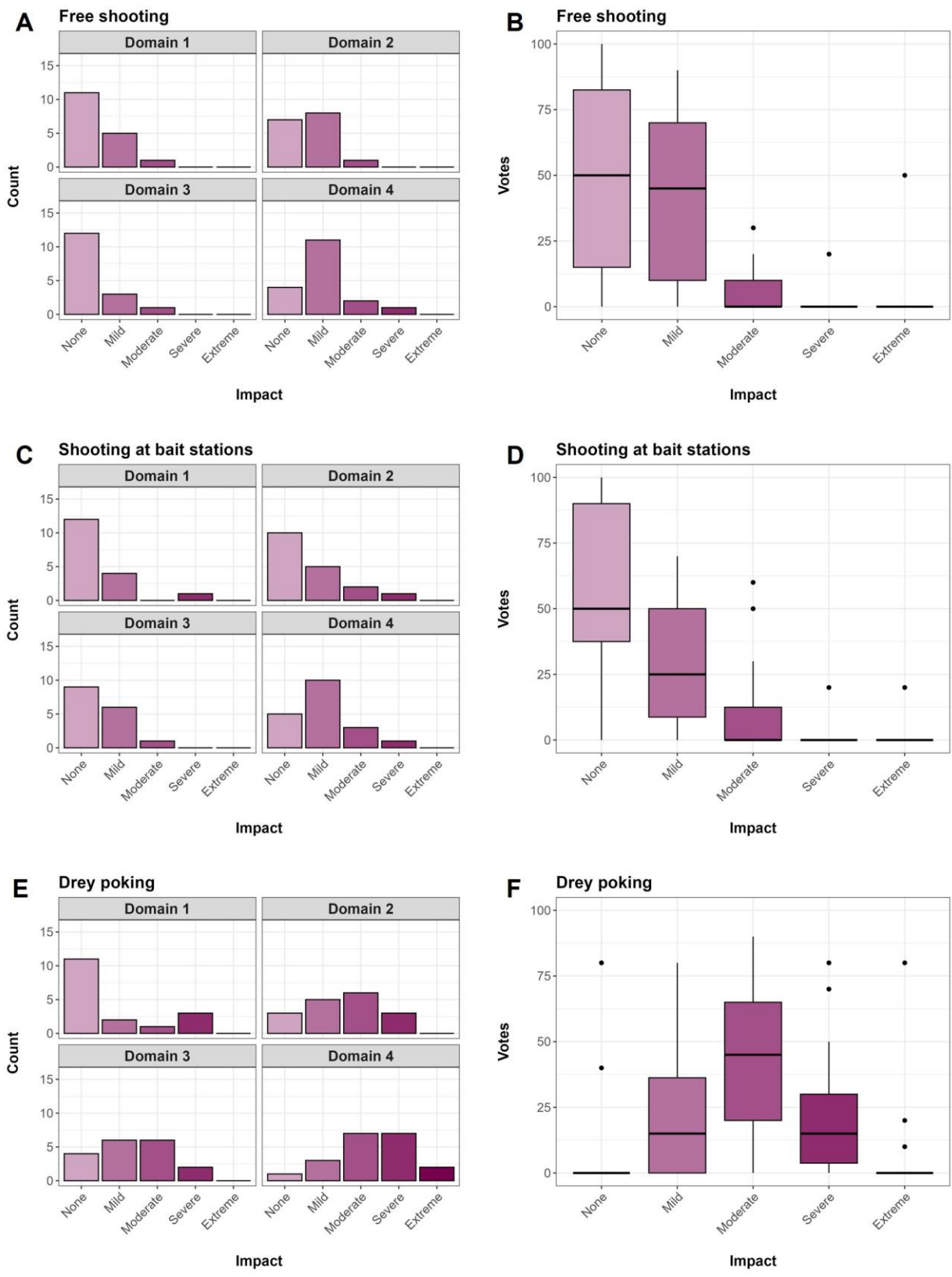


Figure A3. Number of experts who selected each impact category for each of Domains 1 to 4 for different types of shooting (left) alongside the spread of the votes for each category for Domain 5 for each corresponding shooting context (right).

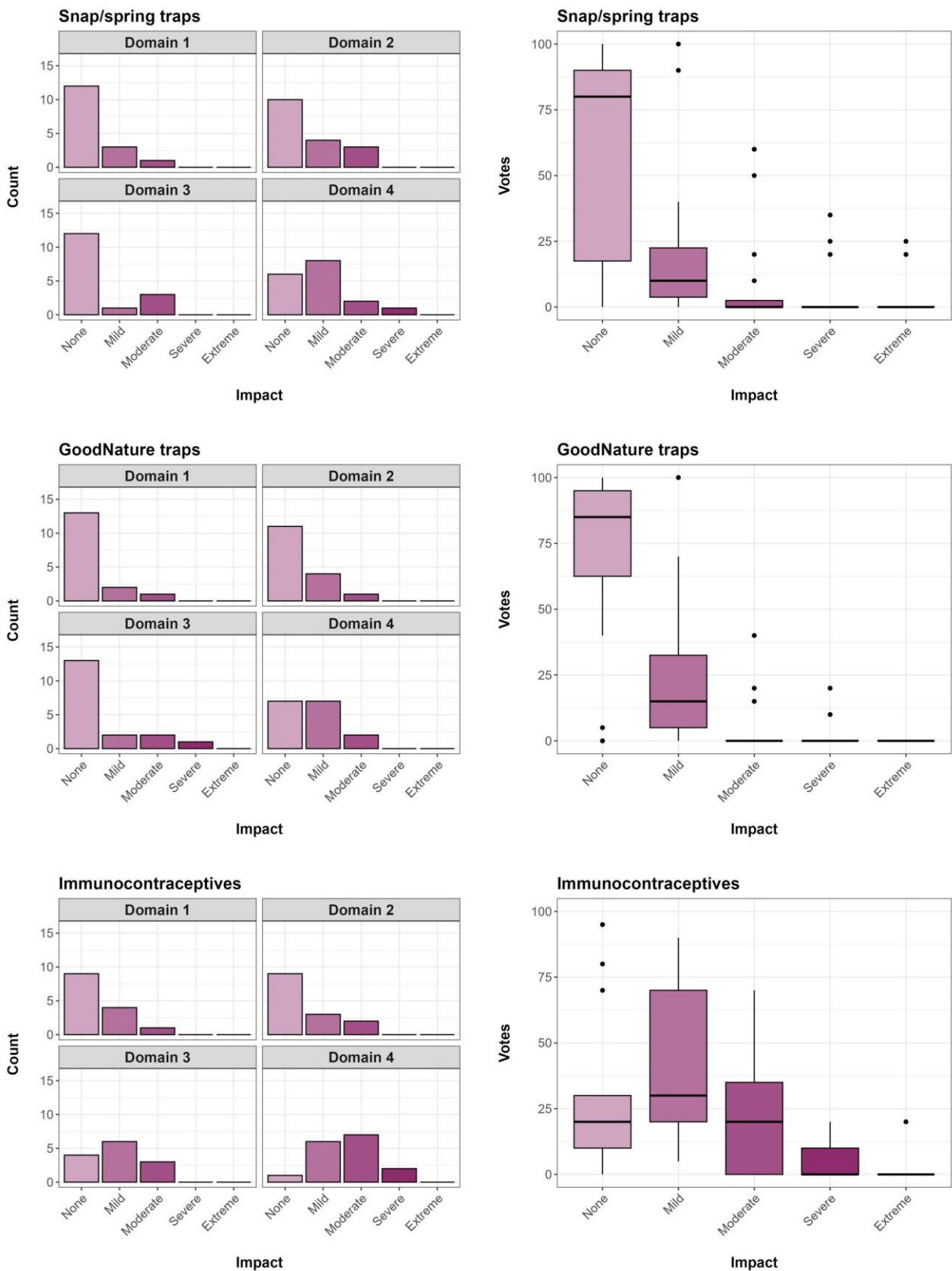


Figure A4. Number of experts who selected each impact category for each of Domains 1 to 4 for different types of kill traps and fertility control (left) alongside the spread of the votes for each category for Domain 5 for each corresponding trapping context and fertility control (right).

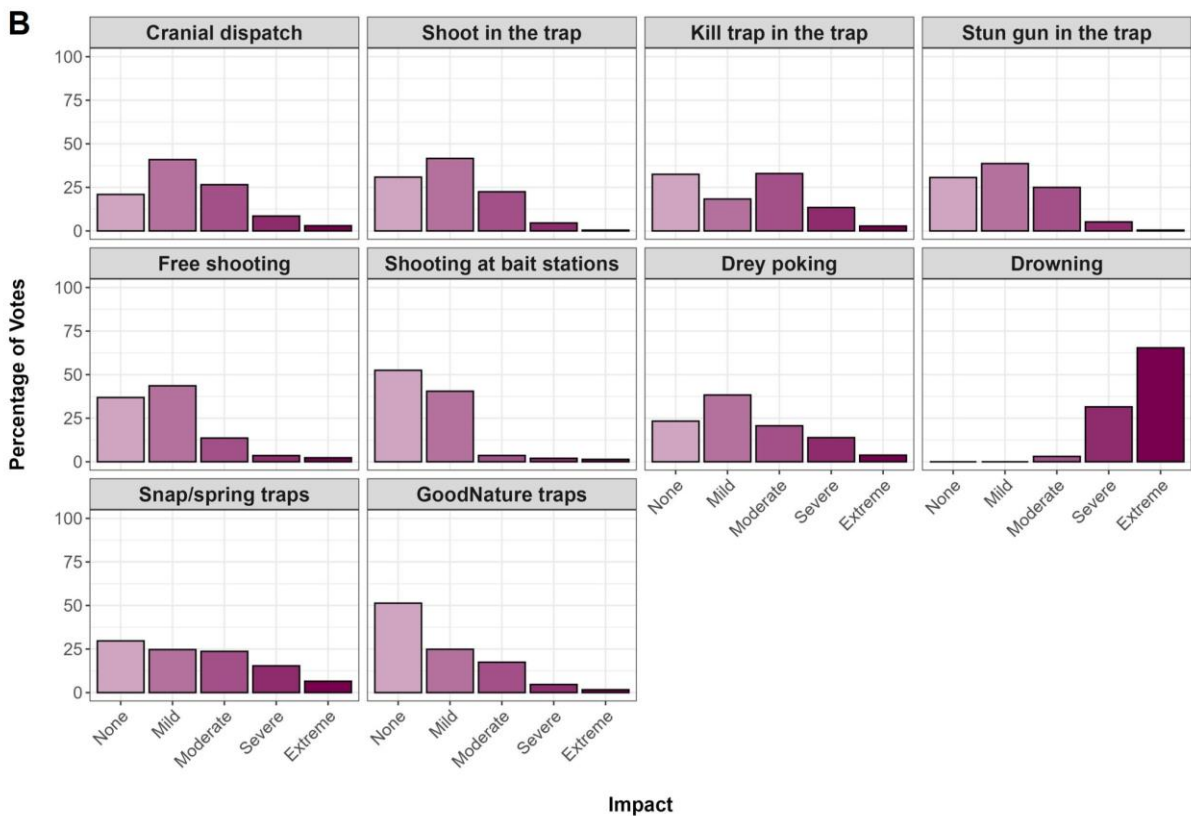
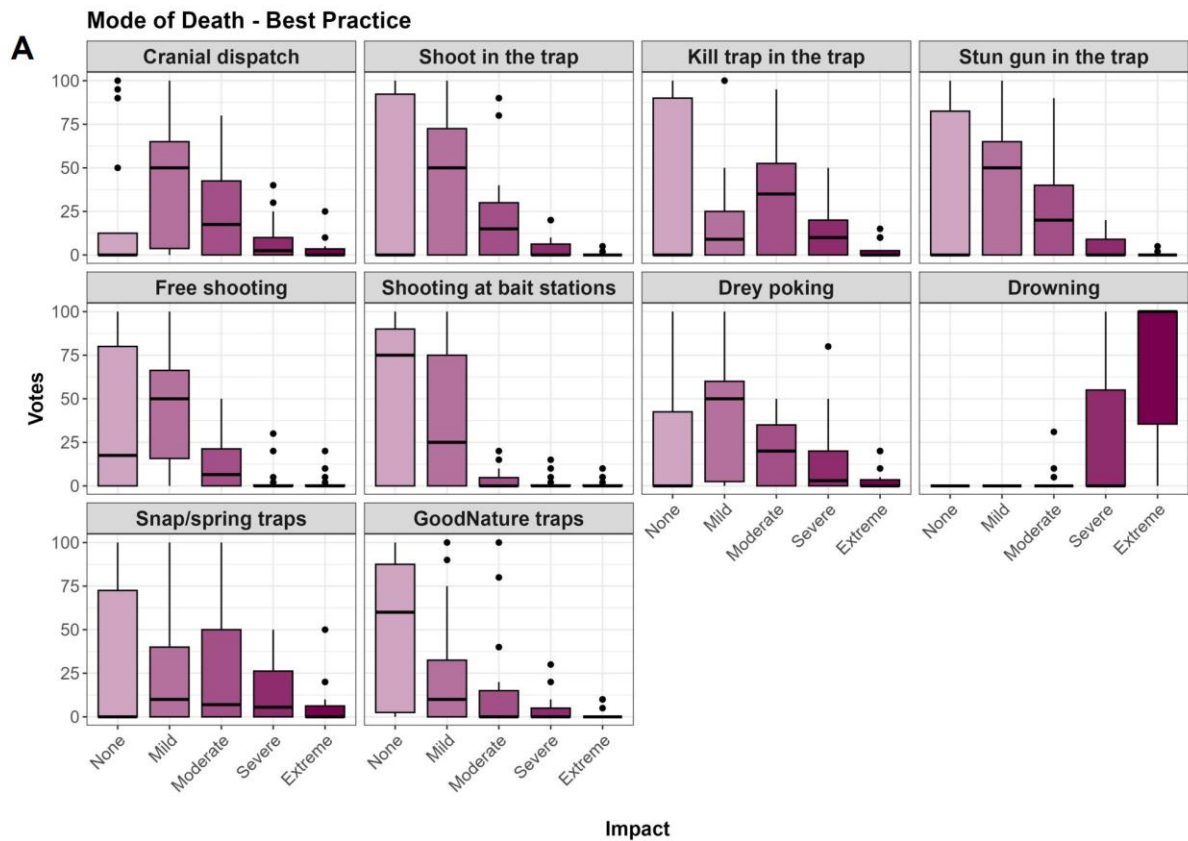


Figure A5. (A) The spread of the votes from all the experts for the level of suffering from each mode of death for the average grey squirrel when conducted under best practice guidelines. **(B)** The percentage of the total available votes that each impact category received.

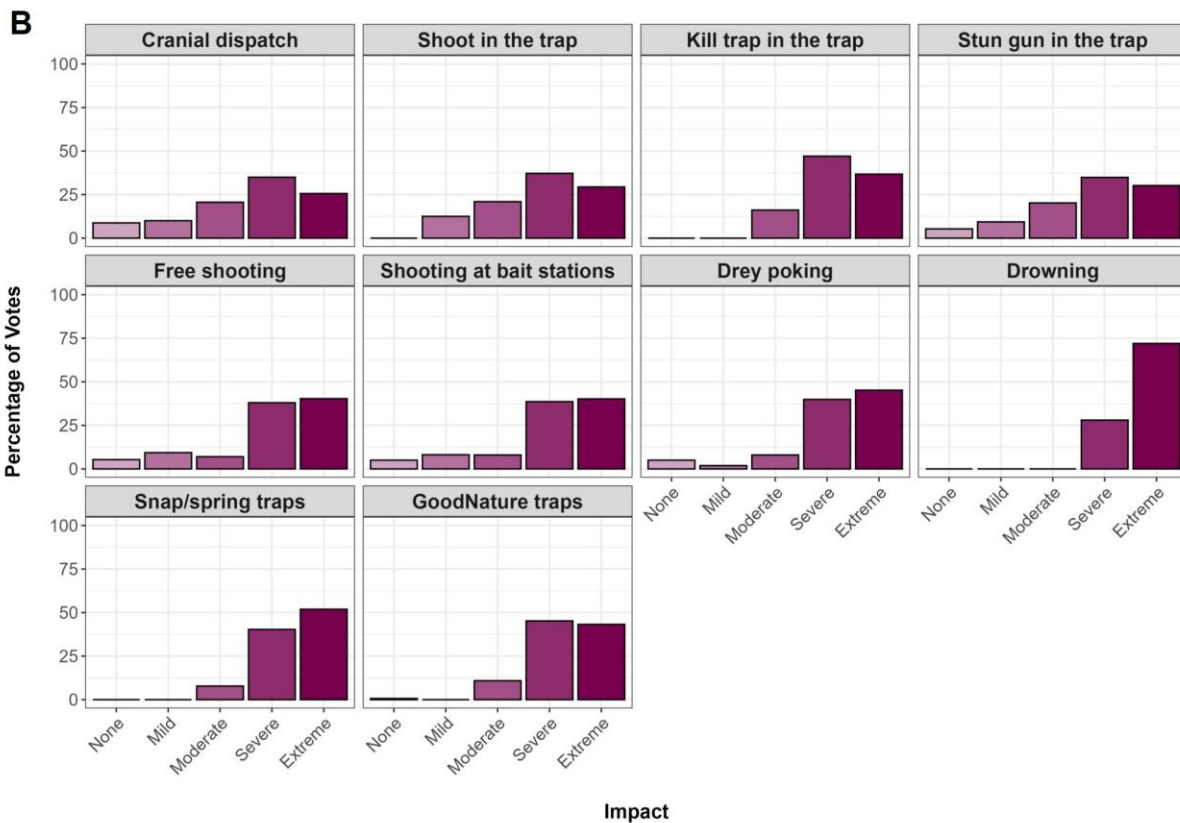
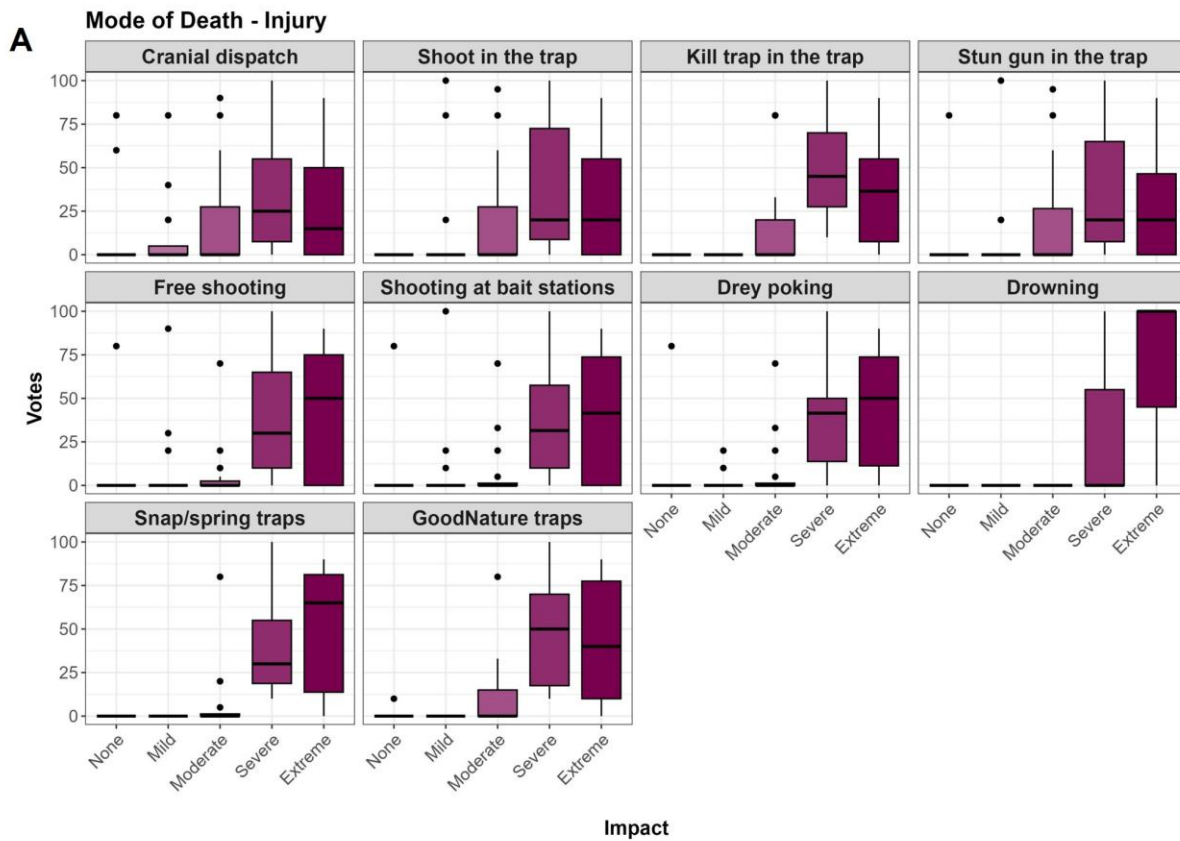


Figure A6. (A) The spread of the votes from all the experts for the level of suffering from each mode of death for the average grey squirrel when something goes wrong with the method, i.e. the animal is injured but killed. (B) The percentage of the total available votes that each impact category received.

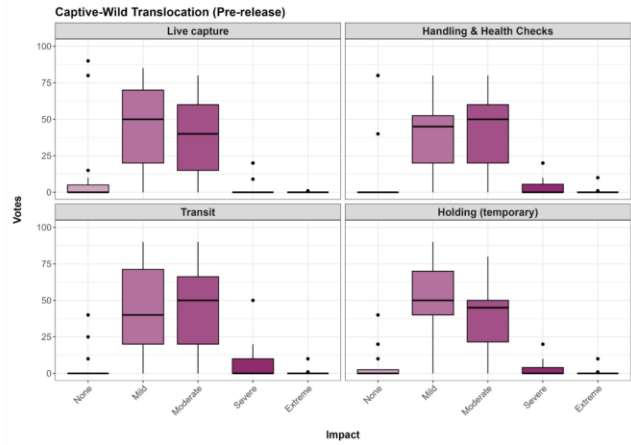
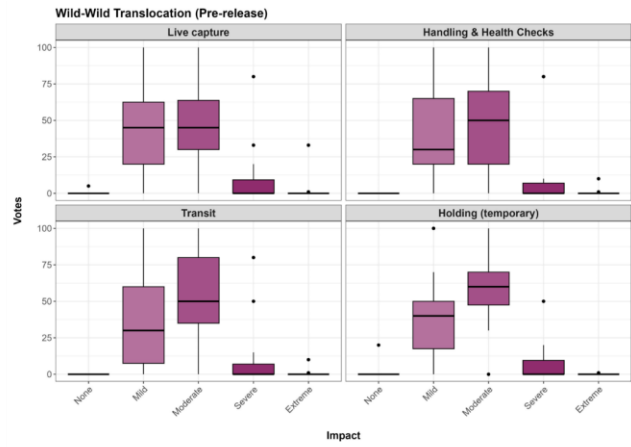
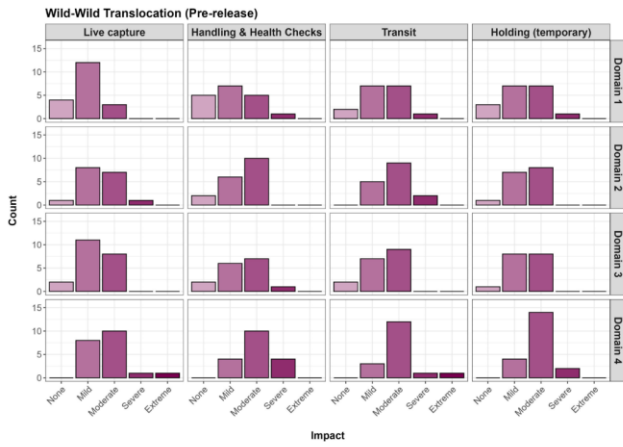


Figure A7. Left: Number of experts who selected each impact category for each of Domains 1 to 4 for four different elements of the pre-release translocation process for both wild-to-wild translocations (top) and captive-to-wild translocations (bottom). Right: Spread of the Domain 5 impact votes for each of the four translocation elements for wild-to-wild translocations (top) and captive-to-wild translocations (bottom).

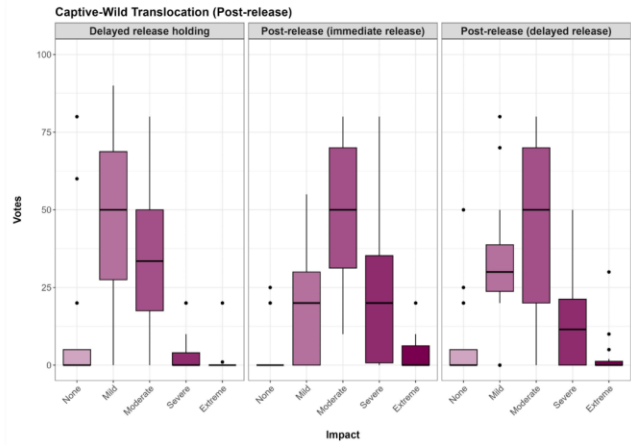
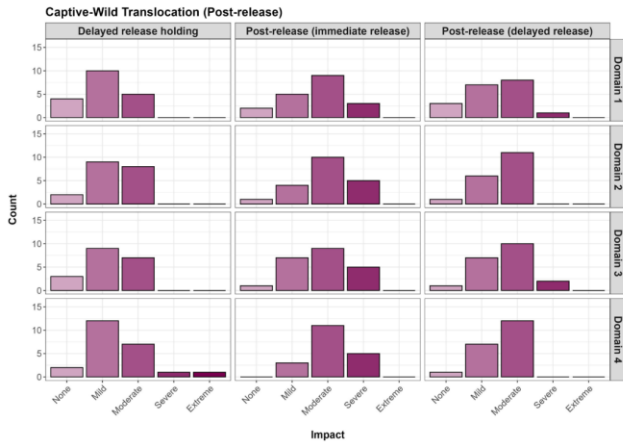
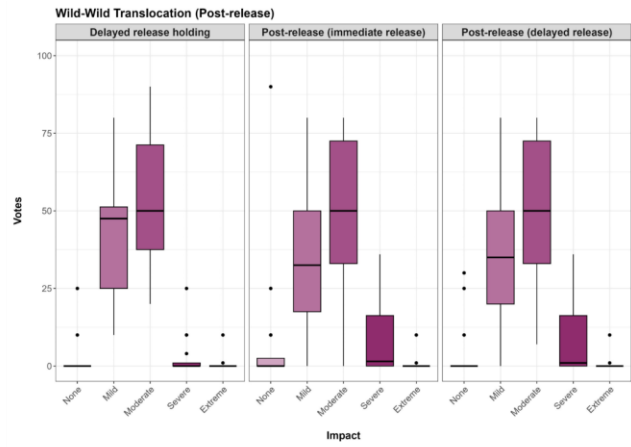
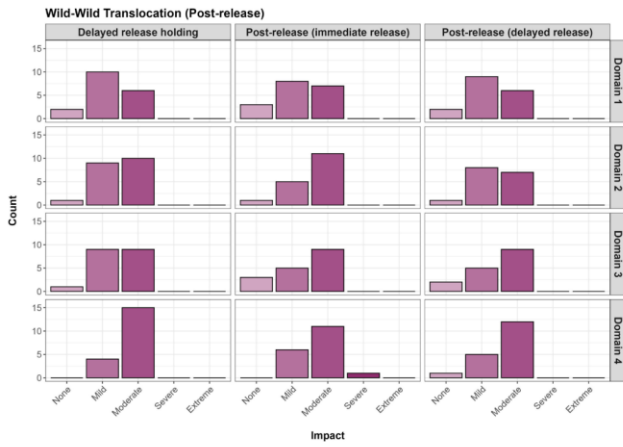


Figure A8. Left: Number of experts who selected each impact category for each of Domains 1 to 4 for three different elements of the post-release translocation process for both wild-to-wild translocations (top) and captive-to-wild translocations (bottom). Right: Spread of the Domain 5 impact votes for each of the three translocation elements for wild-to-wild translocations (top) and captive-to-wild translocations (bottom).

