Using remote activated cameras to estimate relative abundance and habitat preference of red squirrels (*Sciurus vulgaris*) [Redacted]

Report No: 672

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Report series:	NRW Evidence Report Series
Report number:	672
Publication date:	February 2023
Contract number:	RS-2021
Contractor:	Bangor University
Contract Manager:	Huw Jones
Title:	**Using remote activated cameras to estimate relative abundance and habitat preference of red squirrels (*Sciurus vulgaris*)**
Author(s):	Shannon, G., Valle, S. & Shuttleworth, C.M.
Technical Editor:	Liz Halliwell
Quality assurance:	Tier 3
Peer Reviewer(s):	Liz Halliwell and Rebecca Clews-Roberts
Approved By:	Huw Jones
Restrictions:	None

Distribution List (core)

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Organisation, Location

Organisation, Location

Organisation, Location

Organisation, Location

Individual, Organisation

Individual, Organisation

Individual, Organisation

Recommended citation for this volume:

Shannon G, Valle S & Shuttleworth CM. 2022. Using remote activated cameras to estimate relative abundance and habitat preference of red squirrels (*Sciurus vulgaris*). NRW Evidence Report Series. Report No: 672. 40pp.

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Crynodeb Gweithredol

Mae’r adroddiad hwn yn cyflwyno dull o fonitro niferoedd cymharol y gwiwerod coch (*Sciurus vulgaris*) mewn coedwigoedd conwydd gan ddefnyddio camerâu a gaiff eu gweithredu o bell. Buom hefyd yn ymchwilio i gysylltiadau’r cynefinoedd o'r data a gasglwyd mewn dwy goedwig (Niwbwrch a Phentraeth) ar Ynys Môn. Cafodd cynefinoedd coetir eu categoreiddio’n rhai llydanddail, conwydd 0-19 oed, conwydd 20-40 oed a chonwydd. >40 oed. Dewiswyd 50 pwynt samplu ledled y pedwar categori cynefinoedd ac fe gasglwyd data manwl am strwythur y coetir mewn pum llain ofodol ym mhob lleoliad samplu. Gwelsom gydberthynas gref (r = 0.78) rhwng nifer y gwiwerod coch unigol a gafodd eu dal yn fyw dros ddeg diwrnod â nifer y delweddau camera o’r rhywogaeth a recordiwyd mewn cyfnod blaenorol o bum niwrnod o fonitro o bell. Roedd y cyfnod rhwng gosod y camera a’r ddelwedd a recordiwyd gyntaf o wiwer goch hefyd yn dangos cydberthynas negyddol sylweddol (r = -0.39) â nifer yr unigolion a gafodd eu dal yn fyw. Mae ein canlyniadau’n dangos y gall camerâu a weithredir o bell fod yn arf addas ar gyfer monitro poblogaeth y wiwer goch ledled ystod o ddwyseddau anifeiliaid a chynefinoedd coetiroedd.

Roedd cysylltiad negyddol rhwng mynegeion ffyniant niferoedd cymharol gwiwerod coch a natur agored y canopi clystyrau, ac roedd presenoldeb pinwydd yr Alban a chynnydd yn amrywiaeth rhywogaethau’r coed yn gysylltiedig mewn modd cadarnhaol â ffyniant y gwiwerod. Roedd gwahaniaeth cryf hefyd rhwng safleoedd a oedd yn adlewyrchu niferoedd cymharol isel o wiwerod coch yn Niwbwrch o’i gymharu â Phentraeth. Coed bedw a welir amlaf mewn coed llydanddail ac roedd y categori cynefinoedd hwnnw’n tueddu i adlewyrchu addasrwydd isel o ran y gwiwerod coch. Mae’r ffaith nad oes cydberthynas gref rhwng oedran y clystyrau conwydd a niferoedd y gwiwerod yn debygol o adlewyrchu’r teneuo trwm ar glystyrau aeddfed yn Niwbwrch a’r lleihau ar gysylltedd brigdyfiant y coed. Archwilir effeithiau rheoli clystyrau presennol yn y dyfodol, a thrafodwn ein canfyddiadau mewn perthynas ag ymchwil cyhoeddedig.

Executive summary

This report presents a method for monitoring the relative abundance of red squirrels (*Sciurus vulgaris*) in coniferous forests using remotely activated cameras. We also investigated habitat associations from the data, which were collected in two forests (Newborough and Pentraeth) on Anglesey. Woodland habitats were categorised as broadleaf, conifers 0-19 years of age, conifers 20-40 years of age and conifers >40 years of age. A total of 50 sample points were selected across the four habitat categories and detailed woodland structure data was gathered at five spatial plots at each sampling location. We found a strong correlation (r = 0.78) between the number of individual red squirrels live-trapped over ten days with the number of camera images of the species recorded during a previous five-day period of remote monitoring. The interval between camera deployment and first recorded image of a red squirrel also showed a significant negative correlation (r = -0.39) with the number of individuals live-trapped. Our results

demonstrate that remotely activated cameras can provide a suitable tool for red squirrel population monitoring across a range of animal densities and woodland habitats.

Red squirrel relative abundance indices were negatively related to stand canopy openness, while the presence of Scots pine and increased tree species diversity were positively related to squirrel abundance. There was also a strong site difference reflecting relatively low red squirrel abundance at Newborough compared with Pentraeth. Broadleaved woodland was often dominated by birch and this habitat category tended to reflect low suitability for red squirrels. The lack of a strong correlation between the age of conifer stands and squirrel abundance is likely to reflect the heavy thinning of mature stands at Newborough reducing tree crown connectivity. The future impacts of current stand management are explored, and we discuss our findings in relation to published research.

Introduction

Red squirrel ecology and forest management

The red squirrel (*Sciurus vulgaris*) is a small native rodent with morphology reflecting adaptation to a forest environment (Shorten 1954, 1962). Adult body weights are typically 270-320g (Tonkin 1983, Holm 1991, Lurz & Lloyd 2000, Wauters & Dhondt 1989), and their diet is dominated by tree seeds but also includes secondary food items such as tree flowers, tree buds, fungal fruiting bodies, insect larvae and, occasionally, bird's eggs and carrion (Bertolino et al., 2004, Mollar 1983, Krauze-Gryz & Gryz 2015, Ognev 1940, Sulkava & Nyholm 1987, Wauters & Dhondt 1992a). There is extensive literature on the diet and scatter-hoarding behaviours of red squirrels in both coniferous and deciduous forests (Lurz & Bosch 2012, Shuttleworth et al., 2015). In deciduous forests animals may put on 10% body fat for winter (Kenward & Tonkin 1986, Gurnell 1991). In contrast, in coniferous-dominated plantations, these increases in body weight are less likely to be observed, and it was postulated that this is because additional weight could adversely affect an individual's ability to forage for cones in the forest canopy (Lurz & Lloyd 2000). In deciduous habitats during late winter red squirrels are aloft in the treetops for only 18-53% of their active periods, as they concentrate on exploiting fallen tree seeds (Kenward & Tonkin 1986). The peak period of arboreal foraging, 80-92% of active time, occurs in the summer (Kenward & Tonkin 1986). When compared with introduced grey squirrels (*Sciurus carolinensis*), red squirrels' canopy activity is consistently higher throughout the year at an average of 67% compared with just 14% for the grey (Kenward & Tonkin 1986).

Squirrel densities fluctuate with annual changes in tree seed abundance (Lurz et al., 1995, Wauters et al., 2008). Higher population densities occur in habitats with a lower annual variation of seed availability (Wauters et al., 2008). Red squirrel densities are seldom greater than two animals/ha although there are a few notable exceptions, including Scots pine dominated Furzey Island with 6.19 ± 0.58 animals/ha (Kenward et al., 1998). Lurz et al. (1995) present average long-term densities of between 0.5 and 1.5 individuals/ha in both conifer and broad-leaved forests, and stress that year-to-year fluctuation can be large and vary with weather and the availability of tree seeds, particularly in monoculture plantation forest (Wauters and Lens 1995). Northern coniferous forests, including Sitka spruce-dominated plantations, have low numbers i.e. 0.02-0.2 animals/ha (Andrén and Lemnell 1992; Lurz et a1., 1995). Body mass, winter survival and reproductive success, are all correlated with tree seed production (Wauters & Dhondt 1989, Wauters & Lens 1995). Consequently, proactive forest management planning for red squirrels focuses on ensuring that enough preferred tree species are present (Slade et al., 2020).

Given that red squirrels are vulnerable to habitat fragmentation (Andrén & Delin 1994, Wauters 1997), another key management target is to maintain landscape connectivity between adjacent woodland habitats (White et al., 2016). Within each discrete woodland, tree canopy structure and inter-crown connectivity must be sufficient to facilitate efficient movement and foraging activity, which also reduces predation risk by minimising the need for travel across the forest floor (Jones et al., 2016, Dylewski et al., 2021). Studies in the 1990s demonstrated that heavy thinning of mature Scots pine (*Pinus sylvestris*) reduced the presence of red squirrels (Gurnell et al., 1997). Subsequently, Flaherty et al. (2012) quantified the importance of mean canopy closure and the total number of trees per plot as key structural variables and strongly recommended that forest canopy structure should be a primary management consideration where red squirrels were present. The evidence consistently shows that red squirrels prefer denser stands and avoid over-thinned and open stands (Gurnell et al., 2002). Therefore, ensuring sympathetic habitat management, especially within multi-objective forests, is a key element in national conservation strategies (Pepper & Patterson 1998, Wales Squirrel Forum 2018, Forestry Commission Scotland, 2012, Slade et al., 2020). This often involves mapping and forecasting how changes in categorised areas of different habitat suitability affect future abundance (Gurnell et al., 2002, Lurz et al., 2003, Shuttleworth et al., 2012, Jones et al., 2016). Predictive planning does of course not guarantee the expected output from scheduled forest operations and therefore it is important that 'ground-truthing' occurs regularly to quantify the actual impact upon red squirrel populations. For example, Flaherty et al. (2014) reported that when forest structure was surveyed and assessed, only 27% of the Abernethy Forest in Scotland was highly suitable for red squirrels.

There are currently three focal areas for red squirrel conservation in Wales: The Tywi Valley (Mid-Wales), Clocaenog Forest (NE Wales) and the island of Anglesey with a small adjacent associated mainland population (Wales Squirrel Forum 2018) (Fig. 1). Limiting the threats of competition (Wauters & Gurnell 1999, Wauters et al., 2000), stress (Santicchia et al., 2018) and disease transmission (Chantrey et al., 2014, McInnes et al., 2013, Rushton et al., 2006) posed by grey squirrels have been a crucial component of applied national conservation where these species are sympatric. However, it has been noted that a cost-effective monitoring tool to assess the effectiveness of grey squirrel control or woodland habitat management on red squirrel populations is lacking:

'*…implementation of effective monitoring of [red squirrel] population sizes at the focal sites has not been possible due to populations having a low density of squirrels over a wide area, particularly in the mainland focal sites. A cost-effective monitoring methodology that would be powerful enough to detect change in population size has yet to be identified.*' – Red Squirrel Conservation Plan Wales: Review of progress and update 2018 (Wales Squirrel Forum, 2018).

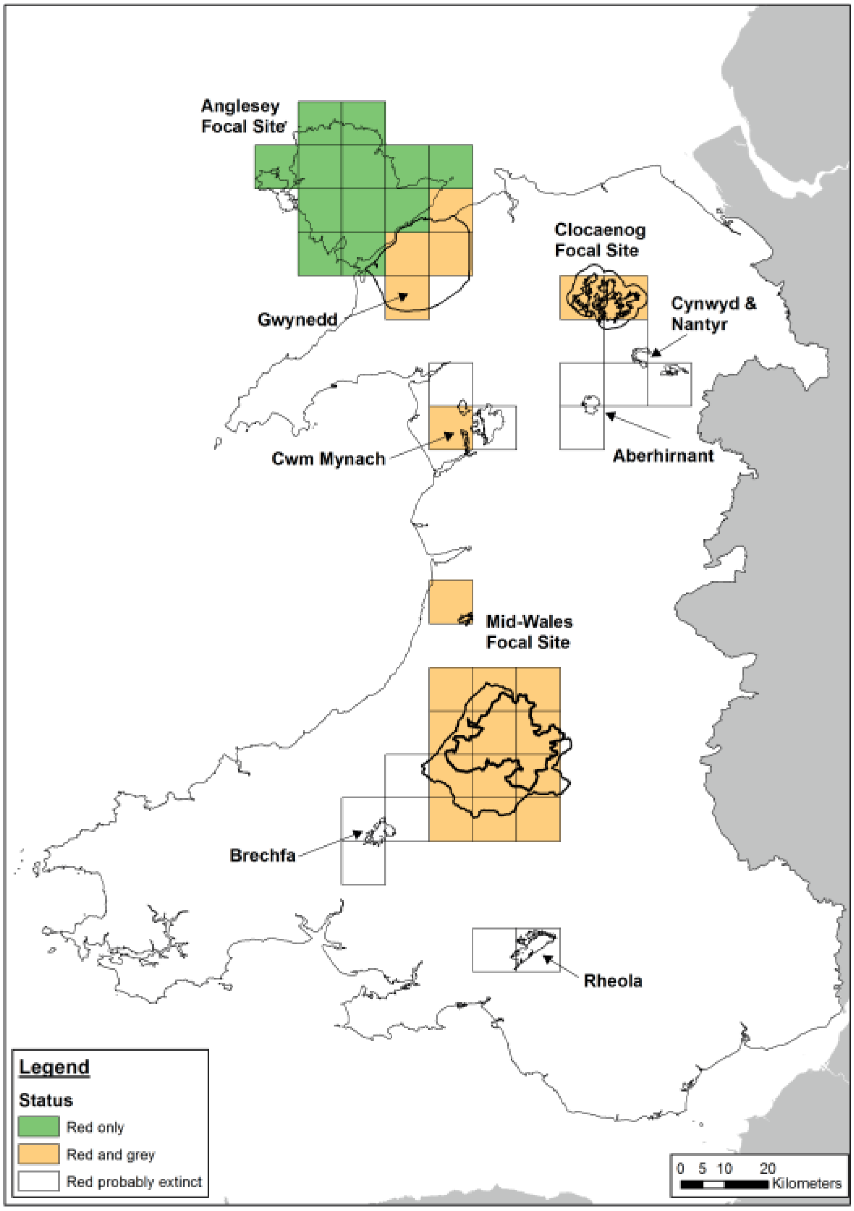

Figure 1. Red squirrel distribution in Wales (© European Squirrel Initiative)

Estimates of population size and trends in local abundance are essential for the development and coherence of conservation and management plans for any wild animal species (Primack 1993, Newson et al., 2008), and they form the cornerstones of the IUCN Red List scheme (IUCN 2022). Ideally, abundance estimates for conservation-important species should derive from high-quality data collected during standardised surveys (Boitani & Fuller 2000, Sutherland 2006). Such surveys should accumulate large numbers of records to allow precise abundance estimation and should account for differences in detectability across sites and species (Buckland et al., 2001). However, the number of species of conservation concern is high and the resources available are limited (James et al., 1999). Accurate estimates can be labour-intensive and invasive as in the case of small and medium-size mammals where the capture and handling of individuals are often required (Bertolino et al., 2009). Thus, there is a need for practical, rapid and inexpensive methods to provide reliable indices of animal abundance (Lancia et al., 1994, Parsons et al., 2021).

Mark-recapture studies provide a proven and effective means of determining local red squirrel populations (Holm 1991, Lurz 1995, Wauters et al., 2008). However, because of legal protections afforded to this species, operatives require a licence to live-capture, handle and mark the species. Trapping is also labour intensive and logistical considerations mean that the scale of any operation is spatially limited. Distance sampling along transects is not a reliable method with low squirrel denisities or in conifer plantations due to the very poor detectability and resulting paucity in sigthings (Gurnell et al. 2001, 2004). Hair-tube monitoring (sections of plastic drainpipe containing double-sided tape to catch body hairs of squirrels attracted by food bait) has historically been used as a non-invasive monitoring tool (Bertolino et al., 2009). However, although no licence is required, the method requires red squirrel hairs to be accurately identified from material caught on internal sticky pads. This time-consuming task requires technical skill and the use of magnification equipment. If grey squirrels are sympatric, then hairs need to be stained and cross-sectioned to confirm which sciurid species they were from. In Wales, red squirrels are frequently sympatric with grey squirrels (Halliwell et al., 2015). DNA testing of hairs collected for the identification of individuals is costly and time consuming (Foran et al. 1997, Trapp & Flaherty 2017).

The increasing technological sophistication, Improved reliability and affordability of Passive Infrared sensor (PIR) triggered wildlife surveillance cameras make their application in squirrel population monitoring attractive. Images can be individually data-logged and visible species identified and recorded without the need for laboratory studies. However, to the best of our knowledge, there are no published studies on the efficacy of camera trap studies as a means of estimating local red squirrel abundance and, to date, they have only been used in occupancy studies (e.g. Sheehy et al., 2018).

Project aims and objectives

This study aimed to provide Natural Resource Wales (NRW) with a robust, inexpensive and standardised method of determining red squirrel local abundance in commercial coniferous plantations. The contract specification required that the ‘annual survey should be deliverable and repeatable utilising no more than 150 hours of surveyor time’.

We defined the following objectives:

i. Determine the relationship between the number of camera trap images of red squirrels and data derived from live trapping at each sampling location.

ii. Investigate whether camera variables (time to first image capture and cumulative number of red squirrel images) provided robust measures of local red squirrel abundance.

iii. Quantify how trap-based estimates of red squirrel abundance relate to habitat characteristics (stand age, tree canopy openness, mean tree diameter at breast height and tree species present).

iv. Outline the strengths and limitations of a camera-trap protocol for monitoring relative abundance.

Methods

Site selection within Welsh Government forests

The study was undertaken in the commercial coniferous forests of Newborough forest (Coedwig Niwbwrch) and Pentraeth forest (Mynydd Llwydiarth) on the island of Anglesey, North Wales (Fig. 2). The forests were established in the late 1950s and early 1960s and contain first and second rotation coniferous stands with small areas of broadleaved woodland.

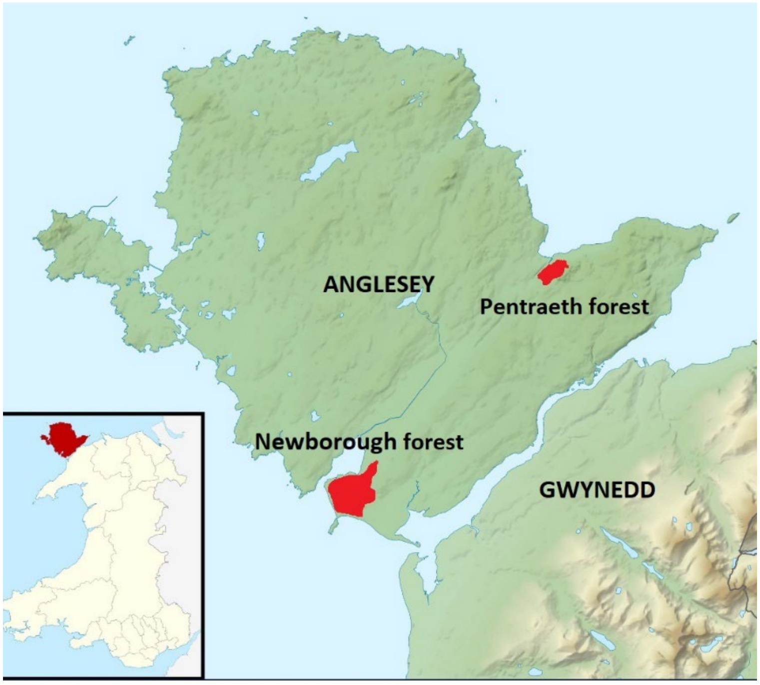

Figure 2. The location of study forests on the island of Anglesey (licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license https://creativecommons.org/licenses/by-sa/3.0/deed.en.Attribution: Contains Ordnance Survey data © Crown copyright and database right)

In the late 1990s, when grey squirrels were abundant on Anglesey, Pentraeth forest was the last woodland found to contain red squirrels (Shuttleworth 2003). Intensive grey squirrel island control facilitated local red squirrel recovery (Schuchert et al., 2014) and in 2004 red squirrels were reintroduced to Newborough forest (Shuttleworth et al., 2016). Anglesey does not currently have an established grey squirrel population, which means that woodland management options are not limited by the need to avoid planting tree species (e.g. oak and hazel), which benefit grey squirrels and exacerbate their competitive advantage over red squirrels (Lurz et al., 2004). However, Corsican pine, Scots pine and lodgepole pine stands are all vulnerable to Red Band Needle Blight (Dothistroma septosporum) (Brown et al., 2003). Consequently, continuous cover selective thinning was put in place in affected coniferous stands to open the forest canopy in order to reduce fungal infection rates by maximising air movement (Browne 2010).

The two island forests are very different. Newborough is 700 hectares of coastal habitat that is dominated by mature Corsican pine (*Pinus nigra*) and which has been heavily thinned in places. Natural regeneration is largely a mix of broadleaved species including the common birch (*Betula spp.*) and willow (*Salix spp.*), while Sycamore (*Platanus orientalis*), hawthorn (*Crataegus monogyna*) and cherry (*Prunus avium*) also occur but are much less common. Coniferous regeneration is limited to areas of Monterey Pine (*Pinus radiata*) and small areas of lodgepole pine (*Pinus contorta*). Both young conifer and older plantations of 20-40 years of age are relatively uncommon, and these are mostly dominated by Corsican pine.

Pentraeth is 244 hectares in size and is a mixture of Sitka spruce (*Picea sitchensis*), European larch (*Larix decidua*), Lodgepole pine and Scots pine. There are small but notable areas of mixed deciduous woodland dominated by beech (*Fagus sylvatica*), sessile oak (*Quercus petrea*) and wych elm (*Ulma glabra*). Young and 20-40 year old plantations are dominated by Scots pine, larch and Sitka spruce, sometimes in monoculture. There are also extensive areas of birch-dominated regeneration. In contrast to the selective thinning of pine at Newborough, coniferous stands in Pentreath are typically line thinned.

Survey design

NRW provided GIS layers for both forests. The information included the area, species composition and planting date for each coupe or spatial forest management unit. We categorised these into four stand types (Fig. 3 & 4, Table 1):

Table 1. Stand types with total extension area and percent of total across the two study sites

Category	Area (sqKm)	% of total
Broadleaved	0.651	7
Young Conifer (1-19 years of age)	0.452	4.8
Conifer 20-40 years of age	1.086	11.6
Conifers 40+ years of age	7.142	76.5

Where coupes had been planted with a mix of species (particularly in Pentraeth), we categorised them according to the dominant species i.e. ≥ 50% of the area planted. Ground truthing revealed that some stands had been clear-felled (see Fig. 3) and these areas were excluded from the study.

Figure 3. 1:25,000 Ordinance Survey map of Pentraeth forest (Mynydd Llwidiarth) with the stand categorisation used in this study

Figure 4. 1:25,000 Ordinance Survey map of Newborough Forest with the stand categorisation used in this study

We initially selected 50 sampling locations across the four stand type categories that would be as central to the coupe as possible (to be most representative of that stand type and least affected by adjacent ones i.e. furthest from the edge) and no less than 250 metres away from any other given sampling location (to maximise independence). Given that both Newborough and Pentraeth are characterised by a heterogeneous mix of different stand types, which vary greatly in size, it was not possible to locate the sampling locations at random without compromising their independence from each other and from adjacent habitats. An initial scoping site visit was conducted to establish their accessibility. Where terrain or site conditions prevented access, or where a point was close to a track or public footpath it was moved to the nearest appropriate location, which resulted in 20 sampling locations in Pentraeth and 30 in Newborough (Figures 3 & 4).

The four stand types differed in extent (Table 1) and therefore the number of sample plots per stand type varied i.e. 11 in Broadleaved, 8 in Young Conifer, in 10 Conifer 20-40 and 21 in Conifers 40+ years of age. At each sampling location, we collected data on vegetation structure and characteristics at its centre and at four equidistant (25 paces) points (see § 'Stand characteristics'). After having recorded habitat data at each sampling location, we ground scattered 1,500 ml of black sunflower seed. Baiting was done within 3 hours of dawn. Five days later a squirrel feeder was erected at the location (again within 3 hours of dawn), and a Browning Recon-force remotely activated camera with a 64GB card was set up using a standard uniform series of settings. (see § *Camera settings*).

Cameras were in situ for five full days (see § *Appendix I* for dates). In the early morning of the sixth day, the camera and feeder were removed, and a live-capture trap was set at each survey point. Trapping was conducted for five cumulative days based on typical methodologies (see Gill et al., 2019 for a review of live-capture approaches). A second five-day trapping session was carried out between 23-45 days later so that for each survey point there was a cumulative ten days of trapping data collected. The second session reflected a likelihood that some animals present at the location may not have been caught during the initial five day trapping period.

Stand characteristics

Five replicate sets of habitat data were recorded at each sampling location. The first set was recorded at the point itself and the remaining four at a 25-pace distance in the four cardinal directions. All these measures were then averaged across sample plots to give a single value per location. At each point, we assessed canopy-openness using a type-A spherical densitometer (Forestry Supplies, Bartlesville OK, USA, Lemmon 1956, 1957, Jennings et al., 1999). This is a pocket-sized instrument with a convex mirror with a grid of 24 squares. The tool is held level at 12-18" from the body and the operator assumes that each of the 24 marked squares is divided into four quarters or smaller squares. Canopy cover is calculated from the number of quarter squares (94 in total) on the mirror filled with vegetation. We instead recorded the inverse, thus the number of open quarter squares. We collected four measurements per replicate, the recorder turning their body 90 clockwise direction after taking each reading and before taking the next until the fourth reading was made. An average of the four could be calculated. Data collected was later converted into 'percentage of canopy openness' (hereafter just 'canopy openness).

A 5m tape was used to determine the species and size of trees contributing to the canopy (including sub-canopy) within a 5-metres radius at each point. The species and Diameter at Breast Height (DBH) in cm of each tree was recorded using a DBH measuring tape. Thus, at each point, a cumulative total of 20 canopy measurements and five sets of DBH and tree species data were obtained. Tree species were later categorised as being of 'low', 'medium' or 'high' value for red squirrels (*as in* Gurnell et al. 2002). Low encompassed willow, alder (*Alnus glutinosa*), birch, rowan (*Sorbus aucuparia*), ash (*Fraxinus excelsior*), horse chestnut (*Aesculus hippocastanum*), poplar (*Populus sp.*), hemlock (*Tsuga heterophylla*), holly (*Ilex aquifolium*), silver fir (*Abies alba*). Medium included oak (*Quercus sp.*), sycamore, Sitka spruce, Weymouth pine (*Pinus strobus*) and Douglas fir (*Pseudotsuga menziesii*). High encompassed Lodgepole pine, Scots pine, Norway spruce (*Picea abies*), hazel (*Corylus avellana*), sweet chestnut (*Castanea sativa*), beech (*Fagus sylvatica*) and cherry. The number of woody stems within a 5 metre-radius was counted at each point and then averaged for each sampling location to provide a measure of forest regeneration. The total number of tree species per point was also calculated. The presence or absence of Corsican Pine, Lodgepole pine, Scots pine and Larch were specifically noted for each sampling point.

Camera settings

Camera settings were standardised. Each remotely activated camera was programmed to take three images per trigger at a high (16MP) resolution setting. Each trigger was followed by a delay of 30 seconds before any further images would be recorded. We used a 'Normal' sensitivity setting and a 'Normal' trigger range. Each camera was positioned so that a wooden squirrel feeder was visible and central in the field of view. The feeder was fixed to a tree trunk at a height of 1.2-1.5 metres. Cameras were attached to a tree 1.2-2.4 metres from the feeder. When a camera was collected after five days operation, the SD card contents were uploaded onto Cloud storage in a folder coded to the sampling point. The camera data were uploaded to the open-soucre software, digikam (www.digikam.org), which enabled the presence/absence of a red squirrel to be tagged in the meta-data of each image. The metadata were then extracted for analysis in R (R Core Team 2022) using the camtrapR package (Niedballa et al., 2016). Two key metrics were extracted from each camera: 1) The total number of red squirrel images over the five-day period, which included a minimum of 10-minutes between successive sightings to ensure that the dataset predominantly focussed on independent foraging events (Parsons et al., 2021, Villette et al., 2017); and 2) the time taken in hours for the first squirrel to visit the feeder.

Live trapping

Live trapping, squirrel handling and marking activities were carried out under Wildlife & Countryside Act (1981 *as amended*) licences (S087309/1-2 & S091126/1) issued by Natural Resources Wales. We used unmodified commercially available Albi™ single-catch

Mink-traps with solid steel doors and treadles. Traps were baited with sunflower seeds in husks. Traps were cleaned with Virkon S™ disinfectant between all captures. All traps were opened early each morning and inspected twice before being closed until the following day. Captured red squirrels were handled by opening the trap door and allowing the animal to move out into a plastic bag before then transferring them into a Virkon S™ sterilised wire mesh handling cone. Individuals were sexed, weighed to the nearest 5g with a 1000g Pesola™ spring-balance, had their hind shin measured to the nearest 0.1mm and reproductive state categorised in earlier studies (Holm 1991, Wauters & Lens 1995). These categories were '*non-breeding*' (vulva small, no longitudinal opening), '*oestrus*' (vulva swollen and reddish in colour), '*pregnant*' (vulva is initially still enlarged, with the longitudinal opening progressively closing to leave a clearly defined central line), '*lactating*' (nipples enlarged with milk excretion on stimulation) and '*post lactation*' (nipples darkened, hair loss in surrounding area significant often with regrowth).

During the first capture each individual was marked using a unique Passive Integrated Transponder (PiT tag; Peddymark™ 1.4 × 10 mm), which was inserted under the skin at the nape of the neck or dorsal area of the back where the skin was relatively loose. This facilitated individual identification by scanning for a PiT tag using a Peddymark™ ISO PM450 Scanner. Individuals red squirrels with a weight greater than 240 g were defined as '*adult*'.We recorded the survey point location for every capture or recapture during both the first and second trapping periods in each forest. If we caught young animals during the second trapping session which would not have been weaned during the initial camera deployment, then these data were excluded from further analysis.

Data Analysis

All statistical analyses were performed in R (R Core Team 2022). A Kruskal-Wallis analysis was carried out initially to compare the number of individual squirrels caught at sites where the cameras detected at least one image of a squirrel (n=35) with those where no images were captured (n=15). A Pearson's correlation was then used to explore the relationship between two key camera trap metrics – cumulative number of images and the time to first image after camera deployment – and the number of individual squirrels that were caught at each site over a period of five days.

The second stage of the analysis employed a Generalised Linear Model (GLM) using the lme4 package (Bates et al. 2015) to explore the habitat characteristics affecting the numbers of individual squirrels caught at each of the survey points (*response variable*). Nine explanatory variables were included in the analyses: *stand type* (broadleaf, conifer 40+ yrs, conifer 20-40 yrs & conifer <20 yrs), *site* (Pentraeth or Newborough), *canopy openness*, *number of stems*, *DBH*, *number of tree species* and the presence/absence of four key tree species: Scots pine, Corsican pine, lodgepole pine and larch.

Data exploration confirmed that the response and explanatory variables met the assumptions of the model (i.e. independence of the data, even distribution of the residuals, correct designation of the variance structure and a linear relationship between the response and explanatory variables). However, two of the stand categories (conifer <20 yrs and conifer 20-40 yrs) were combined due to the limited sample size preventing model convergence. This led to there being three stand types - broadleaf, conifer <40 yrs and conifer >40 yrs).

A total of 53 candidate models were generated from the nine predictor variables, which included a null model, all single-factor and two-factor model combinations and 10 three-factor models. Akaike's Information Criterion adjusted for small sample size (AICc) was used for model selection (Burnham and Anderson 2002). The AICcmodavg package was used to extract AICc scores and model weights for each candidate model (Mazerolle, 2016). Model averaging was conducted across models accounting for ≥0.95 of the AICc weight to extract parameter β estimates and their 95% confidence intervals (CI). The significance of the results was assessed by whether the 95% CI overlapped zero.

Results

Trapping summary

A total of 118 individual squirrels were caught across the 50 survey points during the two five-day trapping periods with a range of 0-8 individual squirrels per sampling point (mean ± SD = 2.4 ± 2.4, see § *Appendix I*).

Camera trapping summary

Thirty-five (70%) of the cameras returned at least one image of a squirrel, while there were no detections on the remaining fifteen cameras (30%). A total of 15,739 images were captured over the five-day sampling period across all 50 survey points. 12,286 of these images were of squirrels (78%). This was then down-sampled to achieve independence between foraging events using a minimum of 10 minutes between successive photos (Parsons et al. 2021, Villette et al. 2017). This resulted in a final dataset of 474 squirrel images. The time to first detection was recorded at the thirty-five cameras (with a confirmed squirrel image) and this ranged from 1hr to 106 hrs (mean ± SD = 28 ± 31) after the survey period began. We also recorded three confirmed images of a single pine marten (*Martes martes*) of unknown age and sex, which was located in conifer habitat >40 yrs of age at Pentraeth. This is the first confirmed sighting of a pine marten on Anglesey (Fig. 5).

Figure 5. First confirmed sighting of a pine marten on Anglesey

Camera trapping as a red squirrel monitoring method

Significantly more individual squirrels were caught at survey points where the camera detected at least one image of the target species compared with cameras that did not record a detection (Kruskall–Wallis χ^2 = 15.187 d.f. = 1, p = <0.001; Fig. 5). The Pearson's correlation revealed a significant positive association between the number of images captured over the five-day study period and the number of individual squirrels caught (Pearson's: n = 50, r = 0.78, p = <0.001; Fig. 6). Similarly, there was a significant negative correlation between the time to first image and the number of individual squirrels caught (Pearson's: n = 35, r = -0.39, p = 0.02; Fig. 7), demonstrating that locations with greater numbers of squirrels detected an individual more rapidly. However, the strength of the association was weaker than for the number of images metric.

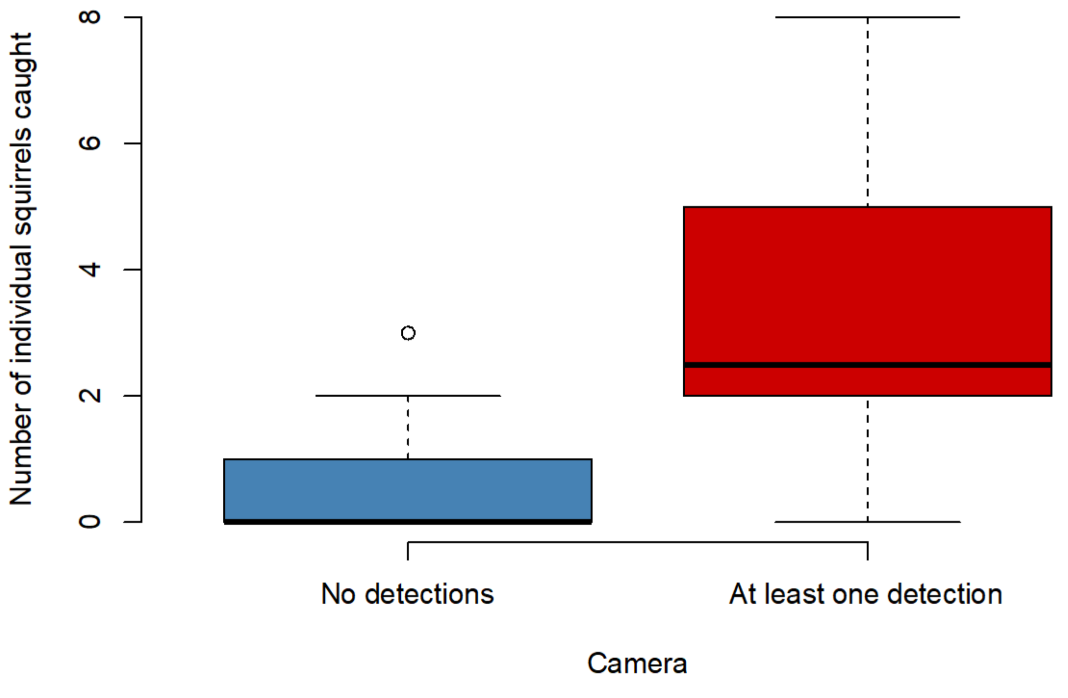

Figure 6. The number of individual squirrels caught at survey points where the cameras had detected at least one individual compared with cameras that had no detections

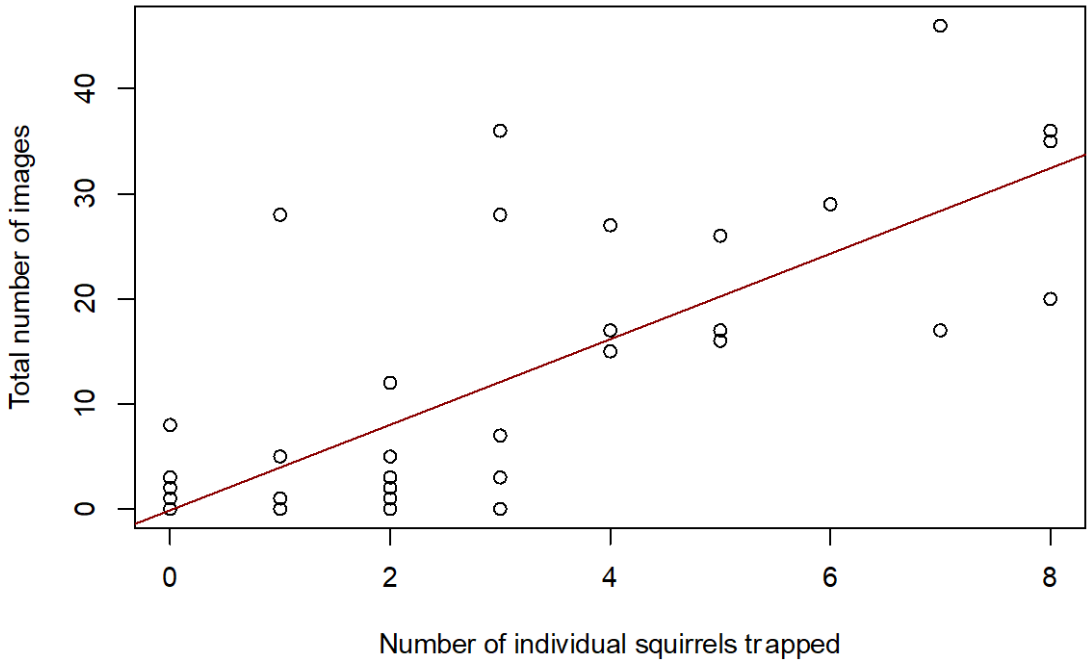

Figure 7. Correlation between the number of images recorded at each survey camera (n = 50) with the number of individual squirrels trapped (r = 0.78).

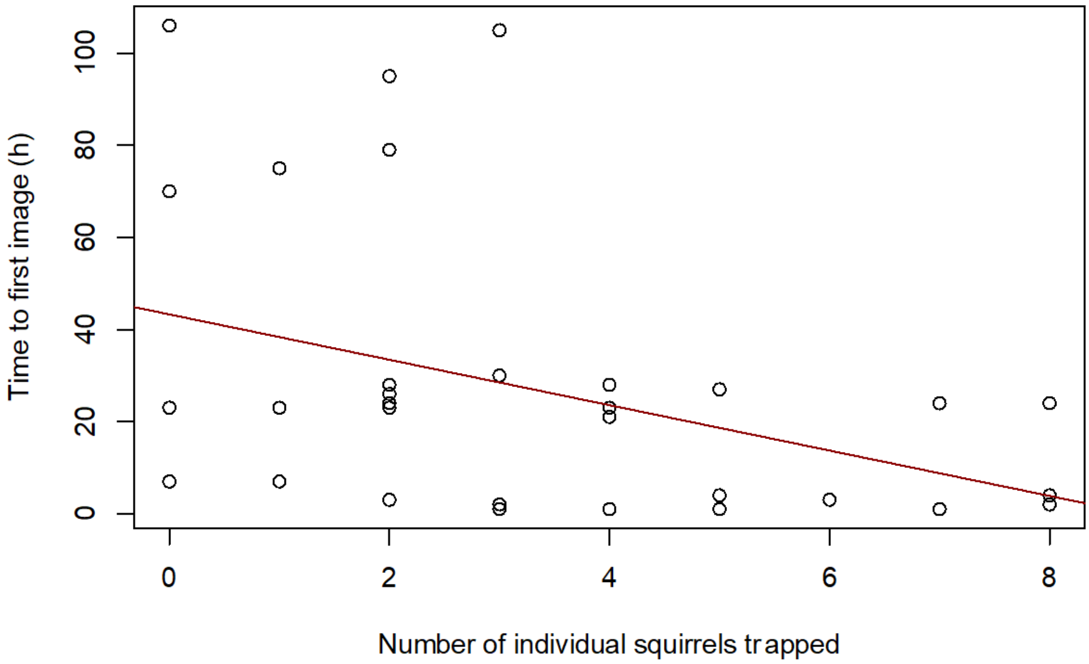

Figure 8. Correlation between the time to first image at each survey camera (n = 35) with the number of individual squirrels trapped (r = 0.39).

The impact of forest stand structure characteristics on red squirrel habitat use

Seven models contributed 95% of the AICc weight for the GLM analysis (Table 2), with the top three models accounting for 77% of the weight. Model averaging revealed that there was a site difference in abundance with more squirrels caught at Pentraeth compared with Newborough (Table 3 & Fig. 8). There was also a negative association between individual captures and canopy openness (Table 3 & Fig. 9), and a positive relationship with captures and the number of tree species (Table 3) and the presence of Scots pine (Table 3 & Fig. 10)

Table 2. Top models accounting for ≥0.95 of the AICc weight.

	K[1]	ΔAIC	AICc
Canopy openness + Site + Scots pine	4	0.00	0.36
Habitat type + Canopy openness + Scots pine	5	0.60	0.27
Canopy openness + No. tree species + Scots pine	4	1.77	0.15

Canopy openness + Site + No. tree species	6	3.78	0.05
Canopy openness + Site + Scots pine	3	3.94	0.05
Habitat type + Canopy openness + Scots pine	5	4.33	0.04
No. tree species + Site + Scots pine	4	4.94	0.03

Table 3. The observed relationship between the response variable (numbers of individual squirrels caught) and the model-averaged parameters from the top models (β-estimate ±95% CI). Bold text denotes β-estimates with 95% CI that do not overlap zero.

Parameter	β Estimate	(95% CI)
Habitat conifers < 40 yrs	-0.11	(-0.83 / 0.62)
Habitat conifers >40 yrs	0.47	(-0.15 / 1.09)
Site (Pentraeth)	0.59	(0.14 / 1.04)
Canopy openness	-0.08	(-0.13 / -0.02)
DBH	0.01	(-0.02 / 0.04)
Stems	0.00	(-0.02 / 0.01)
No. of tree species	0.11	(0.01 / 0.21)
Scots pine (presence)	0.72	(0.26 / 1.18)
Corsican pine (presence)	-0.18	(-0.86 / 0.5)

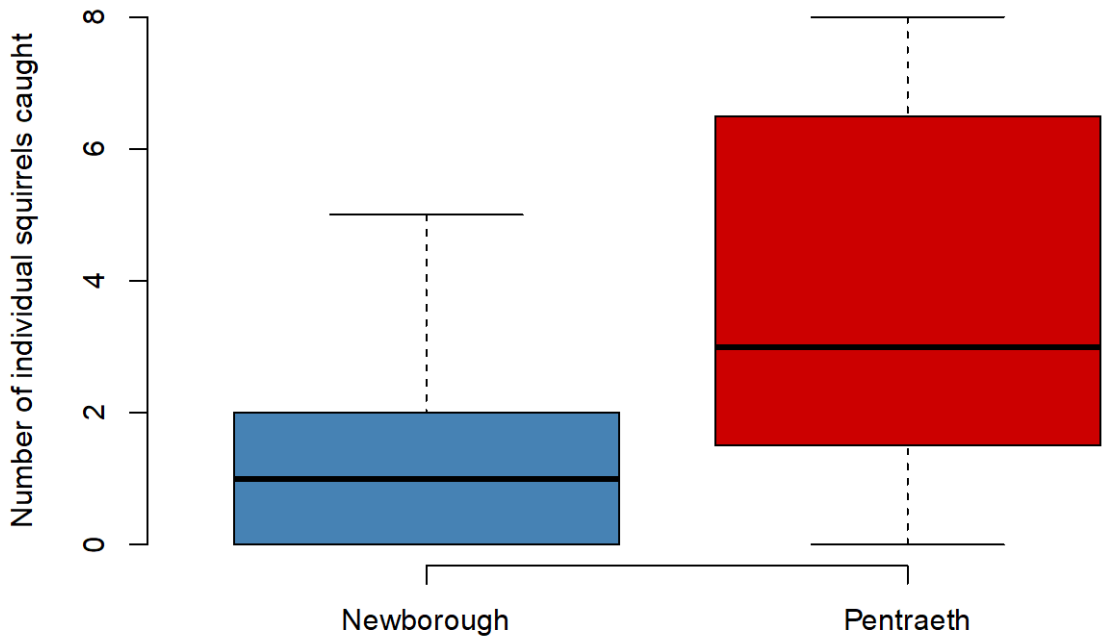

Figure 9. Boxplot comparing the number of squirrels caught at the two study sites (Newborough & Pentraeth).

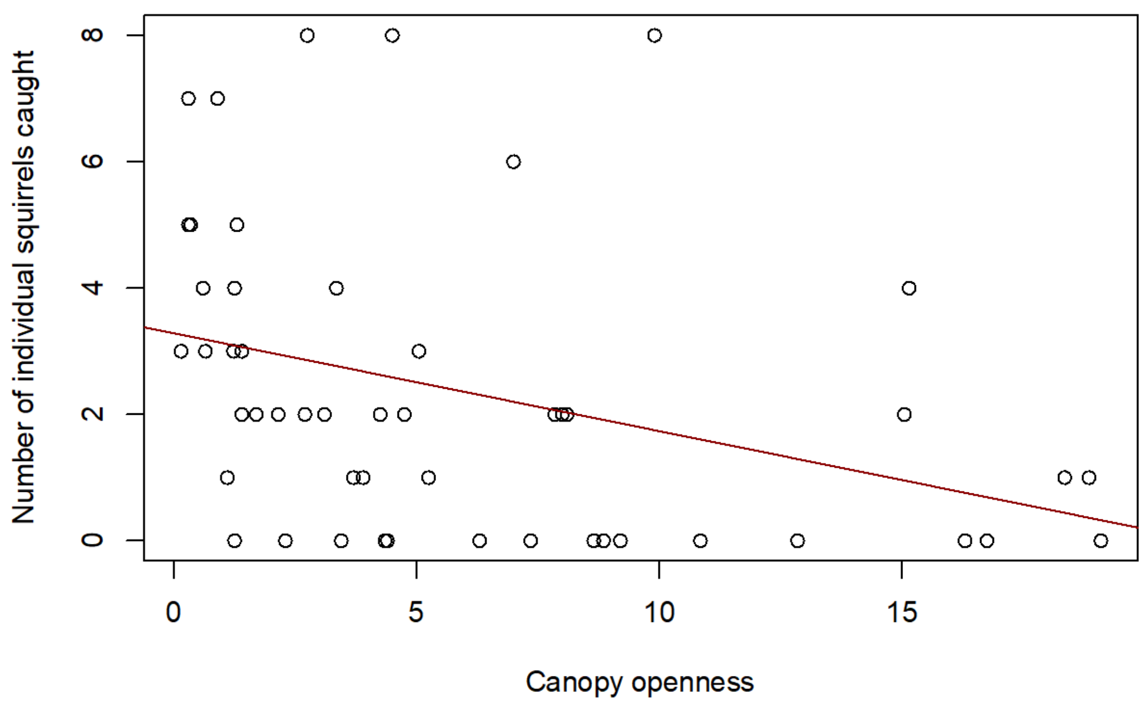

Figure 10. Relationship between the metric of canopy openness and the number of squirrels caught at each survey point (n = 50).

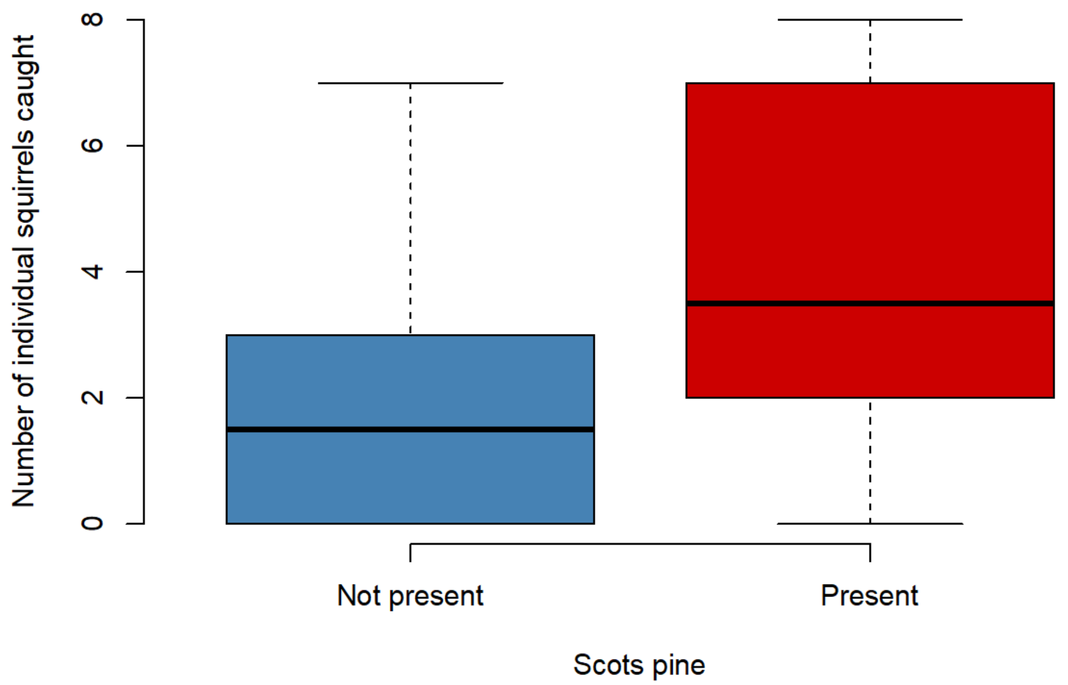

Figure 11. Boxplot comparing the number of squirrels caught at survey points which had Scots pine present or absent.

Discussion

Camera trapping as a method for monitoring red squirrels

Carbone et al. (2001) first found a relationship between local densities and rates of camera trap capture for tigers (*Panthera tigris*), proposing this as a new method to collect crucial demographic data on a wide-ranging and elusive species. There was initial scepticism around the calibration of the method and as to whether it would be useful to monitor other species (Jennelle et al., 2002). Nonetheless, the idea behind this paper was soon welcomed by conservation scientists and practitioners and has been since tested and used on several taxa ranging from large carnivores (Linkie et al., 2006) and forest ungulates (Rovero and Marshall 2009) to ground-dwelling birds (Samejima et al., 2012).

The strong correlation demonstrated by our study between the number of live captured red squirrels and the number of camera trap images recorded, further supports the use of this approach as an index of relative abundance for a small arboreal mammal. Furthermore, the time to first image of a red squirrel also performed reasonably well as an indirect measure of density but was ultimately a cruder metric that only utilised cameras that recorded images of squirrels, while not accounting for the extent of activity across the full five-day survey period. Of course, there are several variables which may further affect the strength of the relationship between camera indices and live captures across different sampling locations e.g differential use of their range, dispersing individuals, etc. (Wauters & Dhondt 1992b). Nevertheless, as demonstrated for a number of other species, indices of density like the ones tested here, can provide a very useful tool in situations where economic resources and/or specialised skills (e.g. squirrel handling) are limited (e.g., Bertolino et al., 2009, Marsden et al., 2016, Villette et al., 2017). The method is expected to be effective and accurate in habitat patches of varying size and with squirrel populations of different densities. Indeed, the assumptions of the method are that the sampling effort is representative of the study area's size and hetereogenity, camera trapping locations are independent from each other and from the habitat's edge (see § '*Survey design*'), and squirrel activity remains constant over the survey period. At very low densities the accuracy of the method may decrease due to the paucity of sightings during the five-day camera trap surveys. However, the method would still provide a relative index of the species rarity at that site. Further investigation would be advisable in these situations using an occupancy modelling framework with the cameras deployed over a longer time period (e.g. a specific season). This method could also be paired with a second intensive sampling strategy, which may include genetic surveillance of hair obtained from sticky pads placed on feeding stations. .

Our study provides further support for the use of cameras in small mammal monitoring. However, it is important to note that the results only apply to red squirrels, and, if deemed appropriate, then other species- and other situation-specific calibrations would need to be investigated. It should also be highlighted that individual squirrels were still caught even where there were no detections by the camera traps (Fig. 5). This may be due to variability in different home range sizes and use between sexes and in different habitats (Lurz et al., 1995, 2000, Lurz & Garson 1998, Wauters & Dhondt 1992b). Thus, the lack of detection by camera traps should not be interpreted as the absence of the species in the area unless confirmed by more intensive monitoring. However, we can infer with reasonable confidence that when camera traps do not detect any red squirrels, the relative density of the species in that area is likely to be low. The two metrics we explored differ in their robustness and in the ease with which they may be used. 'Number of images' is a better predictor of local abundance (i.e. stronger correlation with the number of individuals captured) but it entails a significantly greater investment in data processing, as all of the squirrel images need to be individually tagged before being sub-sampled to ensure that duplicates are removed and there is a minimum period between successive images (10 minutes in this study). Although 'time to first image' is a much easier metric to extract from the data, it is also a weaker predictor and should be used with greater caution (e.g. with a larger sampling effort or in areas where the species is more abundant). Finally, it is crucial to underline that the robustness and usefulness of both metrics as a proxy for local abundance are conditional on an adequately rigorous and unbiased sampling strategy that strives for spatial and temporal independence between sampling locations and foraging events (Sutherland 2006).

Red squirrels' habitat association on Anglesey

Research by Flaherty et al. (2012) and Dylewski et al. (2021) looking at pinecone exploitation rates by red squirrels indicate that heavily thinned and open canopy plantation forests are of low suitability for the species. Our research now reveals that the number of animals caught in standardised trapping operations (and camera indices) was similarly negatively associated with canopy openness. Although red band needle blight is partially defoliating Corsican pine stands on Anglesey (Shuttleworth et al., 2012) and may be a contributory factor, it is notable that infection was also present in stands with greater connectivity where squirrels were more frequently found. Red squirrels preferentially forage close to the forest edge, which is characterized by low understory cover and high canopy closure where trees typically produce larger cone crops than those growing towards the centre of the stand (Dylewski et al., 2021, Turkia et al., 2018). Thinning can increase canopy openness and therefore cone (seed) production throughout a stand by facilitating greater numbers of reproductive trees and greater cone production per tree (Otto et al., 2012), but any significant structural connectivity loss would have potential energetic and predation risk implications for red squirrels whilst foraging for the seed Flaherty et al, 2012).

There is evidence that certain prescriptive thinning regimes may have negligible effects on red squirrel space use (de Raad et al., 2021). However, the scale and nature of each specific forest thinning operation can vary widely, and it is important not to assume that every operation will have minimal consequences for squirrels. Only one of our survey points had been subjected to a thinning operation in the previous winter, the remaining points had not been thinned for at least four years and therefore we can conclude that the dataset reflected long-term effects of forest operations and earlier canopy fragmentation. Such fragmentation of the canopy may result in animals having to move along the forest floor if they are unable to travel arboreally between trees. If such a situation occurs with sufficient frequency, then this could ultimately have considerable energetic and fitness costs particularly in a stand of tall mature trees where the canopy is much further above the ground than younger plantation crops. It is noteworthy that North American pine squirrels (*Tamiasciurus hudsonicus*) in physically substandard condition (body mass to structural size ratio) were significantly more vulnerable to predation than individuals in good condition (Wirsing et al., 2002). Thus, increasing canopy openness may indirectly elevate predation risk by lowering body condition (due to additional energetic costs associated with inter canopy travel) as well as directly raising risk due to increased travel across the forest floor where they are at risk from mammalian predators such as red fox. Further, limiting arboreal escape routes for animals attacked by raptors or arboreal predators whilst they are foraging in the canopy may also increase the risk of predation. The confirmed detection of pine marten on the island is consequently an important consideration because this predator is currently recolonising Wales and will prey on red squirrels (Twining et al 2020).

Our methodology for assessing forest tree canopy openness is relatively quick to conduct. It is therefore possible to apply the technique widely, and alongside published data on the relative habitat values of tree species type and their planting year (stand age) to gain a general overview of stand suitability for red squirrels within Anglesey coniferous plantations. The results indicated that older coniferous stands had greater squirrel abundance indices than younger stands and broadleaved habitats. However, the Confidence Intervals overlapped zero and this relationship is likely confounded by canopy fragmentation that is common among stands >40 years of age. Whereas the low red squirrel presence in broadleaved woodland with comparatively intact canopy cover probably reflects the dominance of birch species, which provide low quality red squirrel habitat (Jones et al. 2016, White et al. 2016, Kortland 2020). Similarly, where >40-year-old coniferous stands had been subjected to heavy thinning in the past, we noted that natural regeneration had established a dense medium storey of birch. Although this may improve the canopy connectivity the lack of optimal food source tree species in this medium layer means that long-term food supplies are lacking once the older conifer has died or been removed.

We observed a significant difference in squirrel density between the two sites and suggest that this reflects historical management approaches. The mixed spruce and pine stands at Pentraeth are managed on a coupe basis, with sequential line thinning occurring through to clear felling and restocking. In contrast, Newborough has been managed using a LISS (Low Impact Sylvicultural System) selective thinning approach with often intensive interventions to reduce the effect of red band needle blight infection. This has resulted in a more open canopy within conifers stands >40 yrs where there is often limited tree regeneration beneath. Finally, positive associations between squirrel abundance metrics and the presence of Scots pine and tree species abundance are likely to reflect food resource availability. Tree species vary annually in their seed production, and a species mix is therefore likely to ensure that at least some will produce seed crops during a given year (Lurz 1995, Lurz et al. 1995). Scots pine produces seed crops at a relatively early growth stage, and on Anglesey, there is some evidence that trees of Scottish provenance may be less affected by needle blight.. Establishing significant underplanted areas beneath open mature stands with Scots pine in Newborough would not only provide a means of progressively improving arboreal structure as the trees grow but also would create a valuable future food source for red squirrels in a way that birch and willow regeneration does not.

Management recommendations and transferability

We recommend that Natural Resources Wales take the following complementary approaches when assessing habitat suitability and red squirrel density during future red squirrel monitoring on Anglesey

1. Quantify habitat connectivity within stands utilising our ‘openness’ method (five measurements per site using a type-A spherical densitometer). We recommend the mapping of 100 random locations overall on Anglesey in stands over 10 years of age. These data can be included in management GIS layers along with details on stand species composition and stand age. We would recommend that that canopy density at all fifty points we surveyed in 2022 continue to be monitored annually, unless the site is clear felled.

2. Additional sites at Cefni and Nant could be included along with key privately owened woodlands e.g. Baron Hill estate, Bodorgan and Plas Newydd.

2. The number of images containing red squirrels collected during five days of camera trapping in early spring (following five days of pre-baiting) should be used as an index of red squirrel abundance. There should be a minimum period of 10 minutes between successive images to account for independence in foraging events. Fifty sampling points could be monitored annually in a rolling sequence when cameras/feeders are limited in availability e.g. we recorded at ten sampling locations at any given time.

3. The collated camera images would provide a means of detecting presence of invasive grey squirrel and also a better understanding of pine marten presence (individual coat bib pattern variation providing opportunities to distinguish between individuals).

Conclusions

Our findings offer a cost-effective and relatively straightforward way of assessing red squirrel abundance using camera traps. Collecting canopy openness readings using a densitometer is quick and easy and provides an essential habitat variable (see § '*stand characteristics'*), especially where data on tree species presence, relative abundance and age data are already known. The utility of our approach is that it can be applied to monitor squirrel numbers at the landscape scale without the need for time-intensive and costly surveying. The estimate of relative abundance provides a very useful metric for land managers, especially those planning selective thinning forest operations while considering the effects on red squirrels. The trapping data have also provided us with a valuable opportunity to explore the key woodland characteristics that are driving variation in red habitat use and activity. Our findings demonstrate a strong site difference between Newborough and Pentraeth, which most likely reflects historical management differences, including the heavy thinning of mature stands at Newborough. Older coniferous habitats with greater canopy closure support significantly higher numbers of squirrels. These structural elements of the woodland are also further enhanced by the presence of Scots pine and greater tree diversity, which provide important food sources for the squirrels throughout the year. Results from this study offer important insights into rapid approaches for surveying red squirrel density as well as guidance on habitat management that can strengthen the long-term viability of populations across the UK.

Recommended future research

- Red squirrels will forage from dense habitat towards the edge of more open woodland habitat. In our study, we did not investigate how the proximity to neighbouring dense habitat affected squirrel abundance metrics. This variable may have contributed to the variation in our observed results across sampling points and is, therefore, a future research priority.

- The discovery of a pine marten in Pentraeth introduces future complexity to red squirrel population monitoring. There is evidence that marten activity around red squirrel supplemental feeding stations can lower red squirrel activity and detection probability (Sheehy et al. 2018). Future research should attempt to quantify how the presence of a predatory species such as the pine marten affects the applicability of a camera-based red squirrel population assessment approach.

- Periods of high seed availability among preferred tree species are known to depress the probability of squirrel capture during trapping programmes. In hardwood stands, seed availability is highly seasonal with peak availability in autumn and early winter. There is a need to understand how this affects red squirrel attendance at feeders and thus the efficacy of camera images in population assessment across the year.

- This study has provided a snapshot of red squirrel density in relation to habitat variation including canopy connectivity. We recommend as a future research priority the forecasting of ongoing and proposed management decisions affecting tree species abundance and stand structure are predicted to influence red squirrel distribution and population viability in key conservation focal sites.
- We recommend that the method detailed in this study is tested further and calibrated in conditions of low squirrell density and/or very fragmented woodland habitats.

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Appendices

Data Archive Appendix

Data outputs associated with this project are archived in NRW's Document Management System on server–based storage at Natural Resources Wales.

The data archive contains: A database named NRW Evidence Report 672 - survey data (Red Squirrel abundance and habitat preference - Anglesey) in Microsoft Excel format.

Metadata for this project is not publicly accessible. It is held by NRW and should access be required, then a request will be considered.

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