Modelling red squirrel population viability under a range of landscape scenarios in fragmented woodland ecosystems on the Solway Plain, Cumbria.

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1. Introduction

The Solway Plain is located in the Northern Lake District, south of the Solway Firth. The landscape matrix is dominated by agricultural land with scattered woodland fragments; the red squirrel (*Sciurus vulgaris*) inhabits of some of these woodland fragments (O'Hare 2005). It is not known, however, if the fragmented woodland ecosystems within the Solway Plain will be able to sustain a viable red squirrel population. Population Viability Analysis (PVA) has been used to predict probabilities of extinction, as well as aid in conservation management decisions, for a wide range of endangered and vulnerable species (Brook et al. 1999). PVA has also been linked with landscape data, combining habitat structure with demographic data to produce metapopulation models (Akcakaya et al. 1995). By linking landscape and habitat data into a PVA it enables the demographic and behavioural characteristics of a species to be applied to specific habitat structures. The need to measure the effects landscape management has on biodiversity has lead to the creation of environmental and biodiversity evaluation tools (Watts et al. 2005). This study uses a combination of these advanced evaluation tools and PVA to assess the population viability of the red squirrel on the Solway Plain and to suggest conservation management strategies.

2. Red squirrel literature Review

2.1. Status and distribution

The red squirrel *Sciurus vulgaris* has been given protection under the Wildlife and Countryside Act 1981 and is classified as a priority species in the UK Biodiversity Action Plan due to a continued population decline within the UK (Cumbria BAP 2007). There are estimated to be 140,000 native red squirrels remaining within the UK, compared to 2.5 million of the introduced grey squirrel *Sciurus carolinensis* (Forestry Commission 2007).

Red squirrels are distributed throughout Europe and were once widespread throughout the UK (Hale et al. 2004). It is thought that competition with the introduced North American grey squirrel, disease, habitat loss and habitat fragmentation have all contributed to the massive decline of the species within the country (Skelcher 1997). Grey squirrels were first introduced into the UK in the late 1800s; by the 1930s concerns were raised about the decline in the red squirrel population and the large expansion of the grey squirrel population (Stewart 1997). Red squirrel populations in Ireland and parts of Scotland went extinct and only recovered in the 19th century due to reintroductions from mainland European (Skelcher 1997). With red squirrels now absent in southern and central England (Figure 1) the decline in the populations and replacement by the greys still continues, increasing the pressure on the remaining red squirrel populations (Gurnell & Pepper 1993; Skelcher 1997). It has been suggested that most red squirrel populations will become extinct in England within the next twenty years (Thomas et al. 2003), leaving the remaining squirrel populations isolated within red squirrel reserves (Gurnell & Pepper 1993).

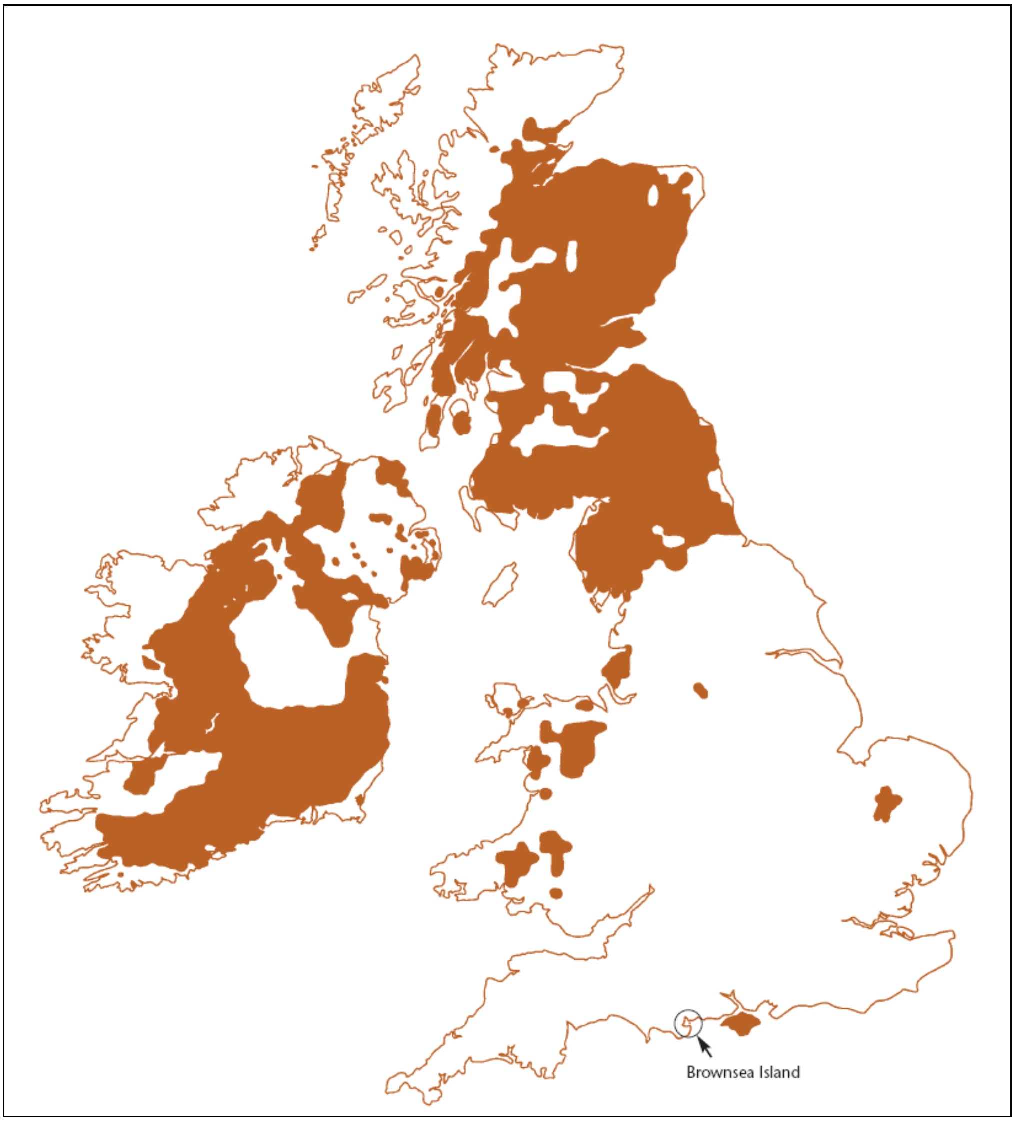


Figure 1: Red squirrel distribution within the UK (Pepper & Patterson et al. 2001)

Despite the expansion of the grey squirrel's range, Scotland remains a strong hold for the red squirrel, with the Lake District and northern England also having reasonable populations (Dutton 2004). Within Cumbria grey squirrels have been steadily advancing from the south, colonising mixed woodlands within South Cumbria (Skelcher 1997). They are already established in the South Lakes and around Windermere and are continuing to increase in number (Skelcher 1997). Sightings of greys have started to rise near Carlisle and Keswick in the north (Skelcher 1997; Tullie House 2007) (Figures 2 and 3) suggesting that the grey squirrels will become established in northern areas soon.

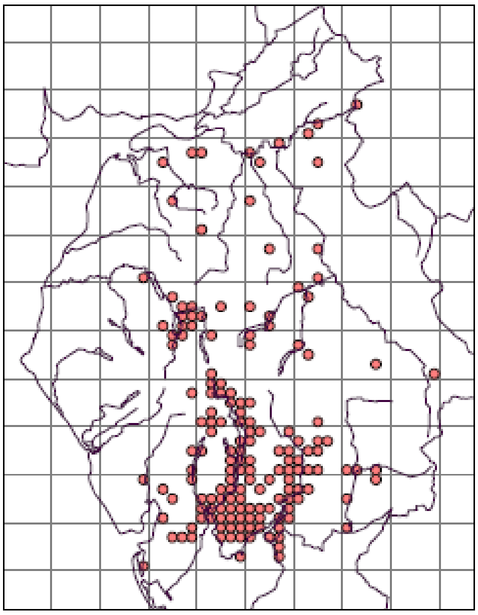


Figure 2: Grey squirrel distribution within Cumbria 2000- 2004 (Lurz et al. 2005)

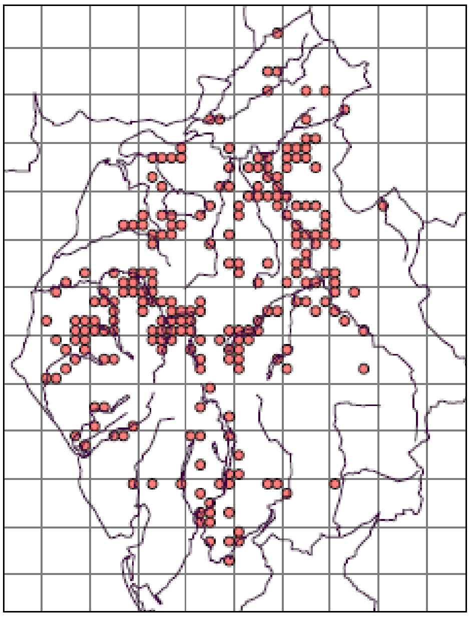


Figure 3: Red Squirrel distribution within Cumbria 2000-2004 (Lurz et al. 2005)

2.2. Genetic history

After the last ice age, 7-10 thousand years ago, the British population of red squirrels became isolated from the populations on mainland Europe (Barratt et al. 1999). Due to the isolation British and Irish red squirrels are considered, by some, as a separate sub species *S. vulgaris leucourus* (Hale & Lurz 2003). The squirrels were thought to be a sub-species due to a unique tail bleaching characteristic; their tails progressively lighten in colour until summer when it becomes a light creamy brown, sometimes looking bleached (Gurnell 1994). In recent years these light tailed squirrels have rarely been seen (Gurnell 1994). It is thought that the British squirrels have bred with introduced red squirrels from Europe, causing their hair to remain dark (Hale & Lurz 2003).

Barratt et al. (1999) studied the DNA of different red squirrel populations within Europe and Britain, the results showed that there are varied levels of genetic diversity but there are no evolutionary differences between the populations, therefore the UK populations are not a sub-species. Hale and Lurz (2003) suggested that the similarities in DNA could be due to the introduced squirrels becoming established in different parts of Britain, such as the Scandinavian introductions becoming dominant in the northeast (Hale et al. 2004). Only the Cumbrian populations are thought to be native and free from introduced stock, making them an important population as many other populations within reserves, such as Formby, have squirrels of European origin (Skeltcher 1997). Recent studies have shown that the Cumbria populations of red squirrels are genetically unique from other red squirrel population within the UK and Europe (Hale & Lurz 2004). There are currently approximately 1000 of these genetically unique squirrels left in Cumbria which makes their conservation critically important if high levels of genetic diversity are to remain within the population (Hale & Lurz 2004).

2.3. Habitat and dietary requirements

Red squirrels are woodland specialists (Verbeylen et al. 2003); their movements and foraging behaviour are concentrated within the tree canopy (Gurnell 1994). The canopy is preferred to the open ground as it provides safety and an abundance of food resources (Gurnell 1994). Although squirrels have been known to survive in all woodland types (Gurnell & Pepper 1993), red squirrels utilize coniferous woodlands with greater ease, with larger densities being found within this habitat (Bryce et al. 2005). Coniferous woodland with an age structure of between 20 and 40 years is preferred as this provides shelter, drey sites and an extensive food resource (Gurnell 1994).

Squirrels will feed upon a wide range of foods, the abundance of which varies seasonally (Shuttleworth 1997). The most important food sources are tree seeds, berries (Gurnell 1994) and fungi (Lurz & South 1998). Conifer seeds provide the squirrels with a high energy diet which they do not obtain from high cellulose foods (Shuttleworth 1997). Halliwell (1997) showed that Scots pine and Douglas fir are the highest ranked used tree species within a home range with radios tagged red squirrels preferring Scots pine over other coniferous tree species. Research has also shown that even with supplementary feeding of peanuts more than 65% of the squirrels diet consists of conifer seeds (Shuttleworth 1997). A squirrel's diet may also include tree flowers, buds, shoots, lichens, bark, and, occasionally, bird's eggs and insects (Lurz et al. 1995; Dutton 2004; Gurnell 1994).

Each red squirrel will select a home range within a woodland dependent upon habitat quality and the abundance of food resources (Wauters & Dhondt 1992). As tree seeds are the most important food type (Gurnell 1994) tree species, age and spacing are key factors that will influence whether a squirrel will permanently inhabit a particular woodland (Gurnell et al. 2002). Although a single red squirrel may only need a few hectares of habitat to survive (Verbeylen et al 2003), their home range may extend seasonally due to sexually activity, with males often having larger home ranges than females (Wauters & Dhondt 1992). Home ranges can range be between 1.52 – 3.59 hectares in large forests, however if habitat quality is low or a seed crop has failed their home range may increased up to 13.5 ha (Verboom & van Apeldoorn 1990). Squirrel home ranges may also overlap with one another (Wauters 1997), suggesting that a number of squirrels may be present within a particular habitat area.

2.4. Reasons for the population decline

2.4.1. Interspecific competition

There are two types of interspecific competition that may occur between red and grey squirrels; exploitation competition and interference competition. The latter can be in the form of aggressive encounters, mating disturbances and by forcing red squirrels out of preferred grey squirrel habitat (Walters & Gurnell 1999). Research has shown that interference competition rarely occurs between the two species (Gurnell et al. 2004), with very few aggressive encounters between species (Walters & Gurnell 1999). Red squirrels will choose to actively avoid grey squirrel core areas just as much as they would choose to avoid another red squirrel core area (Walters & Gurnell 1999). Male and female red squirrels will forage in close proximity to one another with out any signs of aggression (Wauters & Dhondt 1987). The only sign of aggression within red squirrel populations occurs as intra-sexual territoriality, where individuals act aggressively towards same sex individuals (Lurz et al. 1997). The grey squirrel has, however, undoubtedly had a detrimental effect upon the abundance and distribution of the red squirrel and has replaced it over much of its former range (Gurnell & Pepper 1993). It is suggested that the reason behind this replacement of reds by greys is due to exploitation competition (Skelcher 1997).

Both species of squirrel have been known to coexist in mixed woodland for numerous years, with grey and red squirrel populations overlapping when their preferred habitats merge into one another (Bryce et al. 2002). It has been suggested that exploitation competition occurs between red and grey squirrel populations, with grey squirrels exploiting deciduous woodland more efficiently than the reds (Skelcher 1997). Grey and red squirrels fill similar niches (Bryce et al. 2002), if both species are forced to live within close proximity to one another in mixed woodlands the reds' fecundity, recruitment, juvenile presence and breeding rate all drop (Gurnell et al. 2004). The grey squirrel is able to utilize its habitat more efficiently it is able to put on more weight in winter than the red (Bryce et al. 2002); the body condition of greys is therefore elevated and they are then in prime condition for mating in the spring (Gurnell & Pepper 1993). As a result the reds will eventually disperse or go extinct as the grey squirrel population increases (Gurnell et al. 2004) replacing the red in that particular habitat (Skelcher 1997). Gurnell and Pepper (1993) have suggested that the primary ecological requirement for red squirrels is the absence of greys.

2.4.2. Disease

Red squirrels are extremely vulnerable to the parapoxvirus carried by the invasive grey squirrels; it is fatal to the reds and yet not to the greys (Tompkins & White 2003). The grey squirrel has been shown to produce antibodies against the virus with no outward visible signs of the disease (Rushton et al. 2000). The grey squirrel therefore acts as host to the virus and has been known to have caused local extinctions and outbreaks of the parapoxvirus within red squirrel populations (Rushton et al. 2000). Red squirrels contract the virus within ten days of being introduced to it and proceed to die within fifteen (Thomas et al. 2003). During this time insitu infected individuals may pass on the virus to their local population causing a localised extinction, freeing the area for grey expansion (Rushton et al. 2000). It is unlikely that infected red squirrels are able to travel far once they have become ill therefore it is unlikely that other populations will be infected (Rushton et al. 2000).

2.4.3. Natural Predators

Red squirrels may be preyed upon by pine martens, goshawks, buzzards, cats, dogs, and foxes but generally predation is not thought to affect red squirrel populations (Gurnell 1994). However, this depends on the red squirrel population size, in a small population the loss of one individual through predation may result in a loss of genetic diversity, this is deleterious to the population and may lead a localized extinction (Frankham et al. 2002).

2.4.4. Habitat fragmentation

Habitat fragmentation occurs when a continuous habitat is separated into a number of smaller habitat patches, most commonly due to anthropogenic changes to the landscape structure (Wauters 1997). Creating or increasing habitat fragmentation effectively reduces species movement between habitat patches, leading to populations becoming isolated and increasing the possibility of local extinctions (Verbeylen et al. 2003). The fragmented populations have reduced gene flow within the population and are more susceptible to inbreeding, genetic drift and other problems of small population (Trizio et al. 2005). Placing physical barriers and larger geographical distances between fragments will undoubtedly restrict the dispersal of populations and therefore effect gene flow (Trizio et al 2005). Although there is no evidence to suggest that inbreeding depression occurs within red squirrel populations, largely fragmented populations with a decreased immigration rate do lose genetic diversity and fragments contain lower densities of red squirrels (Wauters 1997; Trizio et al. 2005).

Species within a metapopulation are able to recolonise habitat fragments after local extinction events, however this is largely due to the dispersal capabilities of each particular species (Verboom & van Apeldoorn 1990). Within agricultural landscapes hedgerows are seen as extremely important landscape elements aiding in species dispersal by acting as corridors between habitat fragments (Gelling et al. 2007). Squirrels found living within a fragmented habitat are often found to have multinuclear home ranges; consequently they use hedgerows and tree rows as corridors when they are moving from one fragment to another and during dispersal (Wauter 1997; Verbeylen et al. 2003). Radio-tracked red squirrels have been shown to cover distances of over 2km in less than 15 hours and may cover up to 4.1km in a few weeks (Verbeylen et al. 2003). Although there is a high predation risk associated with using habitat corridors and small woodland patches, within a fragmented landscape this behaviour may be essential to enable the squirrel access to sufficient food resources (Wauters 1997) and enable them to disperse further than 1km from their natal range (Verbeylen et al. 2003; Rodriguez & Andren 1999).

A study conducted by Verbeylen et al. (2003) found habitat fragments of lower than 3.5ha were never occupied by squirrels and up to 96% of patches <10ha were also unoccupied. Rodriguez and Andren's (1999) predicted that there is a higher probability of finding squirrels in fragments if they are larger than 10ha in size and are within 600m of a source population. Squirrels, however, do use smaller fragments <10ha (Verboom & van Apeldoorn 1990; van Apeldoorn et al. 1994; O'Hare 2005) and it is both the size and quality of the woodland fragment which determine squirrel presence and density (Verboom & van Apeldoorn 1990). Squirrels may also use more than one woodland fragment (Waulters 1997). Small and medium size fragments in many studies are found to be just as valuable as large patches (Lindenmayer et al. 2008). It is suggested that the use of these smaller fragments is dependant upon the landscape matrix, fragment quality and metapopulation dynamics (van Apeldoorn et al. 1994; Verbeylen et al. 2003). It is possible to conclude from these studies that within fragmented landscapes it is crucial that the landscape structure contains suitable habitat corridors to aid in movements and although small fragments may not be occupied they are still vital as a food resource and to aid in dispersal.

2.5. Current conservation strategies

There are numerous conservation strategies which have been researched to conserve the red squirrel for example eradication of the grey squirrel, immunocontraceptive vaccine for the greys, vaccine for the reds against parapoxvirus and captive breeding of the reds (Gurnell 1994; Moore 1997; Sainsbury et al. 1997). In the North West of England, red squirrel conservation efforts are largely centred on specialist reserves (Simon O'Hare pers. comm.). Gurnell and Pepper (1993) suggest that in order to conserve a viable population of red squirrels they should live within a habitat of at least 2000 hectares. Within smaller woodlands it will only be possible to conserve the red squirrel if there are numerous connected small woodlands with at least 200 ha of conifers (Pepper & Patterson 2001).

Many experts state that red squirrel reserves may be the only way of preventing the extinction of the red squirrel within England, with large coniferous forests being seen as the only place where red squirrels have a competitive advantage (Lurz et al. 1995). Larch *Larix spp* and Sitka spruce *Picea sitchensis* plantations, although not the preferred tree species are more likely to contain low densities of red squirrels if grey squirrels are encroaching within the surrounding area (Bryce et al. 2005). Grey squirrels have been found to rarely use larch and Sitka spruce and therefore these plantations could provide a refuge (Bryce et al. 2005). However, grey squirrels are found to utilize coniferous woodlands at greater densities if their preferred large seeded broadleaved woodland is found less than 500m away (Smith & Gurnell 1997; Lurz et al 2005). It is therefore particularly deleterious for red squirrels to have large seeded broadleaved species such as beech *Fagus sylvaticus*, oak *Quercus spp* and sweet chestnut *Castanea sativa* in close proximity to their coniferous habitat as it will encourage grey squirrel colonization and threaten the reds (Gurnell & Pepper 1993). Within Cumbria there are 19 woodland sites which could potentially be designated as red squirrel reserves (Bruemmer & Bentley 1999). The management of these woodlands is important as red squirrels must be supplied with a constant food source throughout the year (Dutton 2004).

2.6. Squirrel signs

Squirrel presence can be detected by feeding signs such as stripped bark and cone cores. The bark can be stripped and trees may have scratch marks on small well used areas (Brown et al. 2004). The scales on the cones are stripped off to enable the squirrel to reach the seeds inside; the cores are then discarded within the area where the squirrels have been feeding (Brown et al. 2004). Other signs to look for are squirrel dreys which are round structures of around 30cm made up of twigs and moss, usually 6-15m from the ground situated against the tree trunk in a fork of branches (Brown et al. 2004). Food stores and foot prints may also be seen, squirrels prints are distinctive as they have only four toes showing on the forelimbs and five on the hind (Brown et al. 2004)

3. Methods

3.1. Mapping red squirrel usage of fragmented woodlands

The initial focus of this study was to work closely with Cumbria Wildlife Trust to map red squirrel usage of fragmented woodlands on the Solway Plain. This is achieved by building upon previous data sets collected by O'Hare (2005) and using the distance sampling and hair tube survey methods as laid out by Gurnell et al. (2001). Any woodland found to have red squirrel presence from either a visual survey or hair tube survey was highlighted on a digital map to give a clear representation of the location of woodlands used by the red squirrel.

During the field work to map red squirrel usage, additional data was collected in the field for use within the Vortex Population Viability Analysis (PVA) (Lacy et al. 2007) and BEETLE (Biological and Environmental Evaluation Tools for Landscape Ecology) modelling. The methods for collecting this additional data are described within this section as the results from some of the methods can be used to aid in others. The distance sampling method not only enabled the establishment of red squirrel presence or absence in each woodland fragment enabling the mapping of red squirrel usage, but also allowed the density of the Solway Plain red squirrel population to be estimated which was later used within the PVA (Gurnell et al. 2001). The results from the habitat surveys were also used to decide which woodlands would require a hair tube survey and the results from the habitat survey and woodland usage results were be used within BEETLE assessments.

3.1.1. Distance sampling method

O'Hare's (2005) study site (Table 1) consisted of 23 woodland fragments varying in sizes from 0.88 – 63.72 ha, the study established red squirrel presence in 6 of the 23 woodlands using the basic visual survey method. Each transect within O'Hare's survey followed the longest straight line across each woodland fragment to standardise the methodology for woodlands of varying shapes and sizes (O'Hare 2005). For the purpose of consistency and to build upon these data sets this study used the same transect lines of the previous surveys. Two preliminary visits were made to the site. The first of which was to gain familiarity of the site and to be shown the location of each of the woodland fragments. The second visit was to establish ownership and access permission for each woodland fragment, along with any anecdotal data which was shared by the local residents.

The woodland fragments were each surveyed once during September to October 2007, with the surveys being carried out between 7.30 -10.30am to coincide with the red squirrels three hours of peak activity just after dawn (Dutton 2004). Each line transect survey was carried out stopping every 100m for 5 minutes for an intensive scan of the tree canopy as described in Gurnell et al.'s (2001) method. During the survey the location of any red squirrel sighting was recorded and the perpendicular distance of the squirrel from the survey line was measured using a tape measure until it became easier to estimate by eye. This measurement enabled the density of red squirrels within the Solway Plain to be estimated using standard distance sampling equations once all the surveys were completed (Gurnell et al. 2001).

Table 1. Solway Plain woodland fragments with grid reference and woodland data.

Woodland No. and name		Grid ref (NY)	Area (ha)	Transect length (km)	2005 Visual count
1	Moorhouse	255 514	17.17	0.66	0
2	Moorhouse Ellers	273 508	3.85	0.45	0
3	Nr. Nealhouse	338 514	1.02	0.15	0
4	Nr. Orton Rigg	330 520	1.87	0.25	0
5	Jeffreys Wood Kennels	346 523	4.35	0.37	0
6	Nr. Field View	334 535	1.38	0.22	0
7	Nr. Scheughmire	348 533	4.77	0.35	0
8	Orton Moss	340 540	63.72	0.97	1 x red 1 x grey
9	Stonerigg	330 556	6.27	0.52	1 x red
10	Thurstonfield	322 563	23.69	0.80	2 x red
11	Woodlands	318 557	3.12	0.29	0
12	Opposite Woodlands	315 557	5.65	0.45	0
13	Bank House 1	305 546	2.38	0.32	0
14	Bank House 2	302 544	2.39	0.26	0
15	Nr. Park House	297 546	1.96	0.27	0
16	Fisher Gill 1	293 541	2.82	0.24	0
17	Fisher Gill 2	291 542	0.88	0.15	0
18	Fisher Gill 3	289 538	1.01	0.13	0
19	Bank House 3	304 551	6.28	0.37	0
20	Border Range 1	285 557	2.04	0.26	0
21	Border Range 2	280 557	1.89	0.19	2 x red
22	Border Range 3	278 555	0.95	0.18	0
23	Finglandrigg South	276 567	46.54	1.30	1 x red

Source O'Hare (2005)

3.1.2. Habitat survey

Once the line transect survey was finished each transect was repeated in order to obtain habitat data and additional species data such as feeding signs and drey sightings. Woodland tree species composition and woodland classification was already obtained from O'Hare (2005) data. Species composition was also noted in this study along with additional data on the age of each tree species which was a required element of the BEETLE modelling for this study. Tree species age was classed as either young or mature, with trees which were of seed producing age being classed as mature and non seed producing age as young, using Savill (1991) for species age guidance (Table 2).

Table 2. Solway Plain tree species composition with age of tree species seed production.

Tree species	Age of first good seed crop	Age of best seed crop
Ash (*Fraxinus excelsior*)	25-30	40-60
Beech (*Fagus sylavatica*)	50-60	80
Downy birch (*Betula pubescens*)	15	20-30
Douglas fir (*Pseudotsuga menziesii*)	30-35	50-60
Holly (*Ilex aquifolium*)	20	40
Norway spruce (*Picea abies*)	30-35	50-60
Pedunculate oak (*Quercus robur*)	40-50	80
Rowan (*Sorbus aucuparia)*	10 (fruit crop)	15 (fruit crop)
Scots pine (*Pinus sylvestris*)	60	After the age of 60
Silver birch (*Betula pendula*)	15	20-30
Sycamore (*Acer pseudoplantanus*)	25-30	40-60

Adapted from Savill (1991)

3.1.3. Hair tube survey

O'Hare's (2005) habitat data as well as the results from this habitat survey, red squirrel visual survey and any feeding or drey sighting data was used as the basis to decide on hair tube survey locations. Woodlands with a large proportion of red squirrel coniferous habitat, feeding or drey signs and no squirrel sightings recorded during the line transect surveys were surveyed again using the hair tube survey method of Gurnell et al. (2001). This is a less invasive method and ensures that red squirrels were indeed absent from the woodland and not just missed during the survey due to human disturbance. Any hair samples found were then analysed in the laboratory using a binocular stereo microscope at x 100 magnification and identified by using Teerink's (1991) identification key.

3.2. Red squirrel Population Viability Analysis (PVA)

This study is using Vortex software version 9.75 (Lacy et al. 2007) to conduct the PVA. Vortex uses an individual species approach, running through the events that may occur within the life cycle of that particular species (Miller & Lacy 2005). The programme includes demographic, environmental and genetic stochasticity enabling the user to understand what factors or events may lead to the extinction of small fragmented populations (Miller & Lacy 2005). Vortex enables the user to change different stimulation inputs to create different scenarios; it is then possible to see what this change would have upon a population's viability, if any. The methods shown within the Vortex manual were followed (Miller & Lacy 2005), entering the stimulation input needed (Table 3) within the Vortex interface. At this point in the PVA no catastrophes were considered and only the number of populations, dispersal, initial population size and carrying capacity were changed within each scenario.

Table 3. A summary of the red squirrel demographic data needed as inputs to run the Vortex Population Viability Analysis.

Input	Value
Age at which first disperse	1 year
Dispersing sexes	Male and Female
Percentage that survive dispersal	16% Male and 15%female
Reproductive system	Polygynous
Age of first offspring for females	1 year
Age of first offspring for males	1 year
Maximum age of reproduction	7
Maximum number of progeny per year	6
Sex ration at birth	1:1.2
Mortality from age 0 – 1	70%
Annual mortality after 1	30%

After Whitfield (2005)

3.2.1. Scenario 1: Connected woodlands

The first scenario was run to determine the viability of a Solway Plain red squirrel population if all the woodland fragments with red squirrel presence (known from the line transect survey and hair tube survey results) were connected together acting as one population. This assumes that the squirrel is able to move between these fragments with no associated cost. The simulation input consisted of all the input within Table 3 and the variable inputs for this particular scenario. In this case there is only one population and therefore it is not subject to dispersal and no dispersal input is required. The initial population size is calculated by taking the total size of the woodland fragments containing red squirrels and multiplying it by the red squirrel density for the Solway Plain (which is calculated using the distance sampling method). For this scenario it is assumed that only the 5 woodland fragments with red squirrel presence are used by the red squirrel and therefore the population is assumed to be at carrying capacity.

3.2.2. Scenario 2: Dispersing within a metapopulation.

All woodland fragments with red squirrel habitat were modelled in this scenario as a metapopulation, with individuals dispersing between fragments. Each of the woodland fragments classed as red squirrel habitat from the surveys were classed as a population. The annual probabilities of individuals dispersing from a source population were then added to the table in the Vortex interface. The probabilities were calculated by measuring the distance between each of the fragments in a GIS and using the log normal probability density function based on the maximum recorded dispersal distance of 4.1 (Verbeylen et al. 2003). The initial population size of each of the 5 woodlands with red squirrel presence was calculated as in 3.2.1; the rest had no squirrel present within the surveys and therefore had an initial population size of zero. The carrying capacity is calculated by taking the total area of all woodlands and multiplying it by the red squirrel density.

3.2.3. Scenario 3: Dispersing between woodlands with red squirrel presence.

This scenario is modelling a metapopulation but only using woodland fragments that are red squirrel habitat and have red squirrel presence. The number of populations for this scenario is 5 and the annual dispersal probabilities are calculated as in 3.2.2. The initial population is calculated as in 3.2.1 using only woodlands which were found to have red squirrel presence. The populations are assumed to be at carrying capacity.

3.3. Modelling Functional Connectivity for red squirrel habitat

Ecological isolation has negative effects on red squirrel population dynamics (Verbeylen et al. 2003; Wauters 1997; Trizio et al. 2005). In order to assess the population viability of the fragmented woodland ecosystems on the Solway Plain it is essential that the functional connectivity is modelled. Functional connectivity is not only based upon the distance or proximity of each habitat fragment, but upon the species dispersal capabilities through the different land cover types which surround the fragment (Watts et al. 2005). As some land cover types may be more permeable to the squirrel than others, woodland fragments which are close in proximity but are separated by a low permeable habitat, such as a river, are less likely to be functionally connected. The modelling for this study was based at the Forest Research Northern Research Station, Edinburgh. Forest Research, the research agency of the Forestry Commission, has developed a suite of tools called ‘Biological and Environmental Evaluation tools for Landscape Ecology’ (BEETLE), within a Geographical Information System (GIS). The least-cost tool analyses the landscape structure (spatial arrangement and organisation of the landscape elements) and landscape function (the interaction of the landscape structure with a given species characteristics and requirements) to evaluate the functional connectivity of the fragmented habitat in question (Watts et al. 2005).

BEETLE uses a focal species-based evaluation process requiring primary data inputs in the form of a land cover module and a focal species module (Watts et al. 2005). Only these two modules are needed as input as methods are defined within the BEETLE software (Humphrey et al. 2007). The model then creates a Home Habitat Output Shapefile, showing squirrel habitat which is defined within the Focal Species module, and a Network Output Shapefile, indicating how these habitat fragments are connected functionally to create a home habitat network showing potential movements of the squirrels. The modules are created within ArcGIS software using the red squirrel presence or absence data and the habitat suitability data obtained in the field surveys, as well as published data on red squirrel ecology and the Solway Plain landscape matrix.

3.3.1. Creating the Land Cover Module

The land cover module controls the models behaviour and represents changes which may be made to the landscape structure (Watts et al. 2005). When creating the land cover module a comprehensive database is created within the GIS comprising of a number of data sets (Table 4). The first layer added within the GIS is the area of interest layer which is created from the Ordinance Survey MasterMap (OSMM) and Lines (OSL) data sets. The area of interest selected comprised the survey area and a 2km buffer of the survey area; it is important to select an area of interest as the OSMM and OSL contain data on the whole of the UK. Other layers are then added from data sets which hold information on the survey area selected. The OSMM, OSL, and the LCM 2000 layers were attached spatially together to create a new land cover layer; this enabled general land cover descriptions found within the OSMM to be replaced with the more detailed LCM 2000 descriptions, which are contained in the attributes table of the land cover layer. These land cover descriptions were checked against information held within the National Inventory for Woodlands and Trees (NIWT) datasets, aerial photos (Google maps) and survey data sets, editing them if the description was incorrect or if the land use had changed.

As none of the previous data sets contained information on the location of hedgerows, OSL which were found to be hedgerows either in an aerial photo or field surveys were selected. These lines were buffered with 2m either side to create hedgerow polygons; this layer was integrated into the land cover layer to complete the land cover module. Each land cover type was then assigned a unique land cover code, a number given to distinguish habitats from one another.

Table 4. A summary of the data set used to create the land cover module in BEETLE.

Data Set	Description	Format	Reference
Ordinance Survey	large scale mapping –OS Master	Vectors – Lines & Polygon; Raster Map; Land Lines	OS (2007)
Land Cover Map 2000	Satellite based habitat descriptions	Vector – Polygons	Fuller et al (2001)
National Inventory of Woodlands and Trees	Provides information on woodlands >2ha and with a minimum 50% canopy cover	Vector – Polygons	FC (2002)

3.3.2. Creating the Focal Species Module

The focal species module is based on the ecological knowledge of the species (habitat requirements and dispersal abilities) and the area of concern (Watts et al. 2005). This was used to define suitable habitat for both red and grey squirrels. Each land cover type within the land cover module was identified as either 0 (suitable habitat) and 1 (unsuitable) within the attribute table. As squirrels are a woodland species (Gurnell 1994) only woodlands are potentially habitat, a combination of tree species composition, tree species age and canopy connection are used to distinguish if woodlands are red or grey squirrel habitat or neither (Table 5). Woodlands which have a connected canopy are potentially squirrel habitat as the squirrels are able to move easily from tree to tree within the canopy without the need to cross open ground. For woodlands to be classed as red squirrel habitat they need to have a closed/connected canopy, with a species composition of either coniferous, large seeded broadleaved or mixed species which are of seed producing age. This ensures that only woodlands which provide protection, food resources and the preferred tree species of the red squirrel are classed as habitat. Deciduous, large seeded broadleaved and mixed woodlands which are seed producing age and have a closed canopy were classed as grey squirrel habitat, with woodlands comprised of young non seed producing or small seeded species being classed as neither red or grey habitat as it does not provide a food resource or protection.

A connectivity module was then created within the focal species module, this models the dispersal capabilities and preferences of the chosen focal species (Watts et al. 2005). Each land cover type was assigned a habitat permeability score for red and grey squirrels, to represent how easily each species may move through the different land cover types (Table 5). The scores, which range from 1 for very permeable land cover types to 10,000 for impermeable types (e.g. buildings) were based upon scores derived through a Delphi process made up of red squirrel experts in the Scottish Red Squirrel Group (2007). The connectivity module enables the identification of the potential habitat networks by analysing the functional connectivity of the fragmented woodland ecosystems (Watts et al. 2005).

3.3.3. Running BEETLE to Create Habitat Networks

Once the modules were created the modelling process followed the BEETLE method described by Humphrey et al. (2007). Red squirrel habitat was selected and the functional connectivity was modelled at the assumed dispersal distance of 2km and 4km with the associated land cover permeability scores. The dispersal distances chosen are based on the assumed foraging or commuting distance a squirrel would be able to travel in a continuous habitat and include the distance it would need to return. Therefore if a squirrel is assumed to be able to travel 2km in a foraging day half of this distance (1km) would be entered into the model to take into account the returning distance. The two distances chosen allows potential dispersal and habitat functional connectivity to be shown at two dispersal distance.

Table 5 Permeability scores of the different land cover types of the Solway Plain.

Land cover code	Source	Land Cover Type	Red squirrel land cover permeability scores	Grey squirrel land cover permeability scores	Red squirrel habitat = 0	Grey squirrel habitat = 0
1	Survey	Scots pine connected	1	1	0	0
2	Survey	Scots pine not connected	7	4	0	1
3	Survey	Large broadleaved connected	1	1	0	0
4	Survey	Young large broadleaved connected	1	1	1	1
5	Survey	Small broadleaved connected	1	4	1	1
6	Survey	Young small broadleaved connected	7	4	1	1
7	Survey	Conifer connected	1	1	0	1
21	NIWT	Broadleaved	1	1	1	0
22	LCM 2000	Scrub, open birch & deciduous, mixed, broadleaved evergreen,	1	1	1	0
23	NIWT	Coniferous	1	1	0	1
24	LCM 2000	Conifers, new plantation & felled (not actually felled)	1	1	0	1
25	Survey	Coniferous/open marsh	7	7	0	1
26	NIWT	Mixed	1	1	0	0
27	NIWT	Shrub	14	8	1	1
101	LCM 2000	Dense shrub (ericaceous / gorse)	35	21	1	1

102	LCM 2000	Open shrub (ericaceous/ gorse	35	21	1	1
103	LCM 2000	Barley, maize, oat & wheat	46	30	1	1
104	LCM 2000	Bare, carrots, beans, peas, linseed, potato, rape, beet, mustard, unknown	46	30	1	1
105	LCM 2000	Orchard, ley, setaside (rotation)	46	30	1	1
106	LCM 2000	Intensive grazing, hay/ silage cut, grazing marsh	46	30	1	1
107	LCM 2000	Rough grass (unmanaged)	43	30	1	1
108	LCM 2000	Calcareous (managed, rough)	43	30	1	1
109	LCM 2000	Acid with juncus Acid Nardus/Festuca/Molinia	37	31	1	1
110	LCM 2000	Bracken	32	22	1	1
111	LCM 2000	Bog: shrub, grass/shrub, grass/herb	94	76	1	1
112	OSMM	Shingle, vegetated shingle, dune, dune shrubs	112	96	1	1
113	LCM 2000	Salt marsh (grazed / ungrazed)	94	82	1	1
114	OSMM	Mud, sand & sand with algae	112	96	1	1
115	LCM 2000	Sea, estuary	144	144	1	1
116	OSMM	Tidal water	144	144	1	1
117	OSMM	Inland water	119	115	1	1
118	OSMM	Inland water, Natural Environment	119	115	1	1
119	LCM 2000	Water (inland)	119	115	1	1
120	LCM 2000	Despoiled / semi-natural	41	36	1	1

121	OSMM	Building	10000	10000	1	1
122	OSMM	Structure	10000	10000	1	1
123	OSMM	Glasshouse	10000	10000	1	1
124	OSMM	General Surface,Road Or Track	19	12	1	1
125	OSMM	Road Or Track	19	12	1	1
126	OSMM	Path	25	16	1	1
127	OSMM	Rail	46	40	1	1
128	OSMM	Roadside	19	12	1	1
129	LCM 2000	Suburban/rural developed	74	57	1	1
130	LCM 2000	Urban residential/commercial	74	57	1	1

(Scottish Red Squirrel Group 2007)

3.4. Combining BEETLE and Vortex software to model a range of landscape management scenarios that will maintain a viable population

Firstly, from the home habitat networks created by BEETLE, the largest habitat networks were identified. Vortex was then used to see whether these individual networks will be able to support a viable population of red squirrels individually. If the large networks were found to be non-viable, networks which had a short highly permeable distance between them were modelled together as one population in Vortex, to see whether joining the networks together would provide enough habitats to maintain a viable population. From this information it is possible to suggest areas where additional habitat could be usefully created or expanded.

Additional habitat was then added to the landscape matrix in BEETLE to test whether the additional woodland fragments would connect all the woodlands which had red squirrel presence within a functional network.

3.5. Modelling the likely movement of the grey squirrel into the Solway plain and red squirrel viability under a range of grey squirrel pressures

3.5.1. Modelling the likely movements of grey squirrels

Grey squirrel networks were created using the same methods as used in section 3.3 by substituting red squirrel habitat and permeability scores with that for the grey squirrels. Dispersal distances of 2km and 4km were used, as for the red squirrel, showing potential areas for colonization as well as enabling comparisons between the two species networks. Following the recent sightings of grey squirrels in woodlands not predicted to be functionally connected at 4km, dispersal distances of 8km and 12km were used to investigate whether these dispersal distance, modified by the land cover permeability, could show the potential networks for grey squirrels. These networks can indicate the potential dispersal routes and colonisation areas for grey squirrel incursions.

3.5.2. Red squirrel viability under grey squirrel pressures

The woodland fragments which could possibly hold viable populations of red squirrels (shown in section 4 Results) were modelled against the effects of parapoxvirus using Outbreak disease modelling software designed by Pollak et al. (2002). The data needed to be entered into the models interface can be classed into two categories squirrel ecology and disease parameters. The data for the squirrel is the same as used for the Vortex modelling (Table 2). The disease parameter data is base on literature on the squirrel poxvirus (SQPV) (Rushton et al. 2000; Tompkins et al. 2003; Sainsbury et al. 1997).

4. Results

4.1. Mapping red squirrel usage of fragmented woodland

Red squirrel sightings were recorded in 4 (woodlands 10, 16, 21 and 23) of the 23 woodland fragments during the visual surveys, with a total number of 6 individuals seen (Table 6). The sightings occurred within mature woodlands which contained Scots pine and numerous squirrel feeding signs (Table 7).

Additional squirrel signs were recorded in four other fragments, however there were no sightings of squirrels in these fragments during the visual survey. A squirrel drey, scratch marks on trees and feeding signs were seen in woodland 3. Squirrel feeding signs were also found in woodlands 1, 8 and 13 (Table 6). All four of these woodlands contained mature tree species, however only three contained a large enough proportion of coniferous species to affect overall woodland classification. The woodland that was not classified as having coniferous species (woodland number 13), actually had two Scots pine trees within it and was less than 600m from small woodland fragment of Scots pine. All four of the woodland fragments with squirrel signs (1, 3, 8 and 13) were surveyed using hair tubes. Red squirrel hair was found in one tube which was located within woodland number 13; none of the other four fragments produced hair samples. The locations of all the woodland fragments found to be used by red squirrels at the time of this study are shown in Figure 4.

Table 6. Solway Plain woodland fragment usage by the red squirrel.

No	Name	Area (ha)	Squirrel sightings	Squirrel signs
1	Moorhouse	17.17	0	Feeding signs
3	Nr. Nealhouse	1.02	0	Feeding, drey and scratch marks
8	Orton Moss	63.72	0	Numerous feeding signs
10	Thurstonfield	23.69	1x red	Feeding and squirrel noises
13	Bank House 1	2.38	0	Feeding signs
16	Fisher Gill 1	2.82	1x red	Feeding signs and a drey
21	Border Range 2	1.89	2 x red	Feeding signs
23	Finglandrigg	46.54	2 x red, 1 x grey	Feeding signs

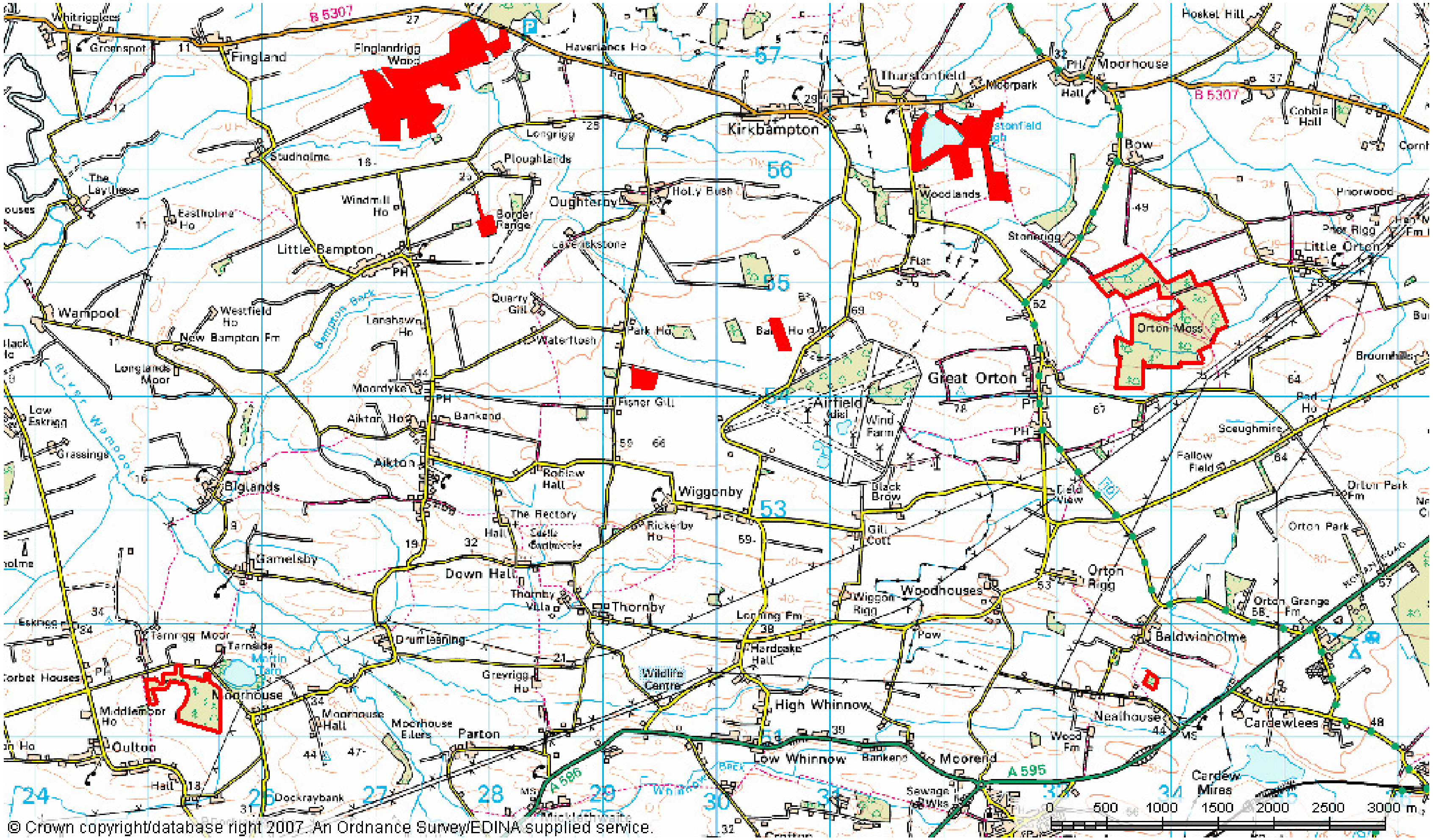
Table 7. Woodland classification and species age of the woodland fragments in the Solway Plain

No	Name	Classification *	Age	Squirrel presence
1	Moorhouse	CSP	Mature	Signs
2	Moorhouse Ellers	LSB	Mature	
3	Nr. Nealhouse	MW	Mature	Signs
4	Nr. Orton Rigg	SSB	Mature	
5	Jeffreys Wood Kennels	LSB	Young	
6	Nr. Field View	SSB	Young	
7	Nr. Scheughmire	LSB	Mature	
8	Orton Moss	MSP	Mature	Signs
9	Stonerigg	LSB	Mature	
10	Thurstonfield	MSP	Mature	Visual sighting
11	Woodlands	LSB	Mature	
12	Opposite Woodlands	SSB	Young	
13	Bank House 1	LSB	Mature	Signs
14	Bank House 2	SSB	Mature	
15	Nr. Park House	SSB	Mature	
16	Fisher Gill 1	MSP	Mature	Visual sighting
17	Fisher Gill 2	SSB	Mature	
18	Fisher Gill 3	SSB	Mature	
19	Bank House 3	LSB	Mature	
20	Border Range 1	LSB	Young	
21	Border Range 2	CSP	Mature	Visual sighting
22	Border Range 3	MSP	Mature	
23	Finglandrigg South	MSP	Mature	Visual sighting

* Based on information taken from O'Hare (2005)

MW = Mixed, MSP = Mixed with Scots pine, CW = Coniferous, CSP = Coniferous with Scots pine, SSB = Small seeded broadleaved, LSB = Large seeded broadleaved.

Figure 4: Red squirrel usage of fragmented woodland on the Solway Plain.



Key for Figure 4: Woodland fragments with squirrel signs but not confirmed presence have a red outline

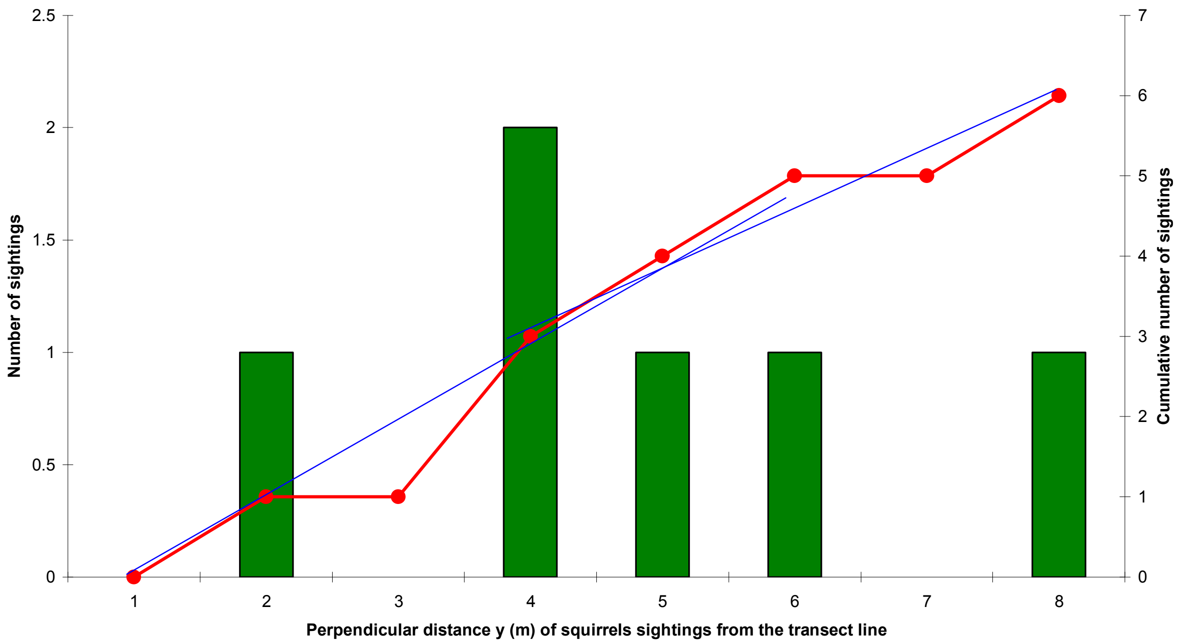
Woodlands with confirmed red squirrel presence are red blocks

4.2. Red squirrel Population Viability Analysis (PVA)

4.2.1. Calculation of red squirrel density for the Solway Plain.

The estimated density of red squirrels within the fragmented woodlands of the Solway Plain was calculated by using the visual survey sightings data (Table 6) and the equation $d = n / (2 \times w \times l)$, where d is the density of red squirrels within an area, n is the number of squirrel sightings along all 23 transects, w is the estimated belt width of the line transect (taken from Figure 5) and l is the length of each transect added together (Gurnell et al. 2001).

Figure 5. Estimation of belt width for Solway Plain red squirrel visual surveys.



Key for figure 5

Cumulative number of squirrel sightings

Line of best fit

Number of squirrel sightings

The woodland fragments of the Solway Plain are estimated to have a red squirrel density of d = 6 / (2 x 5 x 9150) = 0.0000655 squirrels m^2 = 0.65 squirrels ha^{-1}. If the squirrels were found to be using all 206ha of the 23 woodland fragments at the density of 0.65 squirrels ha^{-1}, the fragmented woodland ecosystems could potentially be holding (206 x 0.65) 133.9 individuals. Red squirrels were, however, only recorded in 5 of the woodland fragments (only 77.32ha), therefore there may only be 50.25 individuals. The number of individuals estimates are based upon the squirrels using the entire available habitat of the woodland fragments they were recorded in, the estimates will be lower depending on habitat quality and the proportions of available habitat actually used.

4.2.2. Population Viability Analysis using Vortex

Woodland fragments 10, 13, 16, 21 and 23 were all found to have red squirrel presence in either the visual survey or hair tube survey (4.1), each of the five fragments may therefore hold a single population of red squirrels or they may all be linked together due to metapopulation dynamics. Assuming that there are no costs associated with dispersing between the five woodlands with red squirrel presence, Vortex has predicted that the red squirrel population would face a 4% chance of extinction over a 100 year time period, with extinction being defined as only one sex remaining within the Vortex software. However, when the squirrel populations are modelled dispersing between the 5 woodland fragments which contain red squirrel presence, Vortex predicts that there is an 87 % chance of extinction. When the 5 populations are modelled dispersing between all woodland fragments with red squirrel habitat the population would go extinct with a 100% chance of extinction with no individuals remaining. Vortex has therefore revealed that when the red squirrel populations are faced with the costs associated with dispersal, the populations would face a higher probability that they would face extinction (Table 8).

Table 8. Vortex modelling scenario results

Scenario	Extinction probability
1, Connected woodlands	4 %
2, Dispersing within a metapopulation	100 %
3, Dispersing between woodlands with red squirrel presence	87 %

4.3. Modelling Functional Connectivity for red squirrel habitat

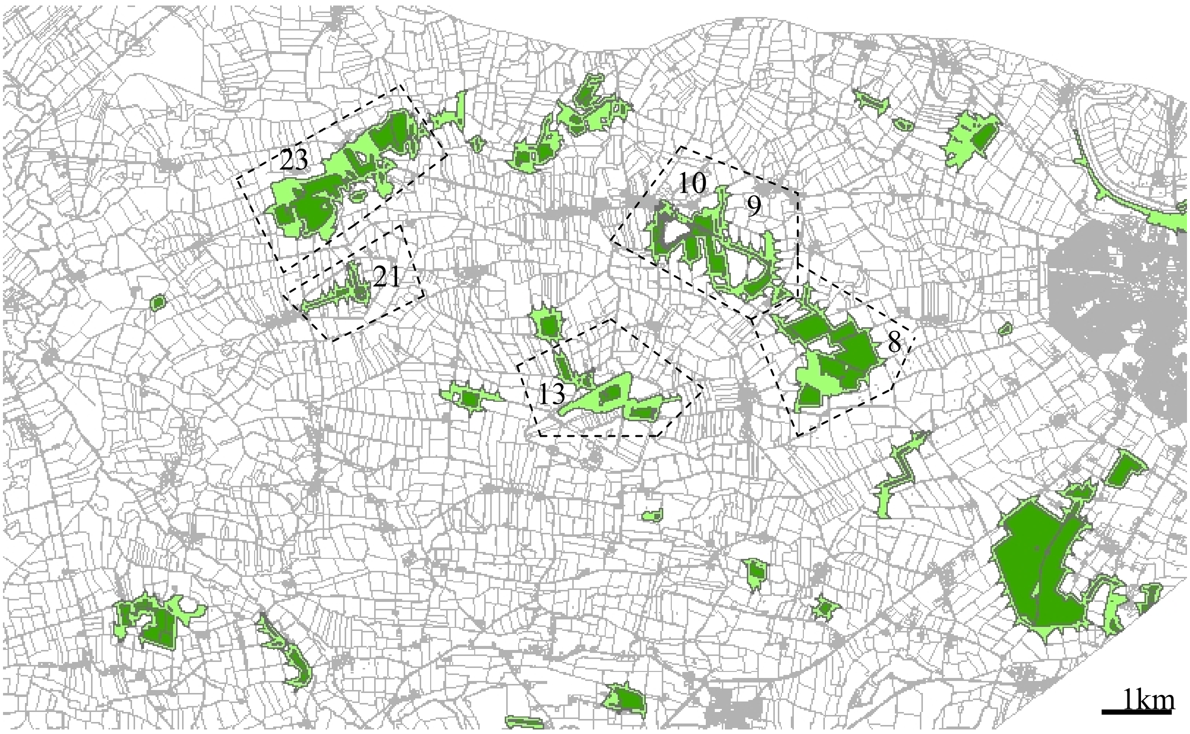
Modelling the functional connectivity of red squirrel habitat at a dispersal distance of 2 km indicated that only two of the surveyed woodland fragments (21 and 22) were connected functionally. However some woodland fragments (23 and 13) were connected functionally to woodland fragments that were either outside of the survey area or were <0.80ha and therefore were not included in the surveys as in O'Hare (2005) study. The 2km modelling shows that although some areas are functionally connected, the majority of the fragmented woodland ecosystems are isolated at this dispersal distance (Figure 6). Even when the landscape matrix is modelled for a future scenario (50 years from now), where four additional woodland fragments are now regarded as seed producing red squirrel habitat, the majority of the woodlands still remain fragmented and the additional woodlands have not affected the original 2km networks (Figure 6 and Figure 7).

Modelling at the dispersal distance of 4km indicated an increase in functional connectivity of the habitats. Woodland fragments 9 and 10 are now shown to be a functionally connected network which also includes one of the small woodland fragments which were not included in the surveys (Figure 8). This network (which will now be referred to as Thurstonfield network) remains unconnected to woodland 8 (referred to as Orton Moss network) although there is less than 10m separating the two habitat networks. The large dispersal distance also reveals a habitat network which is comprised of woodland 13 and the small woodlands located within Watchtree Nature Reserve (NY310540). Three possible networks which may potentially be large enough to sustain a viable population of red squirrels on the Solway Plain are selected from the 4km results. These are Thurstonfield network, Orton Moss network and woodland 23 habitat network (which will now be referred to as Finglandrigg network).

Figure 6. BEETLE red squirrel habitat network at a dispersal distance of 2km. Dark green areas represent red squirrel habitat, light green areas represent potential dispersal areas. Functional networks are considered to be where the light green areas connects the habitat fragments. The dashed lines highlight networks created using a dispersal distance of 2km.

Figure 7. BEETLE red squirrel future habitat network at a dispersal distance of 2km. Red areas represent woodland which is likely to become red squirrel habitat once it has matured, dark green areas represent existing red squirrel habitat light green areas are the potential dispersal areas.

Figure 8. BEETLE red squirrel habitat networks at a dispersal distance of 4km



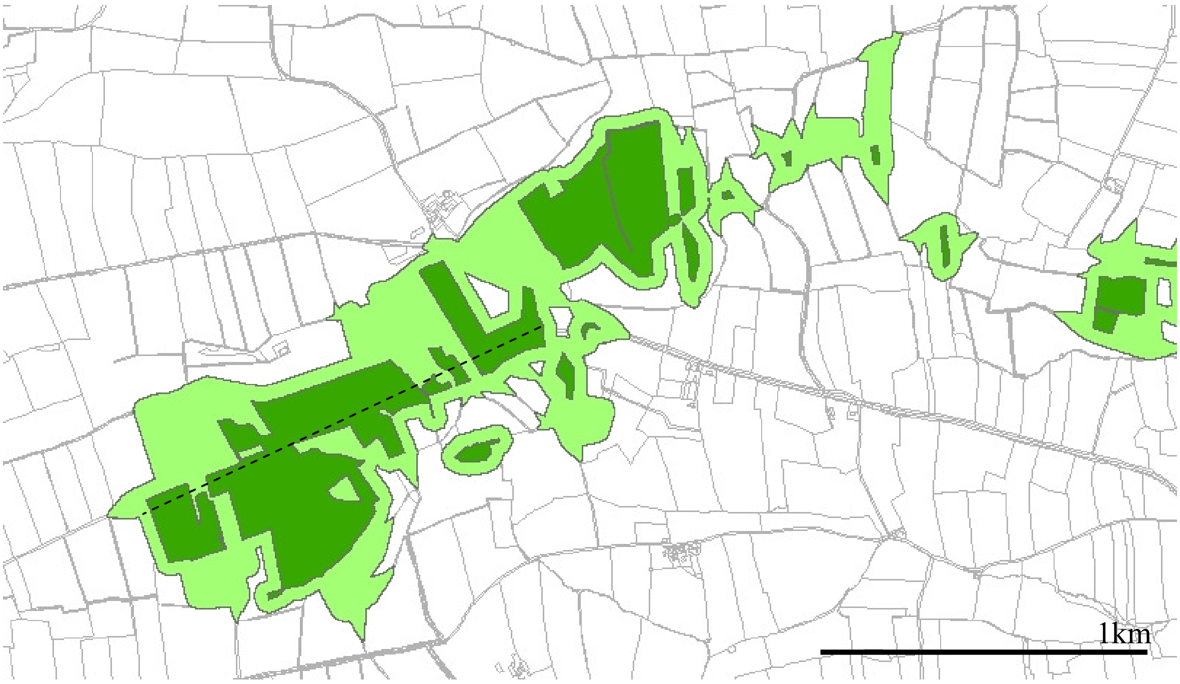
4.4. Combining BEETLE and Vortex software to model a range of landscape management scenarios that will maintain a viable population

The combination of Vortex and BEETLE modelling has enabled two habitat networks to be identified which could both potentially sustain a viable population of red squirrel on the Solway Plain separately.

4.4.1. Finglandrigg network

Vortex revealed that the Finglandrigg network could provide enough habitat to sustain a viable population of red squirrels with an 8% probability of extinction, assuming that the population is using all of the 66ha of available habitat at a density of 0.65 squirrels ha^{-1} (Figure 9). As the visual survey was only carried out in fragment 23 and not in the other fragments which comprise the Finglandrigg network, red squirrel presence or absence is not known for the other fragments. If the red squirrel population only uses fragment number 23 and not the additional habitat shown within the Finglandrigg network, the red squirrel population in this area would face an 80% probability of extinction. The large difference in extinction probability results caused by reducing habitat usage by 22ha indicates that the minimal dynamic area (MDA) of the Solway Plain red squirrel population should not be any lower than 66ha of good red squirrel habitat to sustain a viable population. Even if red squirrels are not present in the additional fragments the initial population concentrated within fragment 23 may start to colonize the other woodland fragments within the Finglandrigg network. If this occurs then the population would face a 13 % probability of extinction.

Figure 9. Finglandrigg network 4km. Note: Dark green areas represent red squirrel habitat, light green areas show potential dispersal areas the habitat networks created by the BEETLE modelling. The dashed line shows the transect.

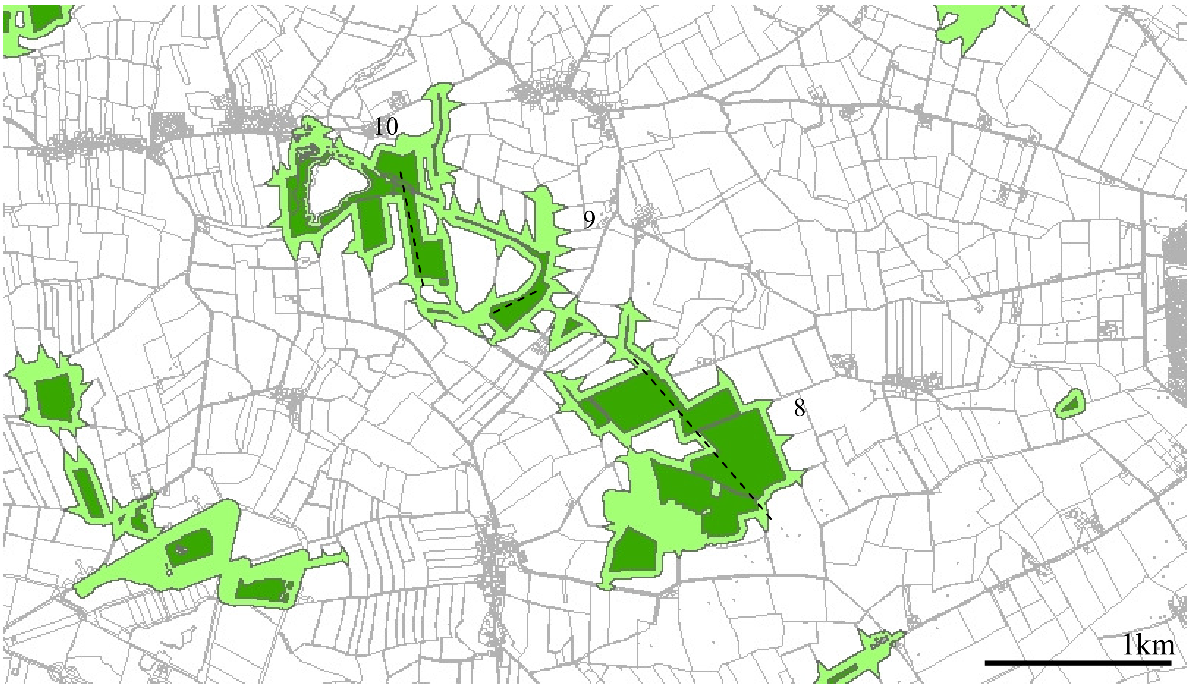


4.4.2. Thurstonfield Orton Moss network

As the minimum dynamic area for squirrels on the Solway Plain is estimated to be 66ha and the Orton moss network has a total of 63.72ha of habitat, the habitat area of this network needs to be increased to meet the MDA. Vortex revealed that if the two woodland fragments (9 and 10) which comprise the Thurstonfield network each had a population density of 0.65ha^{-1} squirrels in each woodland fragment, the population would have a 100% probability of extinction.

As the non-viable Thurstonfield network and the potentially viable Orton Moss network are separated by a Euclidean distance of 10m it could be possible to join the two networks together by adding a small amount of woodland to create one large network with a total habitat of 93.68ha. Assuming that these networks are connected and that each fragment contains a red squirrel density of 0.65ha^{-1} the probability of extinction would be 1%. However, although red squirrel signs have been recorded in woodland fragments 8, 9 and 10 previously, during this survey squirrel presence was only recorded in woodland 10 (located within the Thurstonfield network). This being the case and the red squirrel have an initial population starting at woodland 10 at a density of 0.65ha^{-1} squirrels and assuming the population would expand into the other fragments the population within the joined networks would have a 0 % probability of extinction.

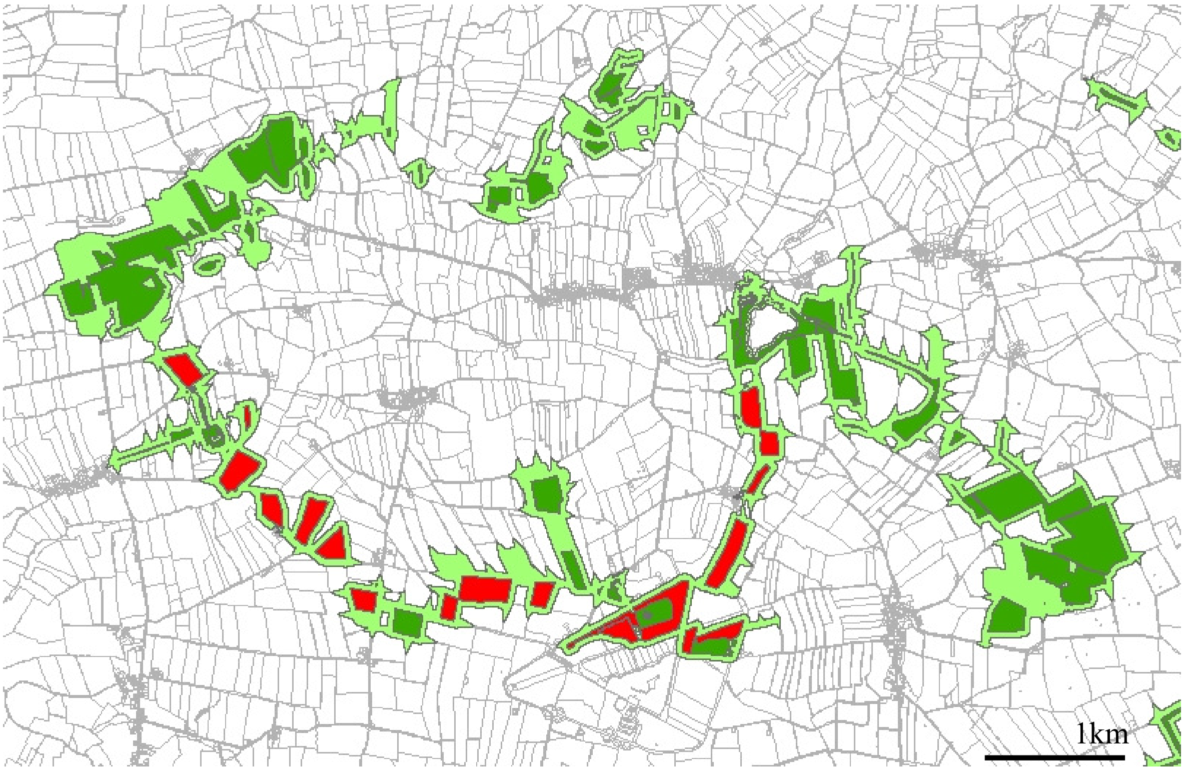
Figure 10. Thurstonfield Orton Moss network at a dispersal distance of 4km. Dark green areas represent red squirrel habitat, light green areas represent dispersal areas in the habitat networks created by the BEETLE modelling. The black dashed line represents the area surveyed.



4.4.3. Connecting woodland fragments with red squirrel presence to a viable population

The Finglandrigg network, Thurstonfield Orton Moss network, woodland 13, woodland 16 and woodland 21 all have had red squirrels sightings or hair samples within part of them. By including all future habitat as well as additional new woodland habitat the BEETLE modelling has indicated that the networks could be connected, enabling each woodland with red squirrel presence to be functionally connected to one of the two viable populations networks (Figure 11). The two viable networks may be functionally connected if the gap between the two newly created networks is closed by planting additional woodland in its place (Figure 11).

Figure 11. BEETLE future red squirrel habitat networks 4km. Future scenarios include the existing woodland which will be mature in 50 years and additional woodland fragments which, if planted now, will potentially aid in future red squirrel dispersal between networks (newly matured and new woodland shown in red). Dark green areas represent existing red squirrel habitat, light green areas indicated potential dispersal in the habitat networks produced by BEETLE.



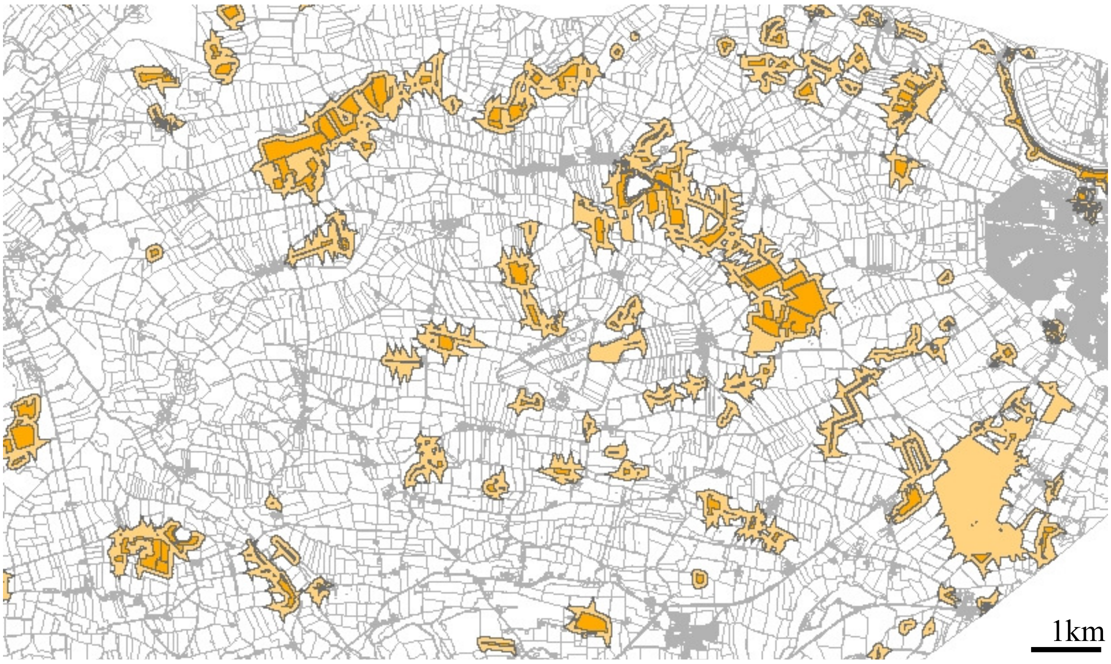
4.5. Modelling the likely movement of the grey squirrel into the Solway plain and red squirrel viability under a range of grey squirrel pressures

4.5.1. Modelling the likely movements of grey squirrels

Modelling the functional connectivity of grey squirrel habitat at a maximum dispersal distance of 2 km revealed a similar functional connectivity of woodland fragments as for the red squirrel, with woodland fragments 21 and 22 forming a network and woodland fragments 23 and 13 being functionally connected to small woodland fragments which were not included within the survey. However, the landscape types have slightly lower costs applied to them for the grey squirrel than for the reds, reflecting how grey squirrels are considered to disperse through the landscape, and therefore woodlands 9 and 10 are also functionally connected at this distance for the grey squirrel (Figure 12 and Figure 6). When the maximum dispersal distance is increased to 4km, 7 habitat networks are created for the grey squirrel, two more than created for the reds at this dispersal distance (Figure 13 and Figure 8). The networks which would provide the red squirrel with viable populations (Finglandrigg network and Thurstonfield Orton Moss network) are also functionally connected networks for the grey and will therefore potentially be used by the grey squirrel if they are present or if they enter the area.

Figure 12. BEETLE grey squirrel habitat network for 2km. Dark orange areas represent habitat and light orange areas the habitat networks created with the BEETLE modelling

Figure 13. BEETLE Grey squirrel habitat network for 4km. Dark orange represents existing grey squirrel habitat and light orange areas the habitat networks created with the BEETLE modelling.



Adding woodlands to increase functional connectivity for the red squirrels will also provide the grey squirrels with habitat which will aid in their dispersal across the landscape (Figure 14). Although the additional habitat may not be favoured grey squirrel habitat it will provide dispersal routes into the area, reflected in the model by a relatively low associated cost. The BEETLE modelling shows that although the grey squirrel habitat networks include most of the additional habitat, there are 4 fragments which are not included at this dispersal distance.

Based upon recent sightings of grey squirrel within woodland fragments 8, 23 and the area surrounding Thurstonfield (O'Hare 2005, Tullie House 2007) the maximum dispersal distance was increased and modelled at 8km and 12km to see if these larger dispersal distances can account for the sightings. The networks produced from these larger dispersal distances indicated that there are mainly two possible routes into the area, following the closest linked habitat networks across the landscape matrix from the southeast and northeast (Figures 15 and 16). Movements from the southeast could result in woodland fragments 7, 8, 9, 10, 11 and 12 being subject to grey squirrel colonization. Many small fragments to the west of Carlisle could possibly enable colonization from this direction. The woodland fragments to the south and west of the survey area remain highly fragmented even at these larger dispersal distance and this suggests that these will be the least likely directions the grey squirrel will take. The closest habitat network connections occur from the southeast and therefore this is possibly the most likely direction for grey squirrel movements.

Figure 14. BEETLE grey squirrel habitat networks 4km with the potential new red squirrel woodlands. Dark orange areas represents existing grey squirrel habitat, light orange areas the habitat networks created with the BEETLE modelling. Red woodlands indicate the additional woodlands which would not aid in grey squirrel dispersal at this dispersal distance.

Figure 15. BEETLE Grey squirrel habitat network 8km. Dark orange areas represent existing grey squirrel habitat and light orange areas the habitat networks created with the BEETLE modelling.

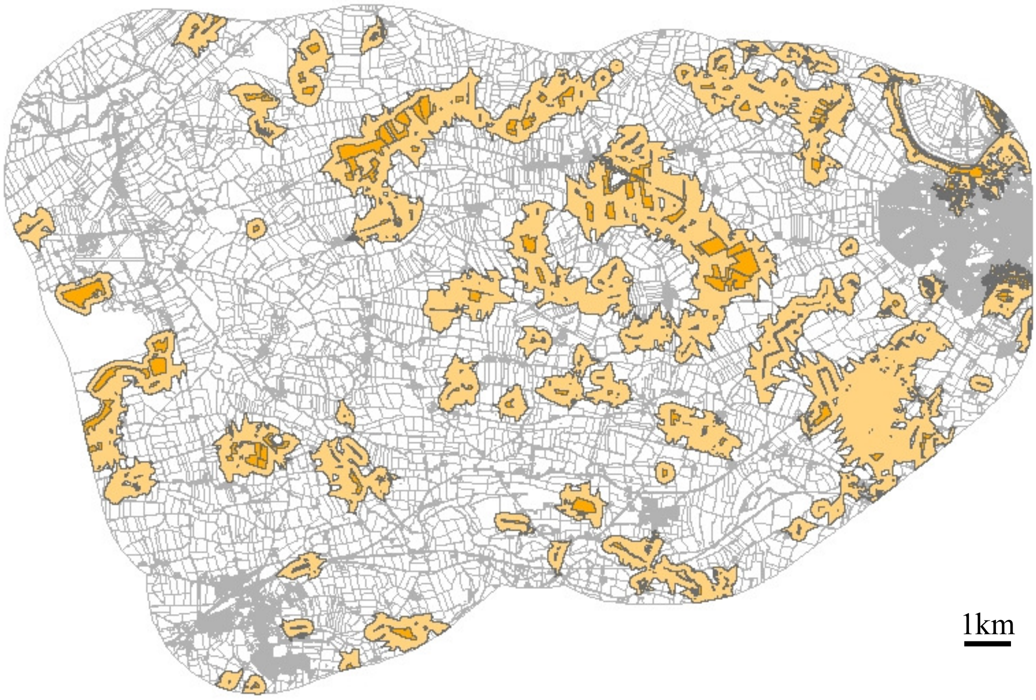
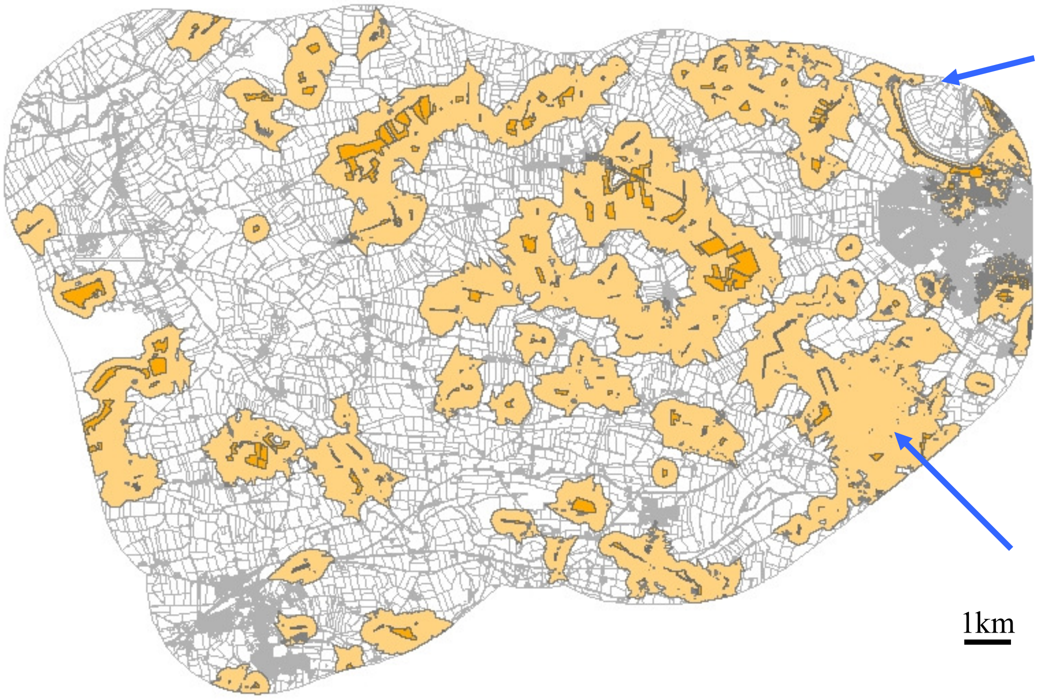


Figure 16. BEETLE Grey squirrel habitat network 12km. Dark orange areas represent existing grey squirrel habitat and light orange areas the habitat networks created with the BEETLE modelling. The blue arrows represent the possible directions of grey squirrel colonization of the Solway Plain fragmented woodland ecosystems.



4.5.2. Red squirrel viability under grey squirrel pressures

The Outbreak modelling reveals that once the small viable red squirrel populations within the Finglandrigg network and the Orton Moss network are subject to high exposure of the SQPV, the populations have a high risk of infection and would go extinct within 1 year of exposure.

5. Discussion

5.1. Mapping red squirrel usage of fragmented woodlands

The knowledge gained from the Vortex and BEETLE modelling can aid in conservation management decisions. The models results are reliant on the accuracy of the information available and gathered on the red squirrel and Solway Plain landscape matrix at the time of this study. It is therefore essential that conservation decisions concerning the population are based upon a combination of current relevant literature, field work and computer modelling.

Squirrel usage of woodland fragments has been shown in previous studies to be influenced by certain factors such as habitat quality, woodland size, distance to a source population, degree of habitat fragmentation and competition (Wauters & Dhondt 1992; Verboom & van Apeldoorn 1990; Rodriguez & Andren 1999; Walters & Gurnell 1999). There may be multiple reasons why red squirrels are not present in all 23 woodland fragments of the Solway plain, some of these reasons can be suggested from the results of the field work.

A previous study has revealed that there is an association between the presence of red squirrels and Scots pine on the Solway Plain. The same study also showed red squirrel usage of unusually small woodland fragments which are lower than 3.5ha (O'Hare 2005). The surveys in this study confirm that red squirrels are using woodland fragments ranging in size from 1.8ha to 63.75ha with 50% of woodlands used at the present time being <3.5ha. They also revealed a change in woodland usage from 2005 to 2007 as woodlands 13 and 16 had not previously been recorded as having red squirrel presence (O'Hare 2005). As red squirrel are now recorded in woodlands 13 and 16, which are both <3ha it can now be assumed that the small woodland fragments are important resources for the red squirrel in this landscape matrix and therefore it is important that they remain intact.

Although there is an association with Scots pine and red squirrel presence, red squirrels were not seen in woodland fragments 1, 3, 8 and 13 even though Scots pine was present. Red squirrel sightings were absent from woodlands 1 and 3, most likely due to the apparent high fragmentation of these particular woodlands (see 5.3). Woodland 1 is also comprised largely of peat bog and contains very wet boggy soil, as Verbeylen et al.'s (2002) study noted that woodlands with very wet soil were never occupied by red squirrels this too could account for the red squirrel absence in this fragment. Woodland 22 was the only woodland with Scots pine that did not contain any squirrel sightings or evidence of feedings signs, however as squirrels choose their home range in relation to tree species composition (Gurnell et al. 2004) squirrels may have by passed this fragment in favour of woodland 21 which is in close proximity and is a higher quality habitat with predominantly Scots pine. An important consideration occurs with the absence of red squirrels in woodland 8 and 9 during this study, which had previously been recorded as having red squirrel presence in 2005 (O'Hare 2005). Most surprisingly no red squirrel sightings or hair samples were recorded in woodland 8 (Orton Moss) even though this woodland has had red squirrel sightings recorded in it for many years (O'Hare 2005; Tullie House 2007). As grey squirrels have recently been recorded within woodland 8 this change in woodland fragment usage by the red squirrel may indicate that the red squirrel population are suffering interspecific competition with the grey squirrels (Walters & Gurnell 1999) or have contracted parapoxvirus and are being displaced in these fragments. This would need further investigation, however if this is the case and red squirrels do not return to woodland 8 which is the largest woodland fragments within the study area (63.72ha), this may have a detrimental effect on the red squirrel population viability in the Solway Plain. It may be more appropriate that conservation efforts focus primarily on the woodland with actual red squirrel presence and conduct additional research into why the red squirrels woodland usage has changed over the two years.

5.2. Vortex population viability analysis

The initial Vortex analysis revealed that when individuals are forced to disperse between the fragmented woodland ecosystems on the Solway Plain the probability that the population faces extinction increases rapidly. The dispersal distance entered into Vortex was based on individuals dispersing away from their natal home range moving a maximum Euclidian distance of 4.1km (Verbeylen et al. 2003). Squirrels may move further than this distance however 4.1km is thought to be the maximum distance moved (Verbeylen et al. 2003), with the majority of squirrels dispersing within 1km of their natal range in fragmented landscapes (Rodriguez & Andren 1999). Rodriguez and Andren (1999) also predict dispersal distances of as little as 600m in fragmented landscapes. If this prediction is correct, then it is not surprising that dispersal would cause extinction on the Solway Plain woodlands that are used by the red squirrel or had feeding signs are mostly more than 600m apart, squirrel would therefore not be able to reach them.

Vortex modelling has revealed that the fragmented woodland ecosystems would not hold a viable population if individuals are dispersing between all woodlands of red squirrel habitat or if they are dispersing between only the woodlands with red squirrel presence. However, it does not take into account woodland fragments which are connected by habitat corridors and small woodland patches which are in commuting distance of each other and comprise a squirrels home range. These home ranges may be comprised of numerous woodland fragments and may be large enough to sustain a viable population of red squirrels without the need of natal dispersal. Verbeylen et al. (2003) class woodland fragments which are up to 160m apart as one habitat because squirrels are able to move easily between them if they are connected by tree rows or hedgerows. In this study the BEETLE modelling is able to represent woodland fragments which are functionally connected and which may therefore show the composition of a squirrel's home range.

5.3. Modelling functional connectivity using BEETLE

The dispersal distance which is entered into the BEETLE model represents an estimation of the distance a squirrel is considered to be able to move from a woodland fragment when foraging or searching for potential new areas of habitat, modified by the land cover permeability scores The dispersal distance therefore includes the distance needed to return to the home fragment but is not based on the maximum natal dispersal distance as these are one way movements. During a homing experiment squirrels have been recorded moving 2.375km in <15hours (Verbeylen et al. 2003). The 2km BEETLE analysis can therefore represent the maximum daily movements of a squirrel. Research has also shown that squirrels can cover 4.1km in a few weeks (Verbeylen et al. 2003) and although it has been shown that individuals dispersing away from their natal range may reach up to 4.5km (Rodriguez & Andren 1999), the 4km dispersal distance in the BEETLE modelling includes the distance of the return journey. The 4km analysis therefore includes squirrels which are perhaps searching for potential new food resources.

The results from the 2km BEETLE modelling indicated that during a foraging day, the squirrels movements are concentrated near to its home woodland fragment, only venturing short distances (in places <100m) away from the woodland in to the surrounding landscape. The 4km modelling also indicated that the squirrel movements are concentrated around the woodlands although they are shown to move slightly further into the landscape (up to 300m) at this distance. In the field Verbeylen et al. (2003) have observed squirrels commuting distances of between 50 – 160m between woodland fragments with the uses of tree and hedgerows within fragmented landscapes. The concentrated movements shown in the BEETLE modelling are therefore highly probable, which means that some of the 23 woodland fragments on the Solway plain are highly isolated in terms of functional connectivity.

The landscape matrix surrounding each of the woodland fragments in the Solway Plain have low permeability as the majority of the landscape is agricultural or arable land (LCM 2000). As squirrels are seen to use tree and hedgerows in this type of landscape (Verbeylen et al. 2003) it can be assumed that the remaining woodland fragments which are not part of a habitat network are either too isolated or there are not enough suitable dispersal routes to provide connection. The habitat networks created within the 2km and 4km modelling all contain woodland fragments that are in close proximity to each other, although the land cover between some of the fragments has low permeability, the habitat networks created by BEETLE indicate that the squirrels are likely to move across the short distances of low permeability to reach the adjoining woodland fragment. It can therefore be assumed that squirrels are more likely to commute between woodland fragments in the Solway Plain if the woodland fragments are in close proximity to each other (up to 300m) and if the connecting landscape includes tree or hedgerows which are considered as highly permeable. Conservation management decisions of any habitat network which has red squirrel presence should take these small commuting distances into account ensuring that the habitats which are chosen as conservation areas or any additional woodland fragments are within this distance.

5.4. Using a combination of Vortex PVA and BEETLE to maintain a viable population of red squirrel on the Solway Plain

5.4.1. Population viability and landscape management considerations for Finglandrigg network

Finglandrigg network is one of the three largest habitat networks chosen from the 4km BEETLE modelling for further analysis. The network can be classed within the Vortex modelling as a continuous habitat as each fragment is indicated to be functionally connected within the BEETLE modelling. Vortex modelling revealed a viable population would only be sustained in the Finglandrigg network if the squirrels use all 66ha of available habitat starting with an initial population size of 30 individuals estimated to inhabit woodland 23. As the remaining woodland fragments that comprise the Finglandrigg network have not been confirmed as having red squirrel presence they are not included in the initial population size. The woodland usage however is based upon the assumption that the red squirrel population would start colonising all of the fragments that comprise the Finglandrigg network using all of the 66ha of available habitat. Further investigation in the field may reveal that red squirrels are already established within these other fragments which would therefore increase the initial population size of the Finglandrigg network. However if they are not present within the other fragments in the network and as Vortex estimates that the red squirrel population would face extinction if they remain only within woodland 23, conservation efforts need to focus on encouraging red squirrel to use all of the available 66ha of woodland habitat as this is the MDA for red squirrel woodland on the Solway Plain.

Although the BEETLE modelling indicated that the woodland fragments that comprise the Finglandrigg network are functionally connected, it is important to remember that the habitat networks created using the BEETLE modelling represent the potential areas of movement across the landscape matrix. Therefore encouraging the red squirrels to use the entire Finglandrigg network's woodland fragments will also involve encouraging the squirrels to move in certain directions and to use suitable highly permeable land cover types such as hedgerow or tree rows (see 5.4.4.). This is essential as these sorts of land cover types have a lower predation risk for the squirrel compared with crossing open ground. None of the surrounding landscape parcels would need to change usage for this network to be viable; however, existing hedgerows and woodland habitat should be improved in favour of the red squirrel (see 5.4.4). It may also be necessary to provide additional trees or hedgerows to aid in dispersal between some of the surrounding small woodland fragments. One of the most noticeable barriers which may cause squirrel causalities in this network is the B530 road which is located just to the north of fragment 23. Although the road does not restrict the functional connectivity of the Finglandrigg network in the BEETLE modelling squirrel populations are susceptible to road casualties. It would therefore be beneficial to encourage the squirrels to use the rope bridge which is already situated on this site which will enable them to cross the road safely minimising the risk of fatalities.

5.4.2. Population viability and landscape management considerations for the potential Thurstonfield Orton Moss network

The creation of a 93.68ha Thurstonfield Orton Moss network would provide a viable population of red squirrel on the Solway Plain, as long as the squirrels use the entire available habitat. As with the Finglandrigg network squirrel presence within the potential Thurston Orton Moss network was only confirmed in one of the fragments which comprise the network, therefore the squirrel population will need to be encouraged, through the correct habitat management to use the additional fragments to increase the population size. Unlike the Finglandrigg network red squirrels have previously been found within two of the other fragments which comprise this network. The reason or reasons why they are no longer using these fragments or were missed during the surveys would need further investigation. If it is due to interspecific competition with the grey squirrel, as suggested in section 5.1, then to maintain a viable population of the reds the greys would have to be removed as suggested by Pepper and Pattenson (2001).

The initial first step to enable the Thurstonfield and Orton Moss networks to function as one functionally connected network would be the addition of a small woodland fragment planted to close the small gap between the two networks. As a road also separates the two networks rope bridges should be put in place to avoid unnecessary squirrel road casualties. The land cover in between each of the woodland fragments within this newly created network will need to contain hedgerows and tree rows and have a species composition which would encourage red squirrel usage and movements in and between all the woodland fragments. It may be possible to change the usage of the land cover that is in between the woodland fragments to create additional small woodland fragments providing additional highly permeable areas within the landscape. However as the addition of one woodland fragment would potentially functionally connect the networks and as the land in between the woodlands is agricultural it may be better to focus on creating additional tree rows and thicker hedgerows first rather than changing the usage of whole parcels of land. This would also enable red squirrel population monitoring to see whether squirrels will actually return to the fragments.

5.4.3. Connection of woodlands with red squirrel presence through additional planting of woodland

Ideally all the woodland fragments with red squirrel presence should be functionally connected to one of the viable populations, as the smaller the population the more vulnerable it becomes to extinction (Trizio et al. 2005). Modelling the landscape using BEETLE has indicated that there is potential to connect Finglandrigg network and Thurstonfield Orton Moss network to create one large functionally connected network of >200ha by additional woodland planting. This would meet Pepper and Patterson's (2001) suggestion that 200ha of coniferous habitat is needed to maintain a small viable population of red squirrels within a fragmented landscape. The provision of additional woodland would clearly depend upon the landowners consent; however it would be detrimental to leave the red squirrel populations within the small woodland fragments of 13, 16 and 21 functionally unconnected to any viable networks (Pepper & Patterson 2001). If possible woodland 21 should be functionally connected to Finglandrigg network and woodlands 13 and 16 to Thurstonfield Orton Moss network. The BEETLE modelling has indicated that to functionally connect Finglandrigg network to woodland 21 one additional woodland fragments will be needed. Connecting woodland 13 and 16 to Thurstonfield Orton Moss network would involve the planting of at least six woodland fragments, if this amount of planting is unlikely to get consent then woodland fragments 13 and 16 should at least be functionally connected to the woodlands contained within Watchtree Nature Reserve.

5.4.4. Woodland, tree row and hedgerow management

Each of the woodland fragments, tree rows and hedgerows need to contain a species composition which favours the red squirrel by providing enough food resources and continuous cover to provide support throughout the year and provide connection (Gurnell & Pepper 1993). It is suggested that large seed broadleaves should be removed from woodlands which are to be managed for red squirrel conservation or at least any additional planting of large seeded broadleaved species should be avoided so not to attract any grey squirrels (Gurnell and Pepper 1993). Hedgerows ideally should also contain tree rows or small woodland patches every 100m with species such as Scots pine. As this is the favoured tree species (Halliwell 1997) it will not only encourage the squirrel to use the habitat corridor to move between woodland fragments but it will also provide food resources along the corridors to keep energy levels up whist commuting.

5.5. *Modelling grey squirrel movements and pressures*

It is important to note that no catastrophes have been included in the Vortex modelling of Finglandrigg network or the Thurstonfield Orton Moss network up to this point. By subjecting the populations to the SQPV the apparently viable networks become highly vulnerable populations and face extinction. It has been suggested that a combination of SQPV and interspecific competition have lead to the decline of the red squirrels within the UK (Ruston et al. 2000). Gurnell and Pepper (1993) have suggested that the primary ecological requirement for red squirrels is the absence of greys. On the Solway Plain the removal of any grey squirrels is particularly crucial if a viable red squirrel population is to be sustained, grey squirrels have already been able to enter the Solway Plain landscape matrix and may have already out competed the red squirrel in Orton Moss (woodland 8) if they also bring SQPV it would not be possible to sustain a viable population of red squirrels on the Solway Plain.

The BEETLE modelling has indicated the potential movement of the grey squirrel in to the Solway Plain and has enabled the identification of certain areas of concern. Grey squirrel removal and monitoring should focus primarily on the two potential routes for greys squirrel colonization which were derived from the 12km grey squirrel BEETLE modelling (Figure 16). A serious threat to the future of red squirrels on the Solway would occur if grey squirrels which disperse into the Solway Plain are carrying SQPV and infect one of the viable populations. As long as they are removed and the disease does not spread to the other population it may be possible that squirrels would either be able to recolonise the woodland fragment or be reintroduced. Connecting Finglandrigg network and Thurstonfield Orton Moss network together by additional planting of woodlands would increase the likelihood that infected red or grey squirrels will be able to infect both populations causing extinction in both networks. Due to this and the recent grey squirrel sightings on the Solway Plain it may be more beneficial to keep the two networks functionally unconnected. Whilst connection would increase the available habitat area to >200ha it may aid in grey squirrel colonization and increase the likelihood of red squirrel encounter with SQPV infected individuals.

6. Conclusion

Modelling the functional connectivity of the woodland fragments on the Solway Plain has revealed how highly fragmented the majority of the woodland fragments are within the landscape matrix. A combination of Vortex and BEETLE modelling has revealed that the red squirrel population which is currently at an estimated density of 0.65 squirrels ha^{-1} will need a minimum dynamic area of 66ha to be viable. The BEETLE modelling has enabled two potentially viable networks to be identified Finglandrigg and Thurston Orton Moss networks; however the viability of both networks will depend upon the red squirrels using the entire available habitat of the networks. Squirrels are likely to commute less than 300m between woodland fragments, therefore it is essential that each woodland fragment within the viable networks is connected by land cover that does not hinder potential movement. Although these viable networks can possibly be functionally connected to include all of the woodland fragments that were found to have red squirrel presence by planting additional woodland, the BEETLE modelling has indicated that these added woodlands have the potential to aid in grey squirrel colonisation of the area. If the viable population are then exposed to the lethal SQPV both the Finglandrigg network and the

Thurstonfield Orton Moss network would face extinction within one year. The two potentially viable networks need to be managed to increase red squirrel numbers and movements, whist protecting these population from the incursion of the grey squirrel.

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