



OLLSCOIL NA GAILLIMHÉ

UNIVERSITY OF GALWAY

Assessing Translocation Outcomes and Revealing
Behavioural Insights in Two Red Squirrel Populations in
the West of Ireland

This thesis is submitted to the University of Galway, in candidature for the degree of
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Declaration

I declare that I am the sole author of this thesis and confirm that it has not been previously submitted, either in its entirety or partially, for any other degree. Unless indicated otherwise through references or acknowledgments, the content presented is entirely my original work.

Signed _____

Date _____

Abstract

The red squirrel (*Sciurus vulgaris*) population suffered a dramatic decline in Ireland following the introduction of the invasive grey squirrel (*Sciurus carolinensis*) in 1911. Two red squirrel translocations, the intentional movement of a living organism from one area to another, were undertaken as part of efforts to conserve the species. These translocations took place in 2005 and 2007 at two sites in the west of Ireland, outside the range of grey squirrels: Derryclare in Co. Galway and Belleek woods in Co. Mayo. In the years following the translocations, monitoring efforts were implemented to observe and assess both populations. The most recent survey, conducted in 2012, provided evidence of the sustained presence and growth of both populations. The core aim of the present study was to investigate the current status of the translocated populations. At this stage the translocated populations were expected to have reached the regulation phase, exhibiting a continued presence and stabilised density.

Following the introduction of the red squirrel population to Derryclare in 2005, the woodland underwent significant changes. Clear-felling operations, both expected and unexpected occurred frequently, owing to the woodland's commercial nature. This activity, combined with a significant forest fire in 2011, resulted in substantial habitat loss. We investigated the extent of this habitat loss and its effects on the carrying capacity of the woodland. We utilised digitised historical maps to compare past and present habitat, revealing a 53% reduction in habitat since 2005. A feeding survey was conducted, and the results were compared to previous feeding survey data, allowing us to track the changes in the estimated squirrel abundance and carrying capacity of the woodland. Carrying capacity estimates declined by 41–81%, with the lowest estimate at 65 individuals. Deterioration of the quality of the habitat, due to a shift in the proportion of tree species towards the less favourable species, further reduced the suitability of the woodland. Feeding surveys estimated a total of 2-4 individuals in the woods, illustrating the negative effects of habitat loss and deterioration.

The Derryclare population was monitored using a combination of non-invasive and invasive techniques from January 2020 to January 2023. Trail camera, hair tube, and feeding survey data indicated a sparse squirrel presence throughout the entire woodland, with squirrel activity concentrated in patches of higher quality. Live trapping data revealed an eighteen-fold decline in density compared to previous estimates, averaging at 0.032 squirrels/ha, or 6.5 total individuals. Breeding and recruitment rates were low, and squirrels were underweight compared to other red squirrel populations, including Belleek. Home ranges, estimated using trapping data, averaged 19.61ha. The large size of these ranges indicates

a poor quality habitat. A feeding survey in nearby woodlands did not reveal any signs of dispersal, making it likely that carrying capacity was never reached in Derryclare. It was deemed that the translocation will ultimately not be successful, due to the low likelihood of the population's recovery.

The Belleek population were monitored from February 2020 to March 2023. Hairtube and trail camera surveys revealed a uniform population distribution throughout the woods. A live trapping study estimated an average density of 0.41 squirrels/ha, or 24.6 individuals, aligning with other healthy red squirrel populations. Breeding, recruitments rates and squirrel body weight were all indicative of a healthy population. Radiotracking was employed, revealing an average home range of 4.02ha. A citizen science survey conducted from March 2021 to January 2023, revealed a significant expansion of the Belleek population's range, estimated to span 738.5km². The success of this translocation was attributed to the maintenance and persistence of consistent suitable habitat and the abundance of food, bolstered by continuous supplementary feeding. In contrast, ongoing loss and deterioration of habitat in Derryclare was believed to be responsible for this population's decline.

The behaviour of individuals in both populations was analysed during live trapping sessions to gain insights into their behavioural diversity. Additional open field tests and mirror image simulation tests were performed on a subsample of individuals in Belleek. While it was hypothesised that these populations would exhibit multiple differences due to their contrasting habitats, only one significant difference was identified. Belleek squirrels displayed a diminished flight response compared to Derryclare, possibly owing to their habituation to humans. A trade-off between reproduction and longevity was observed in Belleek females. In Belleek males, boldness was found to be associated with smaller individuals and increased longevity, while in Belleek females, boldness was linked to larger individuals and a higher reproductive output. These personality differences impact population dynamics and therefore have implications for conservation management.

The recent resurgence of the pine marten has caused a decline in the invasive grey squirrel in Ireland, allowing for a red squirrel population recovery. The coevolutionary history between the red squirrel and pine marten, and the naivety of the grey squirrel to this novel predator are thought to be responsible for the contrasting outcomes of both squirrel species. We used trail cameras to record pine marten and red squirrel visits to feeders, and analysed the behaviour of the red squirrel following recent pine marten presence. We found that red squirrels visiting within 48 hours of a pine marten displayed an enhanced antipredator response involving increased sniffing and vigilance, and decreased feeding. These results

support the hypothesis that red squirrels have avoided predation by the pine marten due to their behavioural adaptations.

The divergent outcomes at Derryclare and Belleek underscore the intricacies of translocation projects, providing valuable insights into factors influencing their success or failure. In particular, this study has provided insights into the importance of habitat quality as a determinant of translocation success. We recommend that future translocation projects choose stable habitats, and place greater emphasis on habitat quality during the planning phase of the project. Additionally, our findings stress the significance of post-release monitoring, suggesting that monitoring is conducted at least until the regulation phase of the project, in order to reveal the true outcome of the project. Additionally, this study yields insights into red squirrel behaviour and ecology, emphasizing the need for behavioural screening in translocation projects. It also contributes to our understanding of the dynamics between red squirrels and pine martens, shedding light on the red squirrel's recovery in Ireland. We believe the insights gained from this study can provide valuable insights for future translocation projects, aiding in their successful planning and execution.

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1 Introduction

1.1 Rodentia

The red squirrel (*Sciurus vulgaris*) belongs to the order Rodentia, which encompasses nearly half of all living mammal species, comprising 29 families, 468 genera, and over 2500 species (Delaney et al., 2018). Rodents are globally distributed, found on all continents except Antarctica (Delaney et al., 2018). The member species are very diverse, both ecologically and morphologically. Ranging from a few grams to 91kg (Mones & Ojasti, 1986; Silva & Downing, 1995), rodents demonstrate a vast range of diets, from seeds and grasses to invertebrates and fish (Kay & Hoekstra, 2008). Herbivory is the most common dietary strategy in rodents, followed by omnivory and carnivory (Verde Arregoitia & D'Elía, 2021). Despite this diversity, rodents share characteristic traits that define this order.

The name 'rodent' originates from the Latin word "rodentem" meaning "the gnawers". All rodents have two pairs of front-facing incisors in the upper and lower jaws. These incisors are quite versatile, having been adapted for digging (Van der Merwe & Botha, 1998) and capturing prey (Renaud et al., 2019). The lack of canine and premolar teeth in rodent dentition creates a gap known as a diastema, allowing for more effective gnawing and chewing (Kay & Hoekstra, 2008). This unique dentition layout is partially responsible for the success of Rodentia (Swanson et al., 2019) and has been made possible by a key evolutionary innovation. A portion of the masseter muscle has shifted forwards in rodents, bringing the lower jaw forward (Böhmer, 2015), aligning the incisors and allowing for a more powerful bite.

1.2 Squirrel taxonomy

The taxonomic classification of the order Rodentia is the subject of much controversy, prompting the use of both morphological and molecular classification methods, resulting in a variety of suborders (Honeycutt, 2009). An early morphological classification by Brandt (1855) suggested three suborders: Sciuromorpha, Hystricomorpha, and Myomorpha. However, subsequent research revealed that some similarities within these groups are a result of convergent evolution (Marivaux et al., 2004; Vianey-Liaud, 1985). Tullberg (1899) classified Rodentia based on the angle of the lower jaw, defining two suborders: Sciurognathi and Hystricognathi. More recently, molecular studies have divided Rodentia into three lineages, encompassing five infraorders and twenty one families (D'Elía et al., 2019). These lineages are as follows: Sciuromorpha (squirrel-related), Supramyomorpha (mouse-related), consisting of Castorimorphi, Anomalurimorphi, and Myomorphi, and

finally, Hystricomorpha (also known as Ctenohystrica) consisting of Hystricognathi and Ctenodactylomorphi (D'Elía et al., 2019) (Figure 1.1).

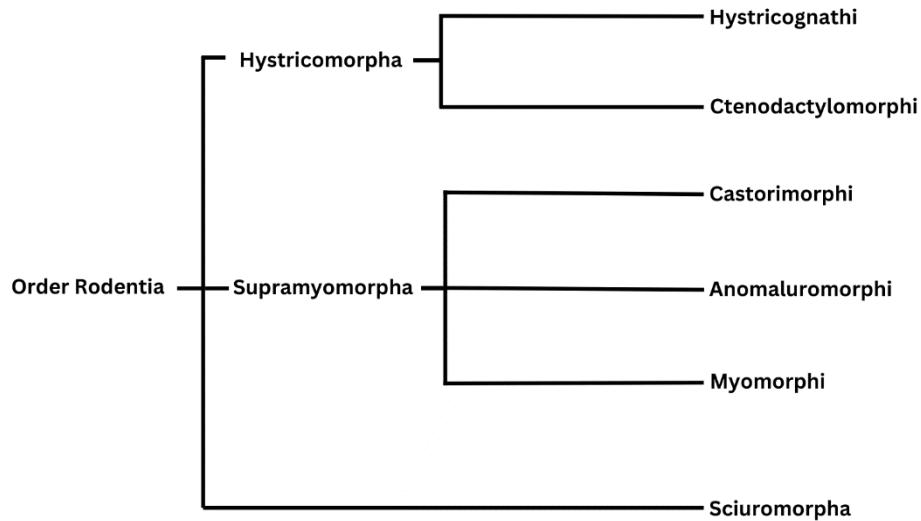


Figure 1.1 Phylogenetic tree of order Rodentia to the infraorder level, according to D'Elía et al. (2019).

The family Sciuridae within Sciuromorpha, includes tree, ground and flying squirrels, as well as chipmunks, marmots and prairie dogs (Nowak, 1999). With 298 species across 62 genera (Burgin et al., 2018), Sciuridae ranks as the fourth most diverse extant mammal family (Vaughan et al., 2013). Sciuridae is further classified into five subfamilies; Callosciurinae (beautiful squirrels), Ratufinae (giant squirrels), Sciurillinae (pygmy squirrels), Sciurinae (tree and flying squirrels) and Xerinae (ground squirrels and marmots) (Abreu et al., 2022; Thorington Jr & Hoffmann, 2005). Within the subfamily Sciurinae, two tribes exist: Sciurini, (tree squirrels) and Pteromyini, (flying squirrels) (Abreu et al., 2022; Thorington et al., 2012) (Figure 1.2).

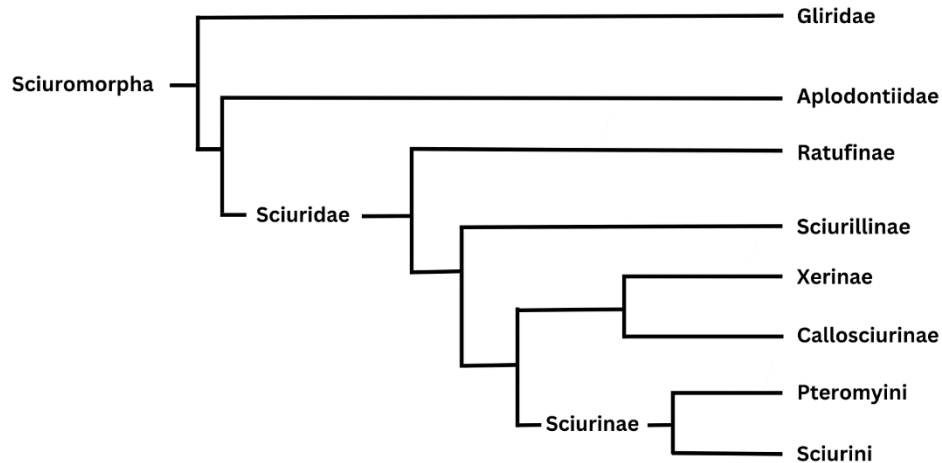


Figure 1.2 Phylogenetic tree of the clade Sciuromorpha, according to Abreu et al. (2022).

Fossil evidence indicates that sciurids, members of the family Sciuridae, originated in North America. The oldest known squirrel fossil is *Douglassciurus jeffersoni* dating back approximately 36 million years (Emry & Thorington, 1982). However, this squirrel lacked a defining characteristic seen in modern squirrels known as sciuromorphy, which refers to an extension of the masseter muscle, allowing for a more powerful bite. The earliest sciuromorphic fossil, *Paleosciurus*, was discovered in Europe from the early Oligocene period (Vianey-Liaud, 1985).

The Eurasian red squirrel (*Sciurus vulgaris*), hereafter referred to as the red squirrel, belongs to the tribe Sciurini. This species has a wide distribution across Eurasia, occupying Palearctic forests from Ireland and the Iberian peninsula to as far east as Kamchatka Peninsula in Russia and Hokkaido, Japan (Asadi Aghbolaghi et al., 2020) (Figure 1.3). Their distribution extends southwards to the Mediterranean and northern Mongolia (Wilson & Reeder, 2005). Throughout its range, red squirrels exhibit huge morphological variation, with coat colours varying from red to brown to black, possibly representing adaptations to different habitats (Finnegan et al., 2009; Wauters et al., 2004b). As a result of the morphological diversity observed in the red squirrel, over 40 subspecies of *S. vulgaris* have been proposed (Corbet, 1978; Ellerman & Morrison-Scott, 1951). However, a molecular analysis conducted by Grill et al. (2009) identified only three subspecies: *Sciurus vulgaris infuscatus* found in Iberia, *Sciurus vulgaris meridionalis* found in southern Italy (which has since been upgraded to full species status, *Sciurus meridionalis* (Wauters et al., 2017)) and a third group comprising of all other individuals.



Figure 1.3 Distribution of the red squirrel *Sciurus vulgaris* (Adapted from the IUCN 2022 data, accessed on 20th of July 2023)

1.3 Red squirrel biology

The red squirrel's body plan is adapted for an arboreal lifestyle, with disproportionately longer and heavier hindlimbs compared to their forelimbs, ideal for climbing and leaping (Shorten, 1962). Their feet are semi-plantigrade and their toes have keeled claws, which have been shown to aid in gripping thin branches, enabling them to navigate the small terminal branches of trees (Samaras & Youlatos, 2010). In contrast to ground squirrels, tree squirrels such as the red squirrel have longer tails, serving as a balance and steering mechanism (Hofmann et al., 2021). Squirrels depend heavily on tree seeds as a food source (Moller, 1983). For this reason, squirrels possess a powerful jaw with sharp and continuously growing upper and lower incisors (Cox & Watson, 2023; Lacher et al., 2016). Squirrels have large eyes, and an ability to see in dim light (Gurnell, 1987). This is essential as although squirrels are diurnal, they are particularly active at dawn when visibility is limited (Gurnell, 1987; Tonkin, 1983). The red squirrel's well-developed sense of smell is utilised in predator recognition (Twining et al., 2020a), mating behaviour (Lurz et al., 2005; Wauters et al., 1990) and food detection (Brzeziński & Zalewski, 2023).

Red squirrels predominantly inhabit coniferous and deciduous woodlands. However, mixed woodlands with a diverse range of tree species offer a more consistent and reliable food source compared to monocultures (Gurnell, 1983; Lurz, 1995). Within mixed woodlands, red squirrels have access to conifer seeds year-round, supplemented by berries, seeds, and fruits from deciduous species when available (Moller, 1983). Red squirrels are a scatter hoarding species (Rice-Oxley, 1993), and rely on cached food when food supply is low (Krauze-Gryz & Gryz, 2015). Sciurids have been found to cache food away from the presence of conspecifics, to minimise pilferage risk (Hopewell & Leaver, 2008; Leaver et

al., 2016). As food availability is the main factor affecting red squirrel densities (Wauters et al., 2008), areas characterized by substantial spatial and temporal variations in food supply tend to support higher squirrel populations (Cagnin et al., 2000; Lurz & Garson, 1997; Wauters et al., 2004a). Monocultures consisting of unreliable tree species with varying mast years, such as Sitka spruce (Broome et al., 2007) have the lowest red squirrel densities (Lurz et al., 1998; Lurz et al., 1995).

Red squirrels have also adapted to populate urban areas, inhabiting urban parks and gardens (Fingland et al., 2022). Urban environments pose significant challenges for red squirrels due to the high mortality caused by road accidents (Shuttleworth, 2001). However, recent studies have shown that the fragmentation and presence of barriers in urban areas do not inhibit dispersal or movement (Fey et al., 2016; Fingland et al., 2022; Hämäläinen et al., 2018). Urban environments offer unique conditions, as they may lack natural predators (Adams, 2009; Twining et al., 2021). Additionally, supplementary feeding, which is often provided by humans in urban centres, has been shown to result in higher red squirrel densities (Magris & Gurnell, 2002). Despite the close contact with humans and other urban stressors like noise and light pollution, urban red squirrels in general are not more stressed than their rural counterparts (Shimamoto et al., 2020). Additionally, squirrel densities have been shown to reach higher densities in urban areas than rural areas (Fingland et al., 2022; Jokimäki et al., 2017; Krauze-Gryz et al., 2021).

Red squirrel activity patterns vary with the seasons (Tonkin, 1983; Wauters et al., 1992). In winter, when the days are shorter, red squirrels rise at dawn and remain continuously active until dusk. However, during the summer, their activity shows two distinct peaks: one a few hours after dawn and the other a few hours before sunset (Gurnell, 1987). Urban squirrels, interestingly, display altered activity patterns compared to their less urbanised counterparts. They display reduced activity throughout the day, with a delayed onset of activity (Beliniak et al., 2021; Thomas et al., 2018). This behavioural change is likely a response to the availability of reliable anthropogenic food sources, resulting in a reduced foraging effort. The red squirrel's active time is mostly spent foraging, which makes up 60-90% of their activities, either in the tree canopy or on the ground (Gurnell, 1987). Red squirrels have two breeding peaks in a year, with litters being born in spring (Feb – April) and summer (May – July) (Lurz et al., 2005). However, in times of low food availability, breeding seasons may be shortened and only occur in summer, due to a trade-off between survival and investing in reproduction (Rodrigues et al., 2010).

The social organisation of red squirrels is based on a dominance hierarchy (Gurnell, 1987). The social status of an individual is determined by its age (Wauters & Dhondt, 1989) and

body weight (Wauters & Dhondt, 1985), with older and heavier squirrels tending to be more dominant. It has also been hypothesised that an individual's personality is linked to their social status (Mazzamuto et al., 2019), although further research is needed on this topic. The social status of the squirrel will affect not only their interactions with other squirrels, but also their home ranges (Wauters & Dhondt, 1992), survival (Wauters & Dhondt, 1992) and reproductive success (Wauters et al., 1990). During the breeding season, typically spanning from December to August (Thorington et al., 2012), mating chases take place, where several males actively pursue a female in an attempt to mate with her. Dominant males, who typically have larger testes, home ranges and body weights, take the lead in the chase and are most likely to succeed in copulating with the female (Lee, 2001; Wauters et al., 1990). The reproductive success of the female depends on factors such as her body weight, age, and social rank (Lee, 2001; Tranquillo et al., 2023; Wauters & Dhondt, 1989). Dominant females are more likely to breed twice in one year (Gurnell, 1987).

Litter size can vary from 1 – 6 young (Lurz et al., 2005), with 3 kits being the most common (Shuttleworth, 1999). When born, young red squirrels are blind, naked and deaf. Complete hair growth occurs around 3 weeks old (Shorten, 1954) and they open their eyes at 3-4 weeks after birth (Fericean et al., 2022). They are weaned by 8-10 weeks (Lurz et al., 2005). Juvenile mortality rates are high, with 75-85% of juveniles dying during their first winter, mainly due to starvation, predation and cold weather (Lurz et al., 2005). Juveniles typically disperse at 4-5 months old, with dispersal times peaking in autumn (Wauters & Dhondt, 1993), but also occurring to a lesser extent in spring (Wauters et al., 2004a). When dispersing from their natal patch and choosing a new territory, squirrels consider various environmental and demographic cues, such as habitat quality and population density (Wauters et al., 2010). Additionally, intrinsic factors such as their individual personalities (Cooper et al., 2017) and life histories (Wauters et al., 2010) can also influence their dispersal decisions. In general, better breeding conditions serve as the primary driving force for dispersal (Wauters et al., 1995). For males, dispersal is best predicted by the distribution of females, and thus their chances of successfully mating (Lurz et al., 1997). Female dispersal is best predicted by food availability, as this directly impacts their reproductive success (Lee, 2001; Lurz et al., 1997; Wauters et al., 1995). Both dispersing male and female squirrels have also been shown to settle in areas with lower densities of the same sex, which reduces their competition for resources and increases mating opportunities (Wauters & Dhondt, 1993; Wauters et al., 2010). A seasonal sex bias in dispersal has been observed, with males more likely to disperse during spring, while females tend to disperse in autumn (Wauters et al., 2004b).

Red squirrels can live for 6-7 years, although adults generally only survive for 2-3 years in the wild (Seinfeld, 1999). The primary causes of death among red squirrels are starvation, predation, disease and human interference (LaRose et al., 2010). Common predators of the red squirrel include pine marten (*Martes martes*), foxes (*Vulpes vulpes*), stoats (*Mustela erminea*), owls (*Asio* and *Tyto* spp.) as well as raptors such as buzzards (*Buteo buteo*), sparrowhawks (*Accipiter nisus*) and goshawks (*Accipiter gentilis*) (Lurz et al., 2005). In urban areas, dogs (*Canis familiaris*) and cats (*Felis catus*) can also cause squirrel mortality (Kopij, 2014). Human activities contribute significantly to squirrel mortality, with habitat destruction (O'Meara, 2018) and vehicle collisions (Shuttleworth, 2001) being notable factors. Additionally, diseases such as leprosy (Avanzi et al., 2016) squirrelpox and adenovirus (Everest et al., 2021), as well as infections of *Staphylococcus aureus* (Simpson et al., 2013a) pose serious threats to red squirrel populations.

1.4 Red squirrel behaviour

Red squirrels lead mostly solitary lives, with each individual maintaining a home range, encompassing the area the squirrel utilises daily, and a core range within their home range which represents the portion of the home range they use most intensively. Home range sizes vary between the sexes, with males typically occupying larger home ranges compared to females (Wauters et al., 1992). The size of the home range is influenced by various factors, including local population densities, habitat quality and the individual's social status (Wauters & Dhondt, 1992). Core range overlap among squirrels of the same sex is less common than overlap between the sexes, resulting in male home ranges that may overlap with several female ranges (Wauters & Dhondt, 1992). Nonetheless, squirrels spend very little time in direct interactions with conspecifics outside of the mating season (Gurnell, 1987). One rare occurrence of close non-aggressive interactions between individuals is communal nesting. Communal nesting may occur during winter and spring when squirrels huddle together to conserve heat (Grönwall, 1982). Squirrels may huddle with individuals that are familiar to them, such as a mother sharing a drey with her offspring (Shorten, 1954). Adults have also been observed sharing dreys in groups of 2-5, although nothing is known about the relationship between these individuals (Gurnell, 1987). Drey sharing has also been observed between mating partners during the breeding season (Wauters & Dhondt, 1990a).

Red squirrels maintain a variety of dreys, typically no more than 8-12, and frequently switch between them (Lurz et al., 2005). Primary dreys are typically used exclusively by a single individual, while other dreys may be used by several squirrels, at different times of the year (Wauters & Dhondt, 1990a). Dominant squirrels use a higher number of dreys compared to subordinate individuals (Wauters & Dhondt, 1990a). It is believed that information about

drey ownership and usage is communicated to other squirrels through olfactory cues (Lurz et al., 2005; Wauters & Dhondt, 1990a).

Scent marking in red squirrels is achieved by various means. Scent glands located in the mouth and on the lips of squirrels (Schumacher, 1924) produce secretions that they may rub onto branches and tree trunks, a behaviour known as face-wiping (Holm, 1990). Additionally, marking with urine is common and has been observed to occur at specific marking points (Holm, 1990; Lurz et al., 2005; Thorington et al., 2012). The olfactory cues contained in these scent markings carry important information about the squirrel that left them, including their identity, home range, reproductive status, and social status (Lurz et al., 2005). Vaginal secretions may also be combined with urine to communicate a female's breeding condition, which can attract males during the mating season (Lurz et al., 2005; Wauters et al., 1990). One significant function of scent marking is territorial marking, which communicates an individual's home range and serves as a warning to subordinates (Wauters & Dhondt, 1990a). Countermarking has been observed at feeding stations (Magris, 1998) and regular marking points (Holm, 1990). More dominant individuals have been observed countermarking the scent of a subordinate (Holm, 1990).

Squirrels also use vocal communication. Red squirrels are capable of making a variety of noises, with each sound serving a different function. Squirrels may vocalise for a variety of purposes, including: to assert dominance, convey information about potential dangers, solicit mates and establish territory (Diggins, 2021). Additionally, squirrels have demonstrated the ability to differentiate between the vocalisation of a conspecific, predator, as well as both competitor and non-competitor heterospecifics (Jayne et al., 2015). Vocalisations of the red squirrel typically consist of chirps, growls, and screeches (Gurnell, 1987) and are often accompanied by a particular body movement or position.

Body language plays a crucial role in red squirrel interactions. Through changes in posture, tail movements and foot stamping, squirrels are able to communicate with conspecifics (Gurnell, 1987). Upon encountering a conspecific, squirrels have been observed adopting an alarm position, standing on their hindlimbs, with their tail positioned close to their back (Bosch & Lurz, 2012). This alarm posture may also involve tail flicking, which is a typical alarm response, often accompanied by a cessation of movement, or freezing (Partan et al., 2009). Aggression is common between conspecifics, particularly between animals of the same sex (Wauters & Dhondt, 1989; Wauters & Dhondt, 1993). Squirrels often display aggression by chattering their teeth and stomping their feet (Eibl-Eibesfeldt, 1967; Lurz et al., 2005; Moller, 1986). Encounters with conspecifics may result in high speed chases, accompanied by screaming (Eibl-Eibesfeldt, 1951).

Body language may also be used to avoid confrontation by communicating submission. For example, during mating attempts, males may adopt non-threatening and vulnerable postures such as standing beside the female with their head turned away (Wauters et al., 1990). The male may also make calls that are typically made by juveniles to reaffirm his non-aggressive intentions (Eibl-Eibesfeldt, 1951). Similarly, subordinate individuals may adopt a submissive posture when approaching dominant individuals, signalling their status and reducing the likelihood of a physical confrontation (Diggins, 2021; Eibl-Eibesfeldt, 1951).

1.5 History of squirrels in Ireland

Red squirrels are considered to be native to Ireland, with a history dating back to prehistoric times (Montgomery et al., 2014). It is unclear if the red squirrel became extinct in Ireland during the last glacial maximum and was later reintroduced from Britain, or if populations survived in refugia and recolonised naturally (Finnegan et al., 2008). The earliest known mention of red squirrels in Ireland can be traced back to the 13th century in historical records of taxes on squirrel skins, which were extensively exported from Ireland at the time, indicating their abundance (Scharff, 1922). References to squirrels in Ireland resurface in the 15th and 16th centuries, with mentions in a list of Irish fur-bearing mammals (Le Fanu, 1922) and an account of exports of squirrel skins (Scharff, 1922). A reference to squirrels in Ireland was made again in the 17th century by an Irish writer named Augustin, referring to them by the name *sesquivolos* (Barrington, 1880). Further confirmation of the presence of red squirrels in Ireland in the 17th century is found in a text from 1684 (O'Flaherty, 1846) and the record of the squirrel skin trade at the end of the same century (Moffat, 1923). They are believed to have become very rare between the 17th and 19th centuries, primarily due to deforestation. However, some records of squirrels still exist from this period (K'Eogh, 1739), leading to the conclusion that some populations persisted in refugia at this time (Finnegan et al., 2008; O'Meara, 2018; Scharff, 1922).

During the 19th century there were at least 10 reintroductions of red squirrels to Ireland from Britain, and therefore, indirectly, from mainland Europe (Barrington, 1880). The original source of the British stock used for these 19th century reintroductions have likely since gone extinct in Britain (Finnegan et al., 2008). Recent genetic studies have revealed that the resulting red squirrel population in Ireland comprises a mixture of native, British and European stock (Finnegan et al., 2008; O'Meara, 2018). Subsequently, the red squirrel population successfully reestablished itself in Ireland, and its range continued to expand until the early 20th century (Shorten, 1954). During the 20th century, a second squirrel species was introduced to Ireland. In 1911, twelve grey squirrels (*Sciurus carolinensis*) were introduced to Castleforbes, Co. Longford (O'Teangana et al., 2000; Watt, 1923), from

an established population in Bedfordshire, England (Signorile et al., 2016). The English population had been introduced to England from the United States in the late 1800s (Middleton, 1931). In just over a decade since their introduction, the grey squirrel had become known as a pest species (Watt, 1923). This classification was primarily due to their adverse impact on forestry, where they caused damage through bark stripping, as well as their ability to outcompete the native red squirrel (O'Teangana et al., 2000).

Following a period of establishment, the grey squirrel range began to expand rapidly, and were soon reported in Longford's bordering counties of Westmeath (Stelfox, 1927), Leitrim, Roscommon (Moffat, 1938) and Cavan (Henderson, 1947). Unpublished internal reports by the NPWS showed the continued rapid expansion of the grey squirrel's range throughout the 1960s and 1970s (Teangana et al., 2000). In 1979, a report by Ní Lamhna (1979), documented that their range had extended into much of the eastern half of the country (Figure 1.4). By 2007, grey squirrels were found to be present in 26 of the 32 counties of Ireland (Carey et al., 2007).

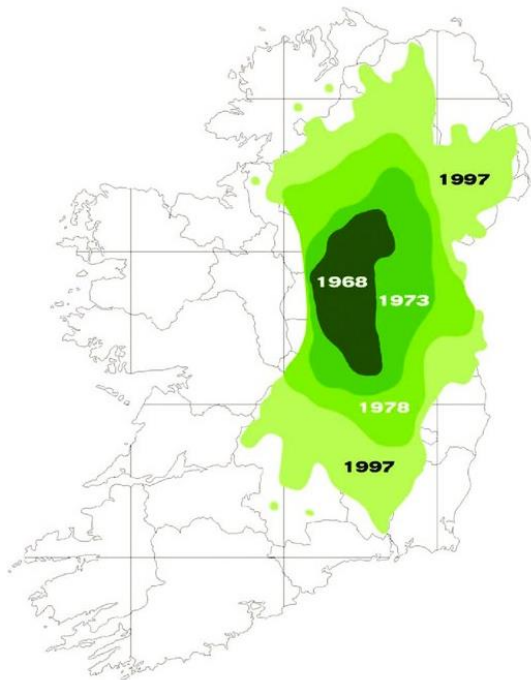


Figure 1.4 The spread of the grey squirrel following its introduction in 1911, as published by Carey et al. (2007), based on information from O' Teangana et al. (2000).

However, the grey squirrel remained absent from the western region of the country, with no grey squirrel populations establishing themselves west of the River Shannon (Carey et al., 2007). This is likely due to the fragmented habitat and lack of suitable corridors in the west

of Ireland, which have created a barrier for both greys and reds (Flaherty & Lawton, 2019; Waters, 2012a). The absence of naturally occurring red squirrels in the far west of the country further supports this observation (Poole & Lawton, 2009) (Figure 1.5).

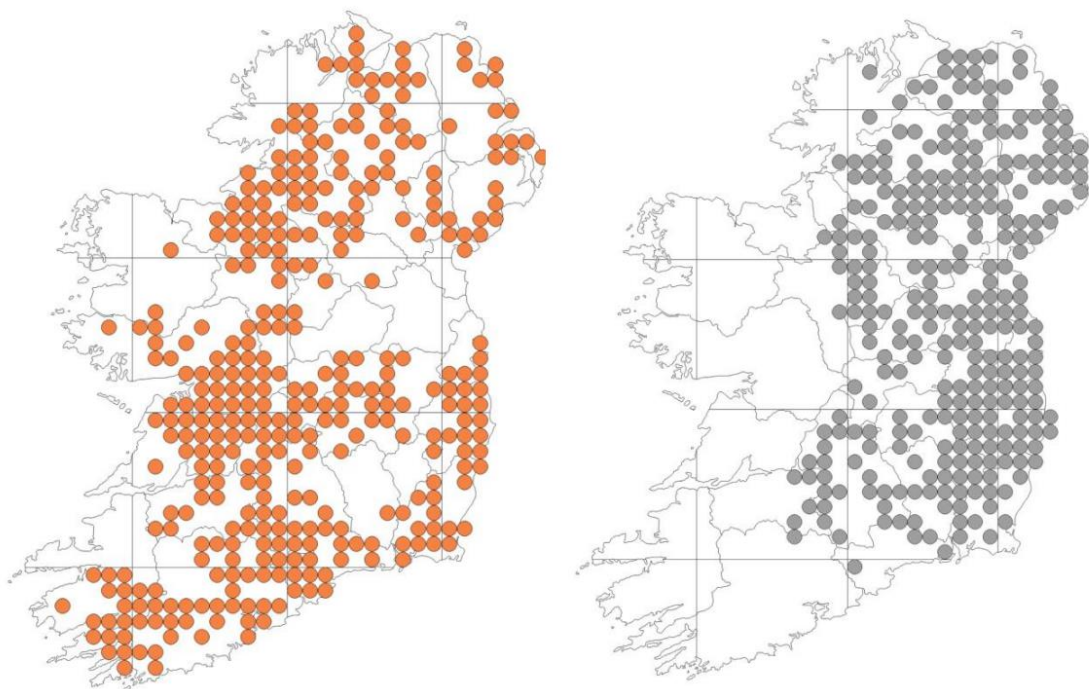


Figure 1.5 Red squirrel (left) and grey squirrel (right) distribution based on 10km squares, as published by Carey et al. (2007).

During this period of rapid grey squirrel expansion, the red squirrel population experienced a dramatic decline primarily due to interspecific competition and the spread of the squirrel pox disease (Carey et al., 2007; Tompkins et al., 2002). Grey squirrels and red squirrels share similar dietary preferences, but the grey squirrel proves to be more adept at exploiting broadleaf food resources (Kenward & Holm, 1989, 1993). Grey squirrels have been found to have higher densities and reproductive rates than red squirrels when both species occur together (Wauters et al., 2000). The presence of grey squirrels adversely affects red squirrel fitness, impacting their breeding and recruitment rates, leading to population declines (Gurnell et al., 2004b). The squirrel pox virus is non-fatal to grey squirrels but causes death in red squirrels within two weeks of infection (Tompkins et al., 2002). The introduction of the grey squirrel is responsible for the transmission of this disease to the red squirrel population (Sainsbury & Gurnell, 1995). The first case of squirrel pox on the island of Ireland was reported in County Down in March 2011 (McInnes et al., 2013). Numerous cases of squirrel pox have been reported since, including a case in Wicklow (Naulty et al., 2013),

and recently, a 2021 outbreak in County Down, resulting in the complete mortality of the red squirrel population (Bell, 2022). A model simulating the presence of squirrel pox in red and grey squirrel occupied habitats found that the presence of squirrel pox accelerated red squirrel replacement by grey squirrels at a rate 17-25 times faster than in its absence (Rushton et al., 2006).

In 2007, it was noted for the first time that the grey squirrel population was declining when it was observed to be absent from parts of the midlands where it had once been common (Carey et al., 2007). By 2012, the contraction of the grey squirrel range became even more pronounced (Lawton et al., 2015a). This trend continued in the subsequent years, with the grey squirrel's range shrinking to only 62% of its 2012 extent, as reported in the All-Ireland Squirrel and Pine Marten Survey of 2019 (Lawton et al., 2019). This contraction in the grey squirrel range was mirrored by a recovery of the red squirrel, who have now become reestablished in much of their historical range (Lawton et al., 2019) (Figure 1.6).

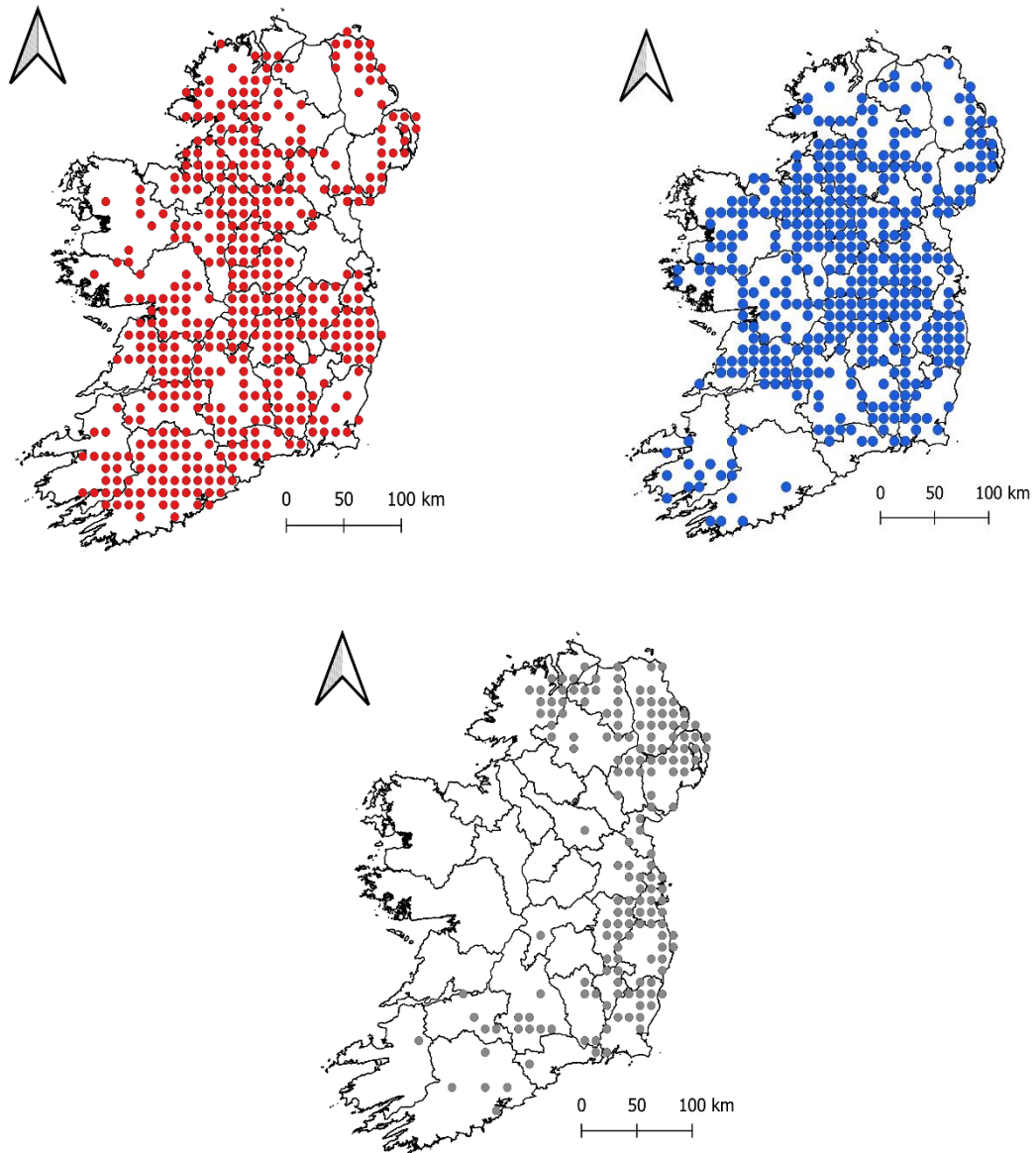


Figure 1.6 Red squirrel (top left), pine marten (top right) and grey squirrel (bottom) distribution, based on 10km squares, published in the All-Ireland Squirrel and Pine Marten Survey 2019 (Lawton et al., 2019)

The initial observations of the grey squirrel decline were anecdotally linked to the resurgence of the pine marten (*Martes martes*) by Carey et al. (2007). The pine marten is a native Irish carnivore known for its tree-climbing abilities and diverse diet, which includes small mammals (Herrero et al., 2016). After facing near extinction due to persecution and deforestation (O'Sullivan, 1983), the pine marten gained protection under the Wildlife Act of 1976, allowing for its subsequent recovery. The 2012 Irish Squirrel Survey revealed a dense population of pine martens in the midlands and west, coinciding with the reduction of the grey squirrel range in the midlands (Lawton et al., 2015a). Subsequent studies revealed a strong negative correlation between the presence of grey squirrels and pine marten, along with a positive correlation between pine marten and red squirrels (Sheehy & Lawton, 2014; Sheehy et al., 2018). These findings are reflected in the 2019 All Ireland Squirrel and Pine Marten Survey, where there is significant overlap between the pine marten and red squirrel, while very little overlap is observed between pine marten and grey squirrels (Lawton et al., 2019). Currently, the grey squirrel is primarily distributed in urban areas such as Dublin and Belfast, which are unsuitable habitats for pine marten (Lawton et al., 2019).

It has been hypothesised that grey squirrels exhibit predator naiveté in response to the presence of the pine marten, a trait not shared by the red squirrel due to its evolutionary history with the pine marten (Sheehy et al., 2018; Twining et al., 2020a). This predator naiveté makes grey squirrels more vulnerable to predation by pine martens, as evidenced by their higher frequency in pine marten scats compared to red squirrels (Twining et al., 2022a). This vulnerability appears to be a significant factor driving the recent changes in distributions of the two squirrel populations in Ireland.

1.6 Translocations

The International Union for Conservation of Nature (IUCN) defines a translocation as the human-mediated movement of living organisms from one area to be released in another (IUCN/SSC, 2013). Translocations may be undertaken for a variety of reasons including conservation efforts, the release of rehabilitated animals, as well as for commercial or aesthetic reasons (Seddon, 2010). The most common reason for translocations is for the purpose of conservation. Conservation translocations (hereafter referred to as translocations) are a critical tool used to prevent the extinction of species and restore ecosystems (Gaywood et al., 2022). With approximately one million species currently facing

the threat of extinction (IPBES, 2019), it is vital that we employ every available conservation method, including translocations.

Translocations may be used to reintroduce animals within their historical range, to areas where it has been lost. Reintroductions have had much success in the conservation of many species (Seddon et al., 2014). However, translocations are extremely complex, requiring extensive knowledge of the target species' behaviour and ecology, sufficient funding, support from local communities, coordination among stakeholders and a well-designed post-release monitoring plan (Berger-Tal et al., 2020). Due to this complexity, combined with poor management in many cases (Griffith et al., 1989), translocations have suffered many failures (Taylor et al., 2017). The potential adverse consequences of mismanaged translocations have been well-documented (Bubac et al., 2019). Relocated animals face the risk of mortality, particularly when they are captive-born (Jule et al., 2008). Resident species may suffer negative impacts, and diseases may spread as a result of this mismanagement (Chipman et al., 2008). However, negative impacts on an ecosystem scale are now relatively rare, with most cases occurring before the 1980s, prior to the introduction of rigorous and regulated translocation guidelines (Novak et al., 2021). These strict guidelines, such as those laid out by the IUCN (IUCN, 1987; IUCN/SSC, 1998, 2013) outline best practices, ensuring translocations are conducted in a responsible and effective manner.

The IUCN identifies post-release monitoring as a vital aspect of a responsible translocation project (IUCN/SSC, 2013). Monitoring the population after release allows for the assessment of the survival of the population and success of the project. Additionally, post-release monitoring facilitates the early detection of potential issues, enabling adaptive management strategies to be implemented (Armstrong & Seddon, 2008; Gaywood et al., 2022). Genetic monitoring is an important aspect of post-release monitoring efforts as it informs researchers about the risk of inbreeding depression (Neaves et al., 2022). By understanding the genetic status of the population, conservationists can take appropriate mitigation responses, such as introducing additional individuals to enhance genetic diversity (Sigg, 2006).

Many translocation projects have been criticised due to their inadequate monitoring practices (Armstrong & Seddon, 2008; Scott et al., 2010). A lack of long-term monitoring or indeed, any monitoring, can lead researchers to prematurely and mistakenly label a project as successful, when the true outcome remains unclear (Fischer & Lindenmayer, 2000). While most failures occur within four years of their initial introduction (Bubac et al., 2019), there have been instances of translocations failing more than a decade after the original

introduction (Bubac et al., 2019; Hambler, 1994), when the majority of post-release monitoring attempts have ceased (Bubac et al., 2019). In order to ensure an accurate assessment of the success of the translocation and avoid premature termination of monitoring efforts, the progress of the project may be measured according to its phase. The three phases of a translocation are the establishment phase, the growth phase and the regulation phase (IUCN/SSC, 2013). Establishment is achieved if the population survives the translocation process and remains in the new environment. The growth phase is achieved when the population expand in density and range. Finally, the regulation phase is characterised by a plateauing in population density, once carrying capacity has been met. Fluctuations in population density, resulting from variations in available resources (Andr n & Lemnell, 1992), as well as density dependent factors (Wauters et al., 2004) may occur during the regulation phase. These phases serve as distinct milestones for assessing the success of the population and encourage long-term monitoring efforts.

Post-release monitoring is also critical for planning future translocation projects (Nichols & Armstrong, 2012). By monitoring the outcomes of a translocation, researchers can identify success factors and potential pitfalls that may be used to inform future projects. Many translocation projects have failed due to species-specific reactions to relocations (Berger-Tal et al., 2020). Behaviours such as dispersal tendencies (Bell et al., 2010; Sasmal et al., 2015), social structures (Shier & Swaisgood, 2012) and habituation tendencies (Valutis & Marzluff, 1999) may all affect the success of a translocation, the effects of which may not be obvious to the researcher prior to the translocation (Berger-Tal et al., 2020). However, once reported, a species-specific adapted strategy may be put in place. Additionally, animals whose life histories may preclude monitoring to the final phase of the project can benefit from the findings of translocation projects involving short-lived animals (Armstrong & Reynolds, 2012).

In conclusion, proper long-term monitoring is crucial not only for the success of the translocation project, but also for optimisation of best practices for future translocation projects.

1.7 Past red squirrel translocations

A total of twelve red squirrel translocation studies have been carried out across Ireland, Britain, and Europe since the 1980s, yielding mixed results. One of the main causes of translocation failures is an inability to address the underlying cause of the population decline (Fischer & Lindenmayer, 2000). For red squirrels, the presence of the grey squirrel has proven to be a significant challenge to translocation efforts. Among the twelve studies, seven were conducted in regions where grey squirrels were present (Lawton et al., 2015b;

Toomey, 2012). Of these, three British projects identified grey squirrel presence and the squirrel pox virus as the primary factors for failure (Bertram & Moltu, 1986; Jackson, 1998; Kenward & Hodder, 1998), with another English study citing these factors as contributing significantly to failure following an initial success (Carroll et al., 2009). However, two projects on Anglesey, Wales, were successful in spite of the grey squirrel presence, and were conducted in conjunction with grey squirrel eradication efforts (Shuttleworth, 2010; Shuttleworth et al., 2009). One project, located in Killiney Hill, Dublin (Toomey, 2012) is currently undergoing mitigation measures, and its outcome is yet to be determined. Among the five projects that did not occur in the presence of the grey squirrel, one Scottish (Dennis et al., 2011), one Italian (Fornasari et al., 1997), and two Irish (Poole & Lawton, 2009; Waters, 2012b) reintroductions were deemed successful. The outcome of a project that occurred in Belgium is unknown (Wauters et al., 1997a). Additional releases of red squirrels in Northern Ireland sourced from a captive bred stock at Belfast zoo have occurred in the last decade, although no formal study has been conducted (Bell et al., 2022).

All successful translocation projects implemented post-release monitoring for at least a year after the release, with durations varying considerably between projects. A range of techniques including live trapping, radio telemetry, drey counts and feeding surveys were commonly used to assess their success. Typically, the health of the population serves as a fundamental gauge of success, with the number of new recruits being used as a success metric in multiple studies (Poole & Lawton, 2009; Shuttleworth et al., 2009; Wauters et al., 1997a). Subsequent monitoring has occurred in six of the seven translocation projects (Carroll et al., 2009; Everest et al., 2012; Fornasari et al., 1997; Ogden & McEwing, 2011; Waters, 2012b), with the frequencies and intervals between monitoring projects varying widely. Although considered successful, the phases which the populations reached are unclear in the majority of the follow up studies. Monitoring of two successful red squirrel translocations, conducted at least ten years after the initial release, revealed instances of disease outbreaks within the populations. In one project, the presence of both squirrel pox virus and adenovirus led to the failure of the translocation (Carroll et al., 2009). The second project was ultimately successful, but the prevalence of adenovirus had a notable adverse impact on the translocation (Everest et al., 2012). These projects highlight the vulnerability of translocated populations and underscore the importance of long-term monitoring.

Two translocations took place in the west of Ireland, as part of an effort to protect the Irish red squirrel population from the threat posed by the grey squirrel. In 2005, nineteen red squirrels were translocated to Derryclare woods in Connemara (Poole & Lawton, 2009). Subsequently, in 2007, fifteen red squirrels were translocated to Belleek woods in Co. Mayo. Insights from past red squirrel translocations informed the selection of translocation

sites and procedures. Both sites are situated in the west of Ireland, where the grey squirrel is absent. At the time of the translocations, Derryclare consisted of 432 hectares of mature woodland, and Belleek consisted of 80 hectares of mature woodland, surpassing the recommended minimum of 50 hectares for a red squirrel translocation (Wauters et al., 1997a; Wauters et al., 1997b). Feasibility studies indicated that the carrying capacities of Derryclare and Belleek were 115 and 65, respectively. Both sites posed their respective challenges to the projects. On one hand, Derryclare, being a commercial woodland, was susceptible to disturbances. On the other hand, Belleek's limited size resulted in a low carrying capacity (Lawton, 2006). Despite these challenges, both locations offered various advantages, including very low grey squirrel threat levels, strong public and management backing, and high-quality habitat conditions.

The source populations were taken from donor sites where the removal of individuals would not adversely affect the populations. These sites were chosen for their proximity to the translocation sites, ensuring genetic continuity within the region and minimal transportation distances. Importantly, source populations did not contain grey squirrels, meaning that translocated individuals were not at risk of carrying the squirrel pox virus. Derryclare squirrels were sourced from Portumna forest in Co. Galway, while the Belleek population was sourced from Lough Key Forest Park in Co. Roscommon, and Union Wood in Co. Sligo. The number of translocated individuals were based on Poole's (2007) Population Viability Analysis, which recommended of a minimum initial breeding population of 13 individuals (including 7 females), with additional squirrels included to account for mortalities. A soft release technique was employed for both translocations, meaning that squirrels were kept in enclosures for several weeks in their new habitat before being released. Soft releases facilitate health monitoring and acclimatisation, increasing their likelihood of remaining in the new habitat (Tetzlaff et al., 2019). A fault in the Belleek enclosure resulted in an accidental hard release, although it was not believed to affect the success of the introduction (Waters, 2012b).

Both translocations successfully transitioned from the establishment phase into the growth phase, with 68% of Derryclare squirrels (Poole & Lawton, 2009) and 67% of Belleek squirrels (Waters, 2012b) surviving to the start of the breeding season. Positive signs of breeding were subsequently observed at both sites during the first breeding season. In the first year of the translocation, seven new recruits were trapped in Derryclare, while twelve new recruits were recorded in Belleek, indicating successful breeding in both populations. A follow-up study in 2012 confirmed the persistence of squirrels in Derryclare, with population estimates peaking at 51 individuals (Waters, 2012b). Additional positive

breeding signs were noted, along with the expansion of the population's range further into the woodland. Both sites were subsequently monitored passively.

1.8 Project Aims

The primary aim of this project was to assess the outcome of two red squirrel translocations in the west of Ireland and identify factors that influenced the success or failure of the projects. Our first aim was to investigate changes to the Derryclare habitat, specifically a deterioration in quality through the loss of habitat caused by frequent felling operations and a significant forest fire in 2011. In contrast, Belleek witnessed no such habitat changes, negating the need for an updated habitat assessment. We hypothesised that the mature habitat available to the population in Derryclare had declined since the introduction of the squirrel population. Our aim was to quantify the extent of this habitat loss and investigate its impact on the carrying capacity of the woods. The effect of this habitat loss on the quality of the habitat will be assessed. Additionally, the outcome of the translocation will also be investigated by estimating changes in the population abundance.

Our second aim was to investigate the distribution and demographics of the translocated populations. Information on presence, range and density was used to assess whether the populations had successfully transitioned from the growth phase to the regulation phase. Additionally, demographic metrics such as weight, shinbone length and breeding status were used to assess the overall fitness of the populations. Home range use data were gathered to assess space use within the woods. An investigation into their distributions extended beyond the woods, encompassing neighbouring woodlands in the case of Derryclare, and neighbouring landscape in the case of Belleek. Signs of a population spread or lack thereof, provided valuable insights into the growth rate of the population, and revealed whether the translocation had achieved the original goal of expanding the red squirrel distribution in the west of Ireland.

Furthermore, we aimed to assess the variations in behaviour between the two populations, which we hypothesised would be influenced by their contrasting environments. We also aimed to explore the relationships between observed behaviours and demographic parameters such as sex, age, breeding status and morphological characteristics, as well as extrinsic factors such as season. Additionally, we aimed to assess the advantages of expressing particular behaviours in relation to the individual's survival and reproductive output.

Finally, we aimed to investigate the response of the red squirrel to the recent presence of its native predator, the pine marten. In doing so we hoped to reveal insights into the

recovery of the red squirrel population following the resurgence of the pine marten, in direct contrast to the decline of the grey squirrel.

In conclusion, this project aimed to assess the outcomes of the two red squirrel translocations in the west of Ireland, while also gathering information on the factors that affected these outcomes, and contributing to the literature on red squirrel ecology. By understanding the factors that influence a translocation outcome, we can provide valuable insights and recommendations that may inform future translocation projects, enhancing their effectiveness. Additionally, the information gathered on red squirrel ecology and behaviour may contribute to the development of more integrated conservation strategies in the future, while also shedding light on the complex and influential relationship between the red squirrel and the pine marten.

2 Investigating changes to the habitat in Derryclare

2.1 Introduction

Translocations, the deliberate movement of organisms from one location to another (IUCN/SSC, 2013), are an effective conservation tool used to recover populations and reduce extinction rates (Berger-Tal et al., 2020). However, translocations are inherently risky and prone to failure (Fischer & Lindenmayer, 2000), mainly due to their low population numbers (Verbeylen et al., 2003) and isolation (Fahrig & Merriam, 1985), making them susceptible to extinction. Generally, the success of a translocation is measured by the establishment of a self-sustaining population (Fischer & Lindenmayer, 2000). However, this definition is controversial as it can only indicate success at the time of assessment and does not necessarily indicate the long-term viability of the population (Seddon, 1999). To address this concern, an alternative approach to evaluating the success of translocations is to define specific objectives for the various phases of the project (IUCN/SSC, 2013). A translocation project may be divided into three distinct phases: the establishment phase, the growth phase and the regulation phase (IUCN/SSC, 2013). The duration of each stage is dependent on the life history traits of the target species, but the success of the stage may be determined by the same general outcomes (Seddon, 1999).

A translocation may be considered to have successfully entered the establishment phase if the initial translocation group survives the translocation process and remains in the new habitat (IUCN/SSC, 2013). The period immediately following release poses considerable challenges, with high mortality rates within the first few weeks (Calvete & Estrada, 2004), mainly due to predation (Calvete & Estrada, 2004; Davis, 1983; Metzgab, 1967) and an increased vulnerability due to handling and relocation stress (Dickens et al., 2010). Homing behaviours and hyperdispersal, which may lead to the departure of part or the entire founding population, also pose serious threats to the success of a translocation (Bilby & Moseby, 2023; Guilbert et al., 2007; Jones et al., 2003; Short & Turner, 2000; Steen, 1994). If the population successfully survives these challenges it will enter the growth phase (IUCN/SSC, 2013). This phase is characterised by the successful reproduction of the founding population and their offspring (Seddon, 1999), and expansion of their range (IUCN/SSC, 2013). However, numerous factors can impede this growth, including predation (Moseby et al., 2011; Plein et al., 2016), competition for resources (Danielson & Gaines, 1987; Losos & Spiller, 1999), and an unsuitable habitat (Blyton et al., 2023; Nafus et al., 2017). Additionally, the failure to remove the original issue prompting the translocation (Fischer & Lindenmayer, 2000; Wilson, 2018) and social structure disruption (Shier, 2006; Shier & Swaisgood, 2012) can also hinder population expansion and survival during the

growth phase. While these factors may not directly cause mortality in the founding population, their cumulative negative effects may become apparent over time, affecting the overall success of the translocation. The final phase of a translocation, known as the regulation phase (IUCN/SSC, 2013), is characterised by the continued presence of the population and a stabilised population density. Threats such as inbreeding depression, disease, human disturbance, and habitat-related factors such as habitat loss and deterioration in habitat quality may all impact the success of the translocation in the long-term (IUCN/SSC, 2013).

Threats to the success of the regulation phase are generally cumulative over time, and do not have immediate effects on the population. Long-term monitoring is required to reveal the extent of these effects on the population, and reveal the true success of the translocation. For example, the effects of habitat-related factors may be delayed, leading to a decline in the population years after the habitat change (Lira et al., 2019). For translocated individuals, the translocation process itself induces a change in their habitat, meaning that delayed responses in the population to their new environment should be expected in the years following their introduction. Habitat-related factors play a crucial role in the success or failure of translocation efforts (Berger-Tal et al., 2020; Bubac et al., 2019). Habitat loss, often cited as the reason for initiating a translocation project (Griffith et al., 1989; Seddon, 2010), can also be a primary factor contributing to its failure in the long term (Bubac et al., 2019). Habitat loss has several negative consequences for a population including a reduced carrying capacity (Devore, 2014), disruptions in the social structure (Verbeylen et al., 2009), heightened predation risks (Lawrence, 1966; Leahy et al., 2016), fragmentation (Stratford & Robinson, 2005), and reduced food availability (Merrick et al., 2021). Habitat loss has detrimental effects on small mammal abundance (Engstrom, 2010; Johnstone et al., 2014; Legge et al., 2008), with some species exhibiting weak to no recovery capabilities in the years following the initial habitat loss (Pardon et al., 2003). As a habitat specialist, the red squirrel (*Sciurus vulgaris*) is particularly vulnerable to habitat loss (Ellis & Coppins, 2007; Sullivan & Moses, 1986).

Poor habitat quality, whether preexisting or as a result of deterioration, is one of the leading causes of translocation failures (Bellis et al., 2019; Griffith et al., 1989; Wolf et al., 1996). The suitability of a habitat depends on characteristics such as habitat structure, composition, and resource availability, in combination with the specific requirements of the target species. Unsuitable habitats may negatively impact reproductive output (Harig & Fausch, 2002), survival (Blyton et al., 2023; Nafus et al., 2017), and population density (Johnson et al., 2018; Moorhouse et al., 2009). For the red squirrel, food availability is the primary factor influencing population densities (Wauters et al., 2008) and is crucial in

determining reproductive output (Rodrigues et al., 2010). Consequently, a decline in the quality of the food source could have severe implications for the population's overall health and long-term viability.

The translocation of red squirrels to Derryclare woods was conducted in 2005 in an effort to conserve the Irish red squirrel population. This site was chosen based on its size, age structure and tree composition (Poole & Lawton, 2009). Additionally, Derryclare woods is free from the presence of the invasive grey squirrel (*Sciurus carolinensis*), the underlying cause for the decline in the red squirrel population (Teangana et al., 2000). The future of the translocated population was investigated during the planning stage. Specifically, a population viability analysis was conducted, accounting for the effects of inbreeding depression, and the mean probability of extinction after 20 years was estimated at 0.125 (Poole, 2007). Monitoring of the establishment phase by Poole and Lawton (2009) from 2005 to 2007 found that 68.4% of the 19 individuals survived to the start of the breeding season, surpassing the target figure of 50% recommended by Venning (1997) in red squirrel translocations. Their initial survival and continued presence in the woodland indicated the success of the translocation through the establishment phase. Subsequent monitoring of the translocated population was conducted by Waters (2012a) from 2008 to 2012. This study revealed that the population was continuing to develop through the growth phase, with an estimated population of 51, as determined through live trapping, and an expansion of their range into new areas within the woodland.

In the years following the introduction of the red squirrels, the habitat underwent several changes, some of which were unforeseen. Expected and unexpected clear-felling operations occurred multiple times in the coniferous section of Derryclare from 2005 onwards, due to its commercial nature. Additionally, the forest suffered from an unexpected and significant fire in 2011. Although no direct squirrel mortalities were found to be caused by the fire or felling (Waters, 2012a), the long-term effects on the habitat and subsequent impact on the red squirrel population, including any possible delayed response to these combined habitat losses, remain unknown.

The aim of our study is to investigate the current habitat available to the population, and determine the impact of clear-felling and fire on the potential carrying capacity of the woodland. Specifically, we will quantify the area lost since 2005 by digitising historical map data of Derryclare and comparing it to the current available habitat. To investigate changes in the carrying capacity of the woodland and variations in actual population size since the translocation, we will conduct a feeding survey. The results of our feeding survey will then be compared to feeding survey data from 2008-2012, allowing us to track the available and

consumed energy for all surveyed years. An additional estimate of the carrying capacity of the woods will be calculated based on the available woodland area, for the year of the initial translocation and the years of the feeding surveys. We hypothesise that there has been a loss of available suitable habitat through clear-felling and fire, and that this in turn has reduced the red squirrel carrying capacity of the woodland. We also predict that this habitat loss will impact the success of the translocation.

2.2 Methods

2.2.1 Study site

Derryclare commercial forest is a 570-hectare woodland located in Connemara, Co. Galway, situated at the foot of Mount Derryclare, one of The Twelve Bens. The forest was planted in the 1960s and is managed by the state-owned commercial forestry business, Coillte. It primarily comprises two coniferous species, lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*). Other species present in Derryclare include heather (*Calluna vulgaris*), Japanese Larch (*Larix kaempferi*) and moor grass (*Molinia caerulea*). According to Coillte data reported in Waters (2012) 31% of the woodland is bare or felled. Adjacent to the commercial woodland is a 19-hectare nature reserve owned by the National Parks and Wildlife Service. Within the nature reserve, 13 hectares comprise mature broadleaf woodland, consisting primarily of oak (*Quercus petraea*), ash (*Fraxinus excelsior*), birch (*Betula sp.*) and hazel (*Corylus avellana*). The remaining area consists of young birch plantations (*Betula spp.*) and wetland.

2.2.2 Investigating extent of habitat loss

The composition of Derryclare has undergone significant changes since the introduction of red squirrels to the woodland in 2005. To quantify these changes, maps from the establishment phase monitoring project (Poole & Lawton, 2009) and growth phase monitoring project (Waters, 2012a), which were based on Coillte data, were digitised manually using QGIS. This process involved overlaying the old maps on a recent map containing woodland stand borders and reclassifying the stands according to the old maps. The resulting maps detailed the habitat composition of Derryclare for the years 2005 and 2008-2011. Precise composition data for other years was not available. The composition of Derryclare in 2021 was mapped on QGIS using recent Coillte data and validated through personal on-site observations.

For each digital map, woodland stands were classified as either mature woodland, immature woodland, bare woodland, or other species (refer to “Study site”). Mature

woodland was categorised as any stand consisting of lodgepole pine or Sitka spruce aged 25 years or older, as this is the age at which stands begin producing a good cone crop (Gurnell et al., 2001). Stands below this age were classified as immature. Immature stands cannot sustain a red squirrel population, although can still facilitate movement through the habitat (Gurnell et al., 2001).

2.2.3 Feeding surveys

Feeding surveys were conducted to assess the carrying capacity of Derryclare and estimate the actual red squirrel population size. The surveys took place in October 2021. Cones were collected along 33 transect lines, each measuring 50m in length and 1m in width. Surveys encompassed all mature stands, as immature, bare and felled areas cannot support red squirrel populations. A small proportion of the mature woodland was inaccessible, and therefore not surveyed, as illustrated in figure 2.1. The starting points of all transects were located at least 100m apart.

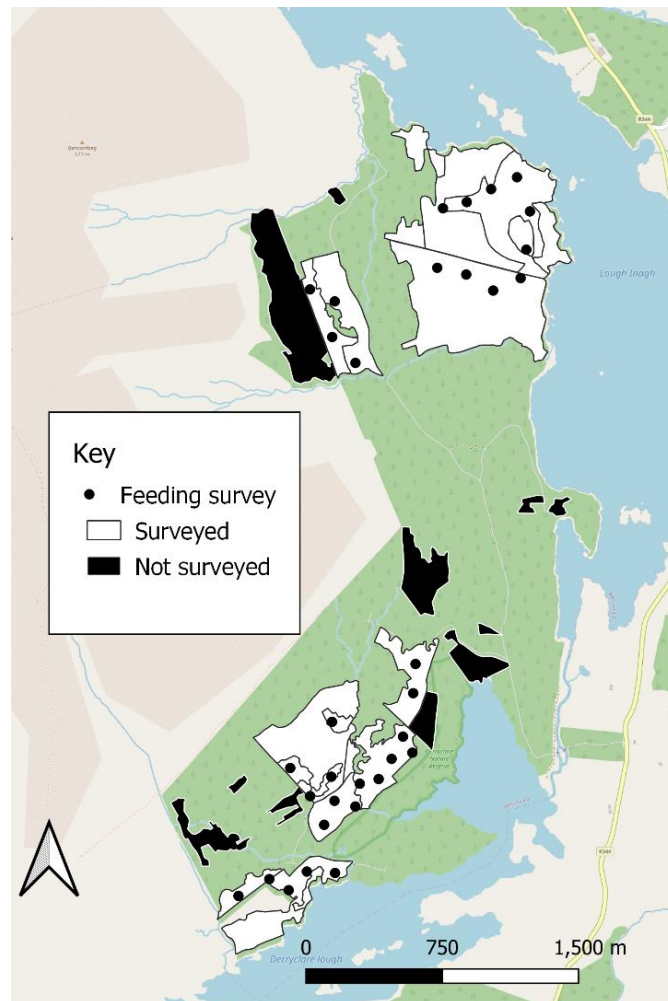


Figure 2.1 Derryclare Woods, depicting mature woodland stands in 2021 and feeding survey transect locations.

During the surveys, unconsumed cones were identified by tree species and counted. Consumed cones were also identified, counted, and collected. Additionally, a sample of unconsumed cones from each block was collected (approximately 5-10 cones per transect of each tree species, depending on availability) for the purpose of estimating seed numbers.

In order to assess the number of squirrels the woodland could theoretically support, it was necessary to calculate the energy values of the cones of both tree species in Derryclare. This was achieved by obtaining the average length of each species' cone, calculating the corresponding number of seeds, and multiplying this by the energy value of each species' seed.

All collected lodgepole pine and Sitka spruce cones were measured and their lengths were recorded. Measurements were made to the nearest 0.1mm using Vernier callipers. To estimate the number of seeds per Sitka spruce cone, a random subsample ($n = 110$) of

unconsumed cones from various stands was selected for scale counting. The lengths of the Sitka spruce cones were then plotted against the corresponding number of scales per cone, and a regression analysis was used to calculate the estimated number of seeds for the average Sitka spruce cone.

Unlike Sitka spruce cones, scale counting is not an accurate method for determining the number of seeds in lodgepole pine cones (Benkman et al., 2001). Therefore, an alternative seed estimation method was used. This involved applying a lodgepole pine-specific equation reported in the literature (McNab et al., 2019) to the average cone length found in Derryclare, to calculate the estimated number of seeds per average cone. The average lodgepole pine cone length was based on a subsample of 179 unconsumed cones from various stands.

The energy values assigned to Sitka spruce and lodgepole pine seeds were 0.04 kJ and 0.098 kJ, respectively, as reported by Gurnell et al. (2001). These values were then multiplied by the number of seeds in the average cone to calculate the energy content per cone. By further multiplying this value by the cone density, the energy per m² was determined. This value was then extrapolated to the mature area in the woodland.

To estimate the potential squirrel population that the woods could sustain, the energy requirements of a red squirrel, ranging from 400 kJ to 700 kJ, as indicated by Gurnell et al. (2001) were utilised. To estimate the number of squirrels present in the woodland, these calculations were repeated using the densities of consumed cones and extrapolated to all mature areas, as positive squirrel signs were observed in all surveyed stands.

Carrying capacities and estimated population sizes during the growth phase monitoring project (2008-2011) were estimated using unconsumed and consumed cone density data reported by Waters (2012a). These surveys were all conducted in late autumn to winter, with the exception of two additional spring and summer surveys in 2010. The average lengths of lodgepole pine cones for these years were obtained from Waters (2012) and substituted into the seed number estimation formula provided by McNab (2019), for consistency. Length data for Sitka spruce was unavailable for those years, so the average length from the 2021 survey was used. Energy values were then determined using the previously described methodology. These values were used to estimate the total energy available in the mature woodland at the time of the survey, as determined by the digitised maps. Subsequently, the total energy consumed by the squirrels was estimated by extrapolating the energy values to the actual area occupied by the squirrels at the time of each survey, as reported in the growth phase study (Waters, 2012a). Carrying capacities

were calculated by dividing the total energy available by the energy requirements of a red squirrel, as described above.

Additionally, an alternative estimation of Derryclare's carrying capacity was conducted, based on a density of 0.32 red squirrels found in a similar lodgepole pine/ Sitka spruce mix woodland in northern England (Lurz & Garson, 1997). This method relies solely on the total area of mature woodland, rather than cone density. The carrying capacity of the woods was calculated using this method for the regulation phase study (2021), considering all available mature woodland. Subsequently, this carrying capacity estimation method was applied to the mature woodland areas available during both the growth phase study (2008-2011) and the establishment phase study (2005).

2.2.4 Composition change

The examination of unpublished data provided by Waters exposed a discrepancy in the mapping, revealing that the true composition of the stands in Derryclare is not accurately reflected by the Coillte map data. Specifically, Sitka spruce was found to be more abundant than recent Coillte data suggested. This inconsistency between the map data and actual composition impacted the carrying capacity of the woodland, prompting an investigation in the present study to reveal the true composition of the stands during the regulation phase study (2021).

To address this issue, a sample stand with a known ratio of lodgepole pine to Sitka spruce, based on unpublished data from Waters, was selected. We compared the percentage composition of trees in this sample stand to the density of cones produced by each species, as recorded in the 2021 feeding survey. By calculating the ratio of cone density to tree species percentage composition, it was possible to apply this formula to the known cone densities of other stands, thereby calculating the actual tree species ratio in each respective area.

By employing this approach, we obtained a more accurate representation of the woodland's current composition. This updated composition was retrospectively used to update the 2021 map of Derryclare, as well as the carrying capacity estimation. All reported results are based on the updated composition described here, unless stated otherwise.

2.3 Results

2.3.1 Change in habitat

The internal structure of the woodland has undergone significant changes since the introduction of the translocated red squirrels in 2005 (Figure 2.2). In 2021, 202 ha are comprised of mature stands, representing a substantial reduction from the 432 ha of mature

woodland present in 2005. This reduction of 53% (230 ha) over 16 years was caused by clear felling (172 ha) and the fire in 2011 (58 ha) (Figure 2.3). The composition of Derryclare in 2021 can be seen in figure 2.4.

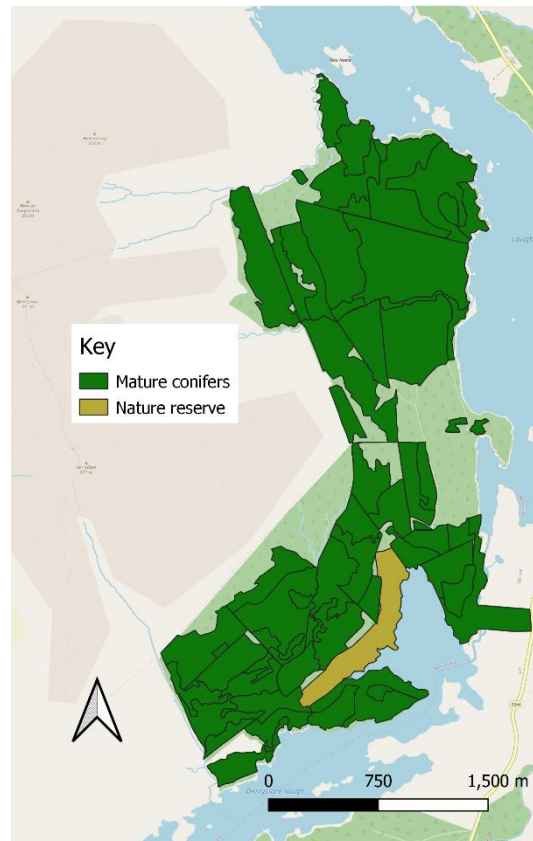


Figure 2.2 The composition of Derryclare in 2005.

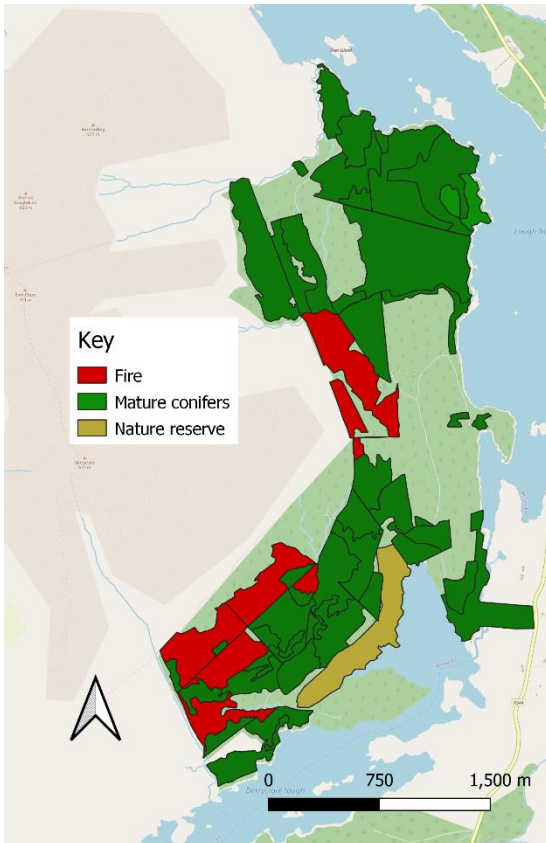


Figure 2.4 The composition of Derryclare in 2011. Areas destroyed by the fire of April 2011 are marked in red.

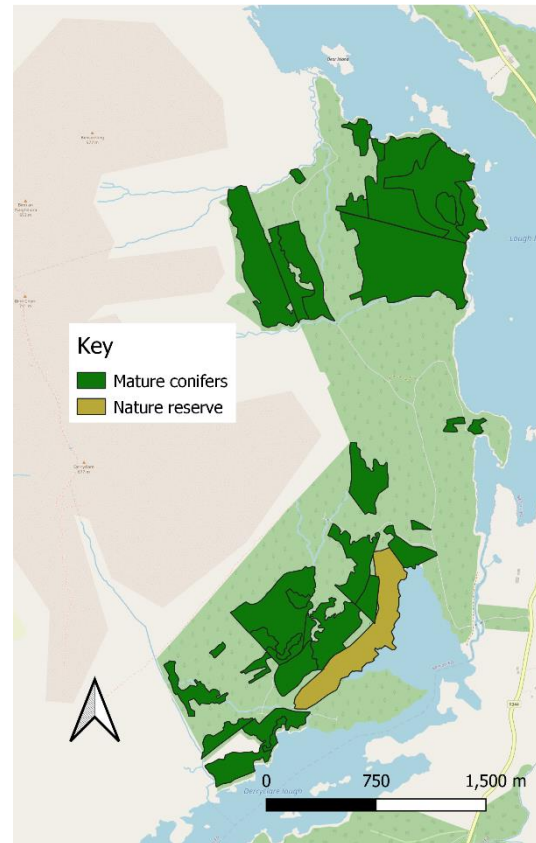


Figure 2.3 The composition of Derryclare in 2021.

In terms of woodland composition, there has been a 42% reduction in the coverage of Sitka spruce, and a 60% reduction in the coverage of lodgepole pine since 2005 (Table 2.1). All Sitka spruce loss is due to clear felling, while 35% (58 ha) of the lodgepole pine loss was caused by the fire of April 2011. Additionally, 21% (35 ha) of the reduction in lodgepole pine coverage can be attributed to misrepresentation on the map, as described in section 2.4.

Year	Broadleaf (ha)	Sitka (ha)	spruce	Lodgepole (ha)	Mature conifers (ha)	Unsuitable (ha)
2005	13	156		276	432	138
2008	13	123		269	392	178
2009	13	108		246	354	216
2010	13	107		226	333	237
2011 (pre fire)	13	93		220	313	257
2011 (post fire)	13	93		162	255	315
2021	13	91		111	202	368

Table 2.1 Composition of Derryclare woodland, during the establishment (2005), growth (2008-2011) and regulation (2021) project phases, including the nature reserve (broadleaf), and immature, felled, or bare stands (unsuitable). All values are rounded to the nearest hectare.

2.3.2 The 2021 Feeding survey

In the 2021 feeding survey, a total of 33 transects were conducted in Derryclare commercial woodland, covering an area of 1650m². During the survey, 1032 lodgepole pine cones were counted, 63 of which were found to have been consumed. A total of 5599 Sitka spruce cones were counted, including 136 consumed cones. All collected Sitka spruce cones (consumed; n = 136, unconsumed; n = 215) were measured and found to have an average length of 48.1mm (n = 351).

A subsample of 110 Sitka spruce cones were randomly selected and a strong positive correlation ($R^2 = 0.7027$) was observed between the number of scales, and therefore seeds, and the cone length (n = 110) (Figure 2.5). The mean number of seeds in a Sitka spruce cone was calculated to be 117.2, with an energy value of 4.686 kJ per cone.

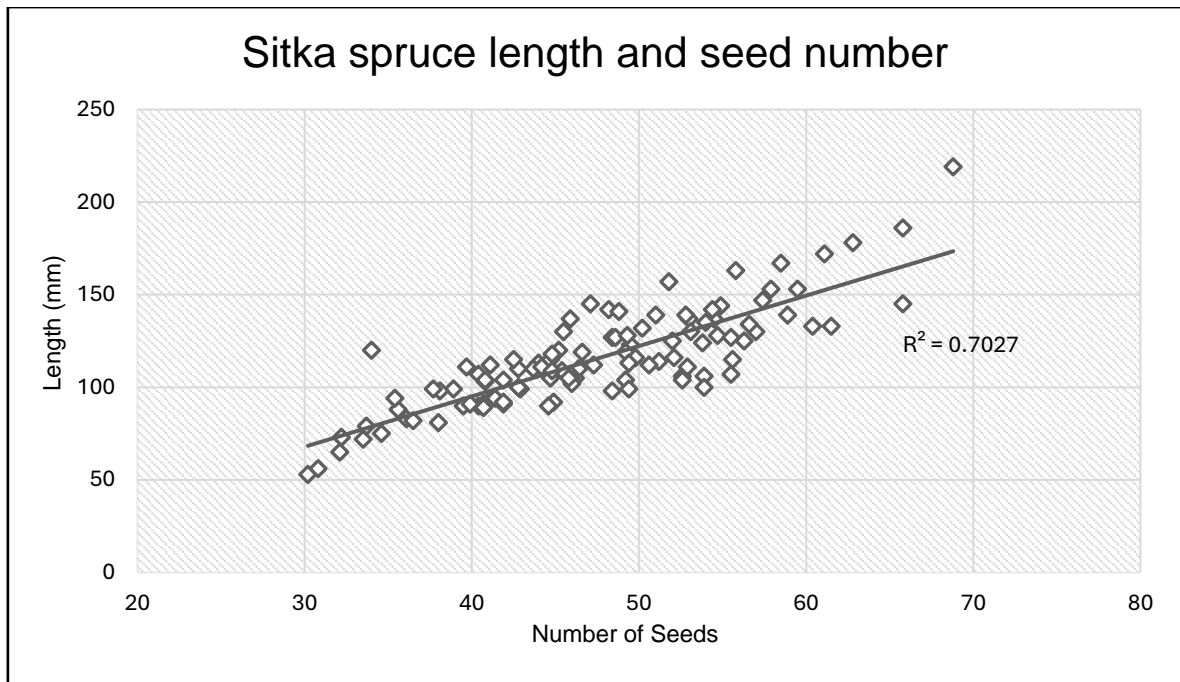


Figure 2.5 The length of unconsumed Sitka spruce cones plotted against the number of seeds counted per cone.

A subsample of 179 lodgepole pine cones were measured and the average length was found to be 42.8mm. The number of seeds in the average lodgepole pine cone was calculated as described above and was found to be 53.9. The mean energy of lodgepole pine cones in this study was calculated to be 5.28kJ.

2.3.3 Comparison with past feeding surveys

The total energy available and total energy consumed during both the growth (2008-2011) and regulation phases (2021) of the project were calculated. The feeding survey conducted in 2011 occurred post-fire. The results are summarised in the table below.

Available cones													
Sitka spruce						Lodgepole						Total energy in woods	
Year	Cones available per m ²	Energy per m ² (kJ)	Mature area (ha)	Total energy	Cones available per m ²	Energy per m ² (kJ)	Mature area (ha)	Total energy					
2008	0.48	2.25	123	2,767,500	3.7	21.84	269	58,749,600			61,517,100		
2009	0.02	0.09	108	97,200	3.37	19.89	246	48,929,400			49,026,600		
2010	5.3	24.84	107	26,578,800	1.42	8.38	226	18,938,800			45,517,600		
2011	2.12	9.93	93	9,234,900	1.35	7.97	220	17,534,000			26,768,900		
2021	4.02	18.83	91	17,135,300	0.63	3.33	111	3,696,300			20,831,600		
Consumed cones													
Sitka spruce						Lodgepole						Total energy consumed in woods	% total energy
Year	Cones consumed per m ²	Energy per m ² (kJ)	Occupied area (ha)	Total energy	Cones consumed per m ²	Energy per m ² (kJ)	Occupied area (ha)	Total energy					
2008	0.00	0.00	0	0	0.53	3.13	74.00	2,314,684			2,314,762	3.76	
2009	0.00	0.00	0	0	0.71	4.19	104.00	4,357,600			4,349,882	8.87	
2010	0.30	1.41	36	507,600	0.20	1.18	119.00	1,404,200			1,911,920	4.20	
2011	0.14	0.66	64	419,866	0.37	2.18	126.00	2,751,417			3,171,411	11.85	
2021	0.08	0.37	91	341,141	0.04	0.21	111.00	234,438			575,690	2.76	

Table 2.2 Cone densities and corresponding energy values per m² for both consumed and unconsumed cones of both species, during the growth and regulation phases of the project. Energy values per m² were extrapolated to show total energy available in the woodland. The total energy consumed was extrapolated to the areas known to be occupied by the squirrels. The percentage of the total energy available in the woods that was consumed is also shown.

2.3.4 Carrying capacity and population estimate changes

The carrying capacity of the woods during all three phases of the project was estimated based on the total mature woodland and the total energy available. Actual population sizes were estimated based on the total energy consumed. The results are presented in the table 2.3 below.

Year	Mature conifers (ha)	Estimated carrying capacity	FS estimated carrying capacity	FS estimated actual population
2005	432	138	-	-
2008	392	125	241-421	9-16
2009	354	113	192-336	17-30
2010	333	107	178-312	7-13
2011 (pre fire)	313	100	105-183	12-22
2011 (post fire)	255	82	-	-
2021	202	65	82-143	2-4

Table 2.3 Changes in the carrying capacity of the woods as determined by total mature woodland area (rounded to the nearest ha) and feeding survey (FS) estimates. Carrying capacity estimates based on total area use a squirrel density found in a similar woodland reported in the literature (Lurz & Garson, 1997), whereas the feeding survey utilises squirrel energy requirements to estimate carrying capacity. Total population estimates based on the feeding survey results are also shown.

2.4 Discussion

The available habitat at Derryclare has declined dramatically since the introduction of the red squirrel population. The area of mature woodland available to the population in 2021 is 47% of what it was in 2005. The effect of this habitat loss on the carrying capacity of the woodland has also been significant, with the carrying capacity estimate based on area declining by 53% and the estimate based on the feeding surveys declining by 41-81%. The substantial drop in the estimated population from 12-22 in 2011 to 2-4 in 2021, as determined by the feeding surveys, reflects the negative impact of this habitat loss on the population. For context, the population estimation in 2011, determined through live trapping, was 51 individuals, significantly larger than the 12-22 individuals estimated by the feeding survey during the same year. It is likely that the estimate of 2-4 individuals determined by the 2021 feeding survey similarly underestimated the population; nonetheless, a significant decline in the population estimations is still evident. The observed consumption of only 2.76% of the available energy in the woods is the lowest recorded proportion in all feeding

surveys conducted in Derryclare. In addition, the proportion of tree species in Derryclare has shifted over the past two decades. Lodgepole pine which comprised 63.8% of all mature woodland in 2005 has declined to 55% in 2021, the implications of which are discussed in detail below.

Translocations are time consuming (Lewis et al., 2012), expensive (Weise et al., 2014), and have a high failure rate (Bubac et al., 2019). Therefore, every effort should be made to ensure its success. Long-term monitoring is recommended by the IUCN/SSC (2013) as an essential part of a responsible translocation project, and should only be omitted when the translocation is risk-free (Pérez et al., 2012). Despite this, the majority of projects only conduct post-release monitoring in the first 4 years after the release (Bubac et al., 2019) due to monitoring difficulties, stemming from the cryptic nature of the translocated species, and a lack of funding (Berger-Tal et al., 2020; Resende et al., 2020). This period is relatively short, generally only encompassing the establishment and possibly growth phases of a translocation, depending on the target species' life history. As a result, projects may be incorrectly and prematurely assessed as successful (Wolf et al., 1996), failing to account for the threats to the translocation project that may occur in the long-term. Long-term threats may be predictable and resolvable, and should be investigated during the planning phase of the translocation, as was the case with the population viability analysis in the Derryclare translocation (Poole, 2007). However, long-term threats may also be unexpected and indirect, caused by complex interactions between the species and their habitat, as evidenced in this study.

The translocated red squirrel population in Derryclare has faced two substantial long-term threats: habitat loss and a deterioration in habitat quality. During the feasibility study of Derryclare as a potential translocation habitat, the carrying capacity was initially estimated at 138 squirrels based on the woods' area. Additionally, the felling plan was assessed and found to facilitate the survival of a healthy red squirrel population, owing to the successive manner of felling, ensuring the retention of sufficient mature woodland (Poole, 2007). However, changes in the felling plans throughout the years meant that the extent of the impact was higher than initially expected. Additionally, the accidental habitat loss caused by the fire of 2011, driven by dry weather conditions (Waters, 2012a), was unforeseen and could not have been planned for. These events significantly reduced the carrying capacity of the woodland, supporting only half of what it could when the original translocation took place, according to the feeding survey results. Interestingly, the area-based carrying capacity estimates are consistently lower than those predicted by the feeding survey (Table 2.3). The area-based estimate was based on squirrel density in a similar habitat type. However, the availability of seeds at this site was patchy (Lurz et al., 1997), demonstrating

how woodlands with very similar compositions may differ internally, potentially affecting their suitability. This underscores the importance of investigating the unique characteristics of potential translocation sites during feasibility studies to accurately assess their suitability.

Commercial woodlands present several challenges as a location for a translocated population. Firstly, the process of clear felling introduces immediate and long-term risks for populations. Risks include direct mortality during the felling operations (Ewacha et al., 2017), disturbance to breeding patterns (Wilson & Wilson, 1975), failure to establish new home ranges, increased predation facilitated by a lack of cover (Pausas & Parr, 2018), and increased vulnerability and stress, impacting fitness (Ewacha et al., 2017). Secondly, the instability of commercial woodlands due to the likelihood of changes in the management's plans means that the future composition is unpredictable, making it a risky choice for a translocation. Finally, forest plantations in Ireland traditionally consist of conifer monocultures (Iremonger et al., 2007). In some cases, a 'nurse' conifer species is planted alongside the primary tree species to aid its growth. The nurse species will naturally self-thin over time, creating a monoculture (Keane et al., 2018). The low tree species diversity of these plantations makes them inherently volatile due to their vulnerability to threats such as pests and diseases (Carnol et al., 2014). It is therefore advisable to explore alternative, more stable and diverse translocation sites where possible.

The habitat loss caused by the fire in April of 2011 is not believed to have caused any direct mortalities, particularly as it primarily affected the base of the trees, without reaching the canopy (Waters, 2012b), where tree squirrels are likely to have taken refuge (Banks et al., 2011; Koprowski et al., 2006). However, the long-term habitat loss resulting from fire, has been found to be more detrimental to a population's survival than initial mortality (Engstrom, 2010). Small mammal populations have been shown to crash in the weeks (Legge et al., 2008) and years (Recher et al., 2009) following a forest fire, particularly if the fire leads to fragmentation in the habitat (Recher et al., 2009). The fire in Derryclare contributed the significant gap between the north and south of the woods seen in 2021 (Figure 2.4). The shortest distance between the two clusters of stands is 839 meters, which is roughly 500 meters greater than the reported mean daily travel distance of 305 meters by red squirrels (Andrén & Delin, 1994; Rodríguez & Andrén, 1999) and the diameter of the home ranges of squirrels in similar habitats (632 meters) (Lurz, 1995). Additionally, squirrels are less likely to travel more than 50m across open areas (Verbeylen et al., 2003). The loss of habitat caused primarily by the fire may isolate the squirrels in the north from those in the south, increasing the overall vulnerability of the population (Crooks et al., 2017). Furthermore, the fire adversely influenced the succession of the woods due to its exacerbated impact on young trees (Waters, 2012a). The deleterious immediate and long-

term effects of habitat loss highlight how the simplicity of estimating carrying capacity solely based on area does not capture the complexity of how changes in the environment influence populations.

The second unanticipated threat faced by the Derryclare translocated population is a deterioration in habitat quality, specifically the replacement of lodgepole pine with Sitka spruce. This is evident in the declining crop yield of lodgepole pine from 2008-2011, and the further drop recorded in 2021 (Table 2.2), in a species which is known for its stable crop yields (Benkman et al., 2003; Lurz et al., 1998; Smith & Balda, 1979). This is likely a consequence of planting lodgepole pine as a nurse species alongside Sitka spruce, as Sitka spruce is known to outgrow this species, suppressing lodgepole growth and production, and ultimately dominating the canopy (Keane et al., 2018). This self-thinning takes effect approximately 40-50 years after planting, with Sitka spruce increasingly representing a larger proportion of the mixture (Mason & Connolly, 2018). This self-thinning management practice was widely employed by Coillte during the period of Derryclare's establishment, with the aim of creating stands of pure Sitka spruce (Keane et al., 2018). However, this information was not known during the translocation planning process.

Based on the self-thinning timescale outlined by Mason and Connolly (2018), the replacement of lodgepole pine with Sitka spruce began in Derryclare between 2000-2010. The consequences of this practice can be seen not only in the declining lodgepole pine crop production, but also in the higher proportion of Sitka spruce recorded in the woods in recent years compared to the original plantation plans (See section 3.1). The negative impacts of this shift in composition may be seen in the decreasing amount of energy available per m² in the woodland. The energy provided by the more favourable and nutritious (Lurz et al., 2000) lodgepole pine crop has dwindled to less than a sixth of its 2005 output. Despite this decline, lodgepole pine remains the preferred food source for squirrels in Derryclare, with 15.86% of total lodgepole energy in 2021 consumed by the squirrels, in stark contrast to the 1.96% of the total energy provided by Sitka spruce being consumed. This result aligns with the findings of Gurnell et al. (2004a), who observed that Sitka spruce cones are favoured the least by red squirrels compared to other cone producing species. Therefore, the loss of lodgepole pine has disproportionately impacted the population. Additionally, the fluctuating crop mast of Sitka spruce (Broome et al., 2007), as observed in the present study (Table 2.2), results in an unreliable food source for red squirrels. The ongoing replacement of lodgepole pine with Sitka spruce will likely have increasingly negative effects on the red squirrel population. Red squirrel population densities are negatively correlated with the proportion of Sitka spruce in a woodland (Lurz et al., 1998). While the replacement of lodgepole pine with Sitka spruce is not the sole factor

contributing to the decline in carrying capacity in Derryclare, it exacerbates the issue and leads to a less favourable woodland.

This further highlights that habitat size alone is not a good enough predictor of the suitability of a translocation site, and instead must incorporate site characteristics and quality (Gilpin, 1986). It is crucial to investigate the specific habitat quality in relation to the target species, taking into account their ecology and behaviour (Seddon et al., 2007). Numerous reviews including those by Griffith et al. (1989), Wolf et al. (1996) and Wilson (2018) have demonstrated that habitat quality is one of the main predictors of translocation success. Another review by Berger-Tal et al. (2020) found that a poor quality habitat was the leading cause of translocation failures in over 25% of cases. In such cases, habitats were either mistakenly perceived to be of higher quality, deteriorated after the introduction, or were selected due to limited options (Berger-Tal et al., 2020). Ideally, animals should be translocated to areas that are as similar to their source habitats as possible (Kenward & Hodder, 1998), with only the best possible habitats being chosen (Moorhouse et al., 2009). Advanced computer systems such as Geographic Information Systems (GIS) can be utilised to identify possible translocation sites based on patch-specific characteristics (Weise et al., 2015), as well as model the future spread of the population (Aurambout, 2005). By incorporating habitat quality assessments into the selection process, the chances of translocation success can be significantly enhanced.

The area and quality of a habitat are dynamic and can change throughout a translocation project, as seen in Derryclare. Consequently, during the initial planning phase the habitat should not be treated as a static factor. A translocation site, like all land, may be exposed to various disturbances and alterations, including anthropogenic, natural and climate-related factors. Therefore, a comprehensive risk assessment of potential disturbances taking into account their direct and indirect cascading effects on the target species should be conducted during the planning phase. The carrying capacity estimate in the present study based on area alone (Table 2.3) fails to take into account the negative effects of such changes in the environment, beyond a simple reduction in habitable area. As discussed above, habitat loss introduces a variety of new risks and challenges for the population that are not accounted for in carrying capacity estimations based solely on area. Additionally, this estimate does not consider the quality of the available area or shifts in this quality over time.

While potential changes in the habitat area and quality are important considerations to make when planning a translocation, we recognise that practical site selection often involves making concessions, as finding the perfect site is rarely possible. For example,

Derryclare was chosen as a translocation site owing to its large size, age structure, accessibility, support of Coillte and the NPWS, and its distance from the range of the grey squirrel (Poole & Lawton, 2009). These factors led to it being deemed the best potential site among several options that were considered in the region. The drawbacks of felling operations and a high Sitka spruce proportion were deemed to be offset by its many suitable qualities. In such cases where practical and balanced decision making results in the choice of a habitat with some suboptimal aspects, intervention may be needed to support the population in the long-term (Grant et al., 2019). Positive changes in the habitat have been shown to increase the chances of translocation success (Wilson, 2018). Supplementary feeding is one such effort that can be employed to support the translocated population and increase the likelihood of successful establishment and long-term regulation (Cabezas & Moreno, 2007).

In conclusion, the translocation of red squirrels to Derryclare has provided valuable insights into the complexities and challenges of conservation translocations. The declining lodgepole pine crop yield and the ongoing replacement by Sitka spruce has highlighted the importance of considering habitat quality as a critical factor in translocation planning. As demonstrated in this study, habitat size alone is insufficient to ensure translocation success; instead, internal habitat characteristics and their potential changes over time should be assessed during the planning phase. We argue that, instead of hindering projects with stringent standards, a nuanced understanding of a site's quality and future serves as the foundation for well-informed decision-making. Additionally, any challenges and potential setbacks may be effectively offset by the establishment of a rigorous long-term monitoring program. This study has highlighted the benefits of conducting long-term monitoring, as the impact of habitat loss and habitat deterioration on the carrying capacity of Derryclare would otherwise have gone undocumented. The success of the translocation is likely to be affected by these factors, emphasising how translocations require long-term monitoring to assess their true outcomes. The lessons learned from this study underscore the need for comprehensive planning, continuous monitoring, and adaptive management in translocation projects to ensure the long-term viability and success of reintroduced populations.

3 Investigating the distribution and demographics of the two translocated populations

3.1 Introduction

Wildlife monitoring can be conducted for a variety of reasons, including for controlling invasive species (Larson et al., 2020), determining hunting limits (Caro et al., 2015), and informing conservation efforts (Hays et al., 2019). Conservation management decisions and legislation are data-driven and rely heavily on accurate data on target species. Similarly, translocation projects depend on precise population information to evaluate how relocated individuals adapt to their new environment, identify challenges that may arise, and assess the overall success of the project. We can assess the success of the project by monitoring its successful progression through the phases of a translocation, from establishment to growth to regulation. Monitoring techniques are selected based on the specific research objectives, target species, and environmental conditions of the project. Several techniques are often used in conjunction with one another to enhance the quality and breadth of the data (Braga-Pereira et al., 2022; Gopaldaswamy et al., 2012). These methods may be categorised as invasive or non-invasive. Invasive techniques involve direct physical contact with the subject, while non-invasive techniques allow researchers to collect data without physically disturbing the subject. The transition into the regulation phase of a translocation, characterised by the continued presence of the population as well as a stabilised density, may be assessed by both non-invasive and invasive techniques. Both types of techniques confer unique advantages and disadvantages.

Common non-invasive methods include trail cameras, acoustic monitoring, scat analysis, hairtubes, environmental DNA (eDNA) sampling, observation and feeding surveys. Non-invasive techniques are capable of generating data on species' distribution (Petrovan et al., 2020), dispersal (Marucco et al., 2022), habitat use (Grimmel et al., 2020), density (Pérez-Granados & Traba, 2021), diet (ter Schure et al., 2021), genetics (Carroll et al., 2018) and behaviour (Harrison & Kelly, 2022). In the context of translocation outcome assessment, non-invasive techniques are particularly useful in generating presence/absence data over long periods of time, allowing for the monitoring of their continued presence in the translocation site. Non-invasive techniques are often more cost-efficient than invasive techniques (Ferreira et al., 2018), making them a more sustainable and economically viable choice for large-scale or long-term projects (Krivek et al., 2022). Due to the minimal training and licensing requirements of non-invasive techniques, the public are often recruited as volunteers, minimising costs, and reducing researcher workload. Citizen science can

significantly expand both the scale and longevity of a monitoring project, resulting in a more comprehensive dataset than could be gathered by an individual or team alone. Public participation in monitoring projects also engenders a sense of environmental stewardship (Plieninger & Bieling, 2012) and increases public engagement with environmental issues (Merenlender et al., 2016; Mitchell et al., 2017). An additional benefit of using non-invasive techniques in monitoring projects is their minimal impacts on an animal's welfare. The use of non-invasive techniques aligns with the principles of the 3Rs proposed by Russell and Burch (1959), which emphasise the importance of replacement, reduction and refinement in animal studies. Non-invasive techniques are recommended as a form of replacement of the direct use of animals (Lindsjö et al., 2016; Zemanova, 2020).

The application of non-invasive monitoring techniques has played a crucial role in advancing our understanding of red squirrel populations. These techniques may be used to detect red squirrel presence (Mortelliti & Boitani, 2008), assess abundance and density (Gurnell et al., 2004a; Shannon et al., 2023), and investigate distribution (Lawton et al., 2019). When used over long periods of time, non-invasive monitoring can give insights into population fluctuations (Gurnell et al., 2004a), range expansions or contractions (Gurnell et al., 2014), responses to woodland or management changes (Gurnell et al., 2009) and seasonal variations in habitat use (Babińska-Werka & Żółw, 2008). In regions where the red squirrel is threatened by the grey squirrel, non-invasive monitoring techniques may be used to assess the level of the threat and their response to conservation management (Everest et al., 2021). Non-invasive techniques are also commonly used in red squirrel translocation projects to monitor their distribution and continued presence. For example, feeding surveys have been utilised in the assessment of post-release settlement patterns (Kenward & Hodder, 1998), allowing the expansion and habitat preference of the population to be monitored. Other commonly employed non-invasive techniques in the study of red squirrel populations include hairtubes, trail cameras, visual sightings, and drey counts. Non-invasive data are commonly used as a precursor to invasive monitoring projects, gathering valuable distribution and abundance data that will inform the planning of subsequent monitoring efforts.

Invasive techniques involve direct physical contact with the study subject, generally through live trapping. Live trapping is often followed by subsequent invasive tests such as radiotracking or behavioural assays. These methods can generate more detailed data compared to non-invasive techniques, enabling more accurate measurements of population sizes (Jolly, 1965), insights into population demographics (Sandercock, 2006) assessments of health (Mathews et al., 2006), investigations into behaviour (Gould et al.,

2009), and habitat use assessments (MacDonald, 1978) among many other applications. Due to their ability to provide detailed information, invasive techniques are commonly employed in red squirrel monitoring projects. For example, mark-recapture studies are frequently used to investigate red squirrel densities (Gurnell et al., 2004a). Radiotracking is used in the assessment of home and core ranges, as well as interactions between individuals (Lurz et al., 2000). Open field tests and mirror image simulation tests are employed to gather data on squirrel personality and behaviour (Mazzamuto et al., 2019; Santicchia et al., 2020). Invasive techniques also play a crucial role in assessing the outcomes of translocations. Determining population sizes and reproductive success (Mitchell et al., 2011) allows for the assessment of density and growth rates, essential for monitoring the successful transition through the various translocation phases. Additionally, invasive monitoring techniques provide data on the overall health and fitness of the translocated population (Gross et al., 2023), offering insight into the long-term prospects of the project and facilitating the implementation of mitigation strategies if needed. However, invasive techniques come with certain challenges, including higher costs due to specialised equipment, licenses, and training requirements. These factors contribute to the barriers facing researchers during translocation projects, particularly when conducting long-term monitoring (Berger-Tal et al., 2020; Bubac et al., 2019).

The selection of technique used to monitor red squirrel populations is influenced by several factors, including the composition and age structure of the habitat, the availability of project resources, and the specific research question. For instance, feeding surveys can provide information on squirrel distribution, densities and habitat use (Lurz et al., 2008), but are only reliable when conducted in conifer woodlands (Gurnell et al., 2004a). Hairtubes, which allow for the collection and identification of squirrel hairs, serve not only for determining presence and distribution (Flaherty & Lawton, 2019), but may also be employed in genetic analyses (Everest et al., 2019). However, hairtubes may be costly in terms of personnel time (Goldstein et al., 2014). Visual surveys are commonly used to detect red squirrels (Gurnell et al., 2001), but are often challenging due to the elusive nature of this species (Gurnell et al., 2004a). However, when the public are engaged in citizen science surveys, the collective effort and expanded observational capacity significantly increases the likelihood of red squirrel sightings. This effect was clearly observed in multiple national squirrel surveys which successfully tracked the changing distributions of both red and grey squirrels in Ireland (Carey et al., 2007; Lawton et al., 2015a; Lawton et al., 2019). Nonetheless, there are limitations to the applicability of citizen science surveys. These surveys exhibit a spatial bias, with densely populated regions providing a disproportionate amount of data compared to remote areas (Blaney et al., 2016). Consequently, they require additional effort and

analysis in rural areas, meaning that other monitoring techniques may be more suitable for these areas. Live trapping provides a wealth of data on red squirrel populations, and allows for subsequent invasive tests to be conducted, but may be unsuitable for certain habitat types. For example, densely populated areas are not conducive to trapping projects, due to the risk of public interference, antisocial behaviour, and logistical challenges. Radiotracking is commonly used to assess the habitat use of red squirrels (Wauters & Dhondt, 1992), however, this technique may be impractical in urban areas or mountainous areas where signals can bounce off structures and mountains, making the process more difficult.

The study of red squirrel demography involves an assessment of the structure of the population, including aspects such as their abundance and density, health and fitness, recruitment rate and habitat use. The density of a population provides an indication of overall health of the population, and may be used to infer habitat quality (Andrén & Lemnell, 1992). Squirrel densities tend to be highest in mixed broadleaf and conifer forests, and lowest in coniferous monocultures (Lurz et al., 1995; Wauters & Lens, 1995). Densities of established populations usually fall within the range of 0.5 – 1.5 squirrels per hectare (Lurz et al., 2005), but are subject to year-to-year fluctuations (Andrén & Lemnell, 1992). The health and fitness of a population are assessed by the general condition of individuals and their reproductive success. A female's chance of reproducing is dependent on her body weight, with females below the weight threshold of 300g in a Belgian population (Wauters & Dhondt, 1989) and 325g in a British population (Magris & Gurnell, 2002) failing to enter oestrus. The average size of a litter is three young (Shuttleworth, 1999). Recruitment rates are used to assess the reproductive success of populations, although in established populations are dependent on resource availability and population densities (Lurz et al., 1997). Home ranges sizes vary between the sexes (Wauters et al., 1992) and depend on both environmental and population factors (Wauters & Dhondt, 1992). Home ranges are smallest in high quality habitats, generally averaging between 2 and 7 hectares (Lurz et al., 2005), and have been observed to be as large as 47 hectares in poor habitats (Münch, 1998).

In this study we aimed to investigate the distribution and demographics of two translocated red squirrel populations, with the primary objective of assessing the outcome of the translocations. We used non-invasive methods to investigate the presence/absence of the squirrel populations in both sites in order to confirm their continued presence, which is an essential requirement for a successful translocation. These methods provided distributional data that we were able to compare to past studies on these populations (see section 1.7) to analyse any changes in their range. Subsequently, a live trapping project was

implemented in both sites with trap placement informed by the distributional data. Mark-recapture techniques were employed to obtain more accurate density estimates, while also assessing breeding rates, recruitment, and the overall fitness of the population. These density estimates helped to determine whether the population has successfully transitioned into the regulation phase (IUCN/SSC, 2013). Radiotracking was employed to assess the habitat use of the squirrels. Additionally, non-invasive monitoring techniques were employed to investigate the spread of both populations beyond their introduction sites. We hypothesise that both populations will exhibit a successful progression into the regulation phase within their respective woodland habitats, characterised by the continued presence of both populations throughout their introduction sites, and a plateaued population density. We expect a spread of the population into neighbouring habitats, due to the carrying capacity of the translocation site being met. Furthermore, we believe that both populations will be reasonably fit and display high levels of reproductive success.

3.2 Methods

3.2.1 Study sites

A description of Derryclare may be found in chapter 2.

Belleek woods is a recreational park situated alongside the river Moy in the town of Ballina, Co. Mayo. The site consists of 61.5 hectares, with 60 hectares comprising of mature mixed broadleaf and conifer woodland. The coniferous species include Norway spruce (*Picea abies*), which is the most dominant, Sitka spruce (*Picea sitchensis*), larch (*Larix kaempferi*) and Monterey pine (*Pinus radiata*). The broadleaf coverage is primarily composed of beech (*Fagus sylvatica*), with oak (*Quercus* sp.), sycamore (*Acer pseudoplatanus*), ash (*Fraxinus excelsior*), birch (*Betula pendula*) and elm (*Ulmus* sp.) also present. The understorey primarily features brambles (*Rubus fruticosus*), holly (*Ilex aquifolium*) and ferns. Belleek woods is managed by the forestry company Coillte, in collaboration with the voluntary community group known as the Belleek Forest Enhancement Committee. The long-term management plan (2009 – 2040) for Belleek woods, as outlined by Tiernan et al. (2009), aims to increase the broadleaf coverage while reducing the coniferous component.

This public park features a network of forest pathways spanning 10 kilometres, which are frequently used by walkers, joggers, and cyclists. There are a number of attractions of historical importance within Belleek woods, including Belleek castle, located in the centre of the woodland and built in the early 19th century by the Knox-Gore family. The forest also features a fairy trail, picnic locations and a duck pond.

Eight red squirrel feeding stations are located throughout Belleek woods (Figure 3.1). The feeding stations are rarely empty as they are regularly replenished with peanuts by the members of the Belleek Forest Enhancement Committee and other locals. This committee, which was established by Cyril Collins in 1998, was instrumental in red squirrel translocation to this woodland.

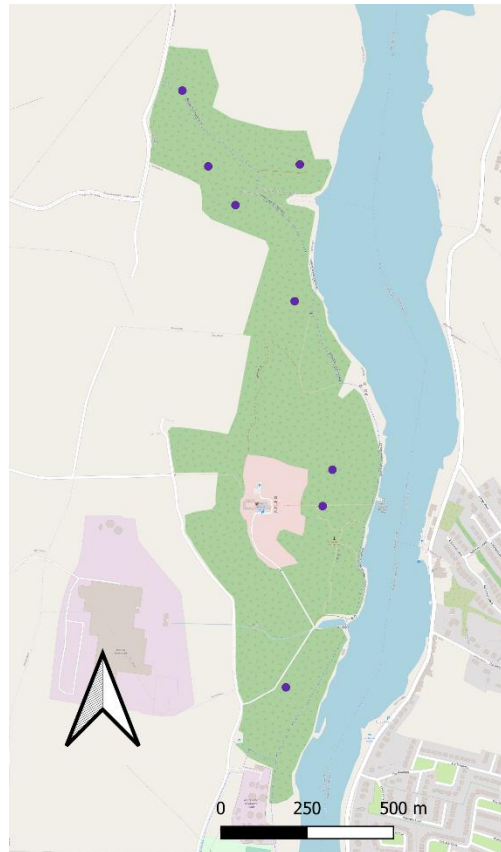


Figure 3.1 The location of supplementary feeding stations in Belleek woods. Stations are filled regularly with peanuts by local volunteers

3.2.2 Population distribution in woodland

Non-invasive methods were employed in both sites to investigate the distribution of both populations within their respective woodlands. The purpose of this monitoring was initially to gather presence/absence data to inform the trap placement, and additionally, to continuously monitor the distribution and density of squirrels in the larger Derryclare woods. Hairtubes, trail cameras and feeding surveys were used in Derryclare, while only hairtubes and cameras were utilised in Belleek. In Derryclare, the hairtube study took place from January 2020 to October 2022, while in Belleek, the hairtubes were deployed from February

Bushnell NatureView and Browning trail cameras were deployed in both Derryclare and Belleek. Four cameras were deployed at each site (Figure 3.3). Trail cameras were positioned at chest height each aimed at a hairtube, and positioned within 6 meters of the hairtube. The video length was set at 30 seconds. The trail camera memory cards and batteries were replaced during hairtube block collection sessions. The data collected from the trail cameras were analysed, and squirrel sightings were recorded, along with the corresponding date and location of each sighting. In Derryclare, trail cameras were deployed from January 2020 until May 2021. In Belleek, trail cameras were deployed from February - March 2020; however, it was concluded that squirrels were present at all camera locations and further presence/absence data was not necessary.

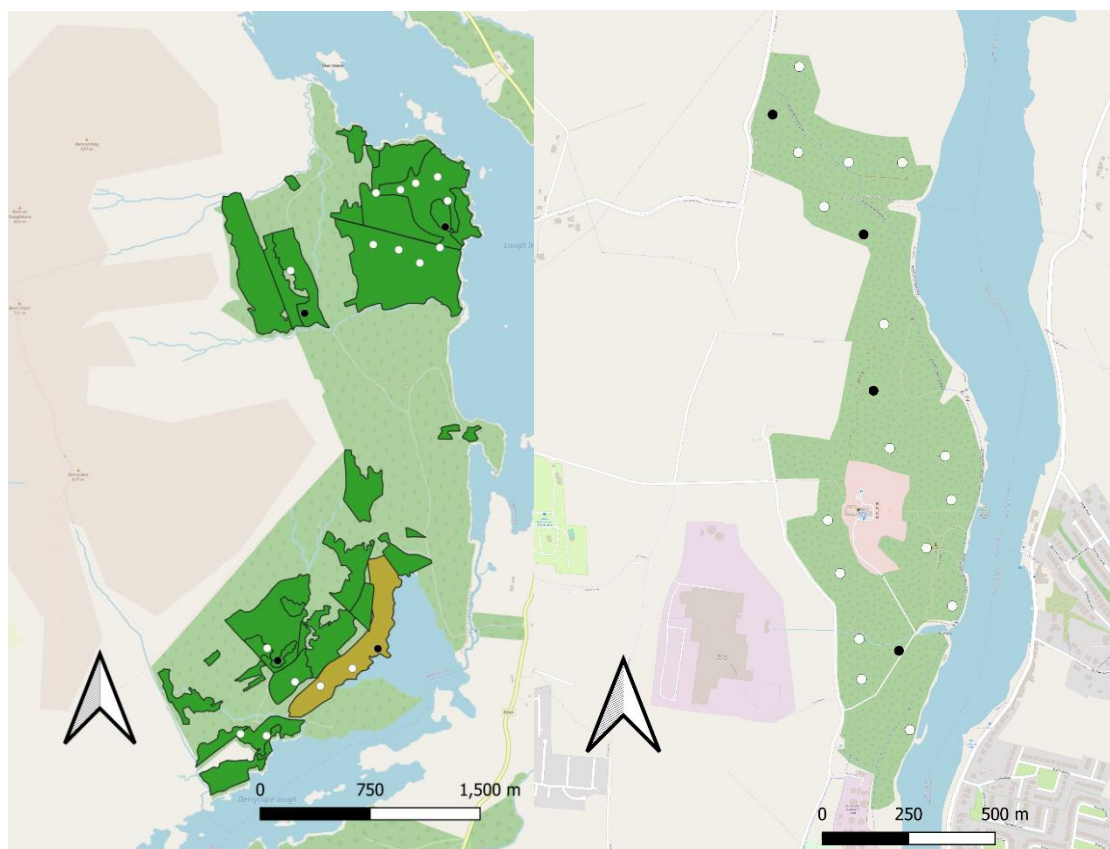


Figure 3.3 The locations of hairtubes and cameras in Derryclare (left) and Belleek (right). Hairtubes without a camera are denoted in white, and hairtubes with cameras are denoted in black. All mature coniferous stands in Derryclare are highlighted in green and the nature reserve is shown in brown.

A feeding survey was conducted in all accessible mature stands of Derryclare to investigate the distribution of the population. Stands in this study are defined as a spatially contiguous grouping of trees, distinct from other blocks of trees. This survey was undertaken in October 2021. The survey procedure is described in the methods section of Chapter 2.

The information obtained from the hairtube and trail camera studies was used to inform the selection of trapping locations in both Derryclare and Belleek. Live traps should ideally be concentrated in the area of highest squirrel abundance, within a compact area to ensure that all traps can be set as close to dawn as possible. For this reason, it was decided that traps in Derryclare must be placed in either the northern or southern end, due to the additional set up time a more widespread trap distribution would incur. In contrast, this was not a concern in Belleek, as it is a smaller area compared to Derryclare and can be covered entirely within a shorter time frame. However, the distribution of the population was still investigated in Belleek to ensure that trap placement was as effective as possible.

3.2.3 Live Trapping

Live trapping was conducted once per month from July 2020 to Jan 2023, with trapping sites alternating each month (See table 3.1 for summary). The locations of traps in both sites were determined by the results of the trail camera and hairtube studies. In Derryclare, traps were concentrated in the southern half of the woods, corresponding with the region in which squirrel activity was most prominent (Figure 3.4). In Belleek, traps were placed uniformly throughout the woodland, with the exception of the castle grounds (Figure 3.5). Twenty traps were placed in both sites, with a minimum spacing of 50m between each trap. In Derryclare, felling operations in September 2022 necessitated the relocation of four traps, which were moved into sites that were deemed promising based on the results of the feeding survey and previous trapping success. These new trapping locations were employed in the final two trapping months (October 2022 and January 2023). In Belleek, which is a public forest park, traps were hidden from view as much as possible to minimise public interference. Traps in this site were locked to trees to prevent removal or tampering. Additionally, a sign was attached to each trap explaining the aims of the project. During the course of the study, no traps were taken or significantly tampered with.

	Derryclare	Belleek
Trapping period	July 2020 - Jan 2023	Aug 2020 - Nov 2022
Trapping sessions	16	14
Total mature woodland (ha)	202	60
Trapping grid (ha)	75.06 (sessions 1 – 14) 54.23 (sessions 15 -16)	42.78
No. of traps	20	20
Trap density (traps/ha)	0.27 (sessions 1 – 14) 0.37 (sessions 15 – 16)	0.47

Table 3.1 A summary of the trapping study in Derryclare and Belleek.

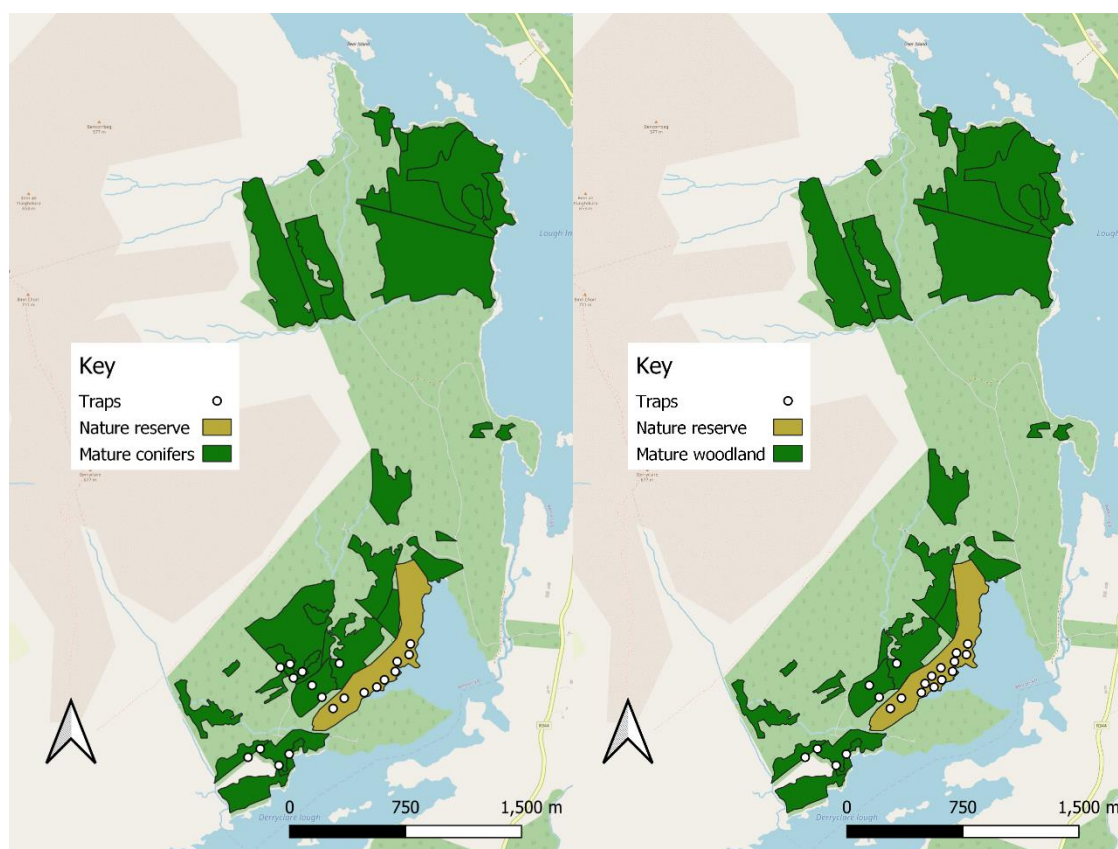


Figure 3.4 Locations of traps in Derryclare before the felling operations in September 2022 (left) and after the felling operations (right).

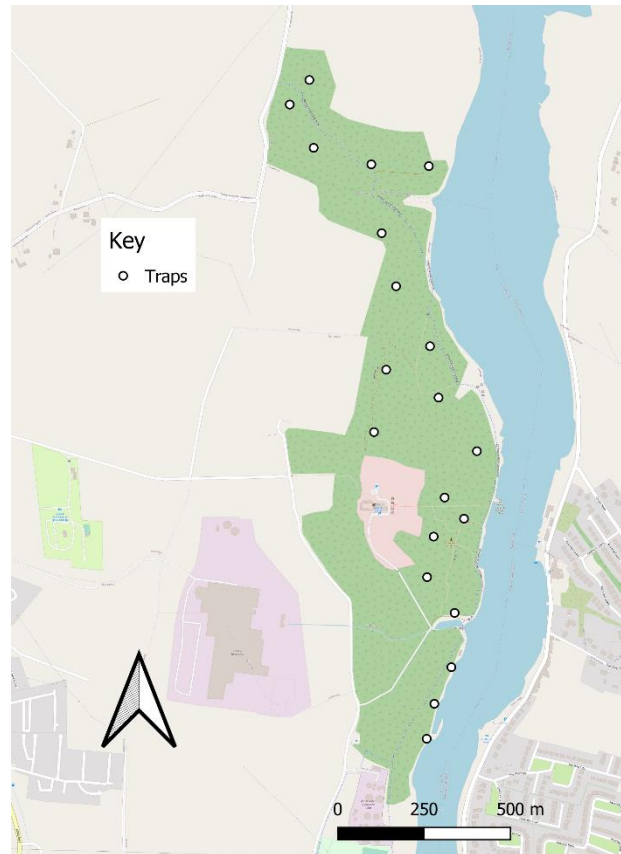


Figure 3.5 Location of traps in Belleek. No traps were moved during the study period.

Traps consisted of a modified mink trap, with a nest box attached to the rear section (Figure 3.6). These traps operated by closing shut when the occupant activated the treadle system near the trap's rear. Traps were placed at chest height on branches of trees or on fallen tree trunks and secured with a thick metal wire and lock. Bait consisted of peanuts scattered on the top and at the entrance of the trap, while hazelnuts were placed behind the treadle. Traps were prebaited twice in the week before each trapping session. During this time, the treadle system was disarmed to allow a visit without triggering the mechanism. In Belleek, the prebaiting duration was reduced from two days to one day from December 2021 onwards as it was noted that Belleek squirrels were highly habituated to using manmade objects through their long-term use of feeding stations. This adjustment was found to have no adverse impact on trapping success. As a result, prebaiting was halted in July 2022 with no apparent deleterious effect. In Derryclare, prebaiting was not conducted in the final trapping month (January 2023). Trapping sessions consisted of three consecutive days of trapping. Traps were set just after dawn and rechecked several hours later. The duration of the rest period between setting and checking the traps was determined by the available

daylight hours, with a minimum of four hours in the winter months and six hours during the summer months.



Figure 3.6 A closed squirrel trap. Bait of peanuts and hazelnuts are visible outside and inside the trap.

Once a squirrel was captured in a trap it was transferred to a hessian sack. The struggle rate, which is further discussed in chapter 4, was observed at this stage. After this measurement was taken, the squirrel was transferred to a handling cone (Figure 3.7). A pen was inserted into the cone beneath the squirrel's feet to prevent it from backing out of the cone.

The sex and breeding status of the squirrel was identified. Adult males with staining on their genitals, caused by scent marking (Gurnell, 1987), were deemed to be actively breeding. Adult females were categorised as pregnant if their nipples were prominent and hairy and the vagina was swollen and perforated. Lactating females were identified based on the lack of hair around the nipples, indicating that they were nursing kits.

A squirrel's weight was measured to the nearest 5g using a 500g Pesola balance, and the weight of the cone and pen were later subtracted. Juvenile squirrels were distinguished as individuals weighing less than 240 grams, as no breeding adults were found below this

weight threshold (Tittensor, 1970). The shinbone of an individual was measured to the nearest 0.1mm using Vernier callipers. The body condition of individuals was calculated by dividing the body weight by the shinbone length (Wirsing et al., 2002). The relationship between these variables was linear.

Individuals were injected with a Passive Integrated Transponder (PIT) tag into the scruff of their neck upon first capture. An individual authorisation was granted by The Health Products Regulatory Authority (Authorisation Number: AE19125/I266) for these purposes. A Trovan PIT tag responder was used to scan for PIT tags and identify marked individuals. All unmarked individuals were assumed to be progeny of resident squirrels due to their isolation from other squirrel populations (Lawton et al., 2019). New squirrels may be captured as juveniles or detected as adults. Vocalisations of squirrels during the trapping process were noted (Diggins, 2021).



Figure 3.7 A squirrel in a handling cone lying on a hessian sack. A pen is inserted into the cone under the squirrel's legs to prevent escape during processing.

3.2.4 Population density estimates

Population density estimates were calculated using hairtube data, as well as live trapping data. The hairtube data were used to estimate the population density of the Derryclare population only. This estimate was calculated using a linear regression equation outlined by Bertolino et al. (2009), based on the proportion of all the hairtubes that were visited by squirrels. The authors recommend that this equation is used in coniferous regions with a density of fewer than 0.5 red squirrels per hectare. As a result, it was not possible to estimate the population density in Belleek using this technique, which did not meet the specified conditions.

Marking individuals with a PIT tag allowed for the abundance estimation of both populations. The mark recapture technique assumes all individuals have an equal chance of being captured, that marking them does not affect their survival and that all marks are permanent. Two population estimates were used in this study. The minimum number present (MNP) population estimate uses the minimum number of individuals present over a specified period, relying on information from prior and subsequent sessions to estimate the population size. Individuals are counted as present if they are captured during that session or were captured in the past and then captured again in a future session (Krebs, 1966). This estimate is useful in small populations where a low trap efficiency leads to a lack of data. However, this estimate is negatively biased, particularly at the beginning and end of a study, where no information on previous and subsequent captures are available (Pocock et al., 2004).

The second estimate used was the Lincoln index, also known as the Lincoln-Peterson index. Bailey's modification, which is used when recaptures are 10 or fewer, was applied (Bailey, 1951). This estimate assumes that the population was closed, and that the population did not change between sessions. The Lincoln index estimated the population size by comparing the number of previously marked individuals in a session to the total number of individuals in a session. It is denoted by the following equation, where r = The number of individuals caught (and marked) in the first session, n = the number of individuals caught in the second session and m = the number of marked individuals caught in the second session from the first session.

$$N = \frac{r(n + 1)}{m + 1}$$

Because trapping sessions in this study were three days long, the first two days were combined to give the number of individuals caught in the first session, and the third day of the trapping was used to give the number of individuals caught in the second session. Using

a three day period to estimate population size reduced the chance of population fluctuations within that time, which as stated, is an assumption of the estimate.

The standard error was calculated using the following formula from Bailey (1951).

$$SE_N = \left[\frac{r^2 (n + 1)(n - m)}{(m + 1)^2 (m + 2)} \right]^{\frac{1}{2}}$$

Monthly population estimates were calculated for both populations using the MNP estimation, while the Lincoln index was only used to estimate the density of the Belleek population, and not the Derryclare population. Due to the low trapping success in Derryclare, the Lincoln index could not be calculated for 56% of trapping sessions ($n = 9$), making it an unreliable estimate. In both sites, population estimates were extrapolated to the total mature woodland using the area of the trapping grid. The trapping grid in Derryclare encompassed all blocks in which traps were situated, giving a total area of 75.06ha. Following felling operations in September 2022, the trapping grid was reduced to 54.23ha. In Belleek, the trapping grid excluded the castle grounds, giving a total sampled area of 42.78ha. The population estimates were converted to density estimates by using the total suitable woodland available.

3.2.5 Radiotracking

Radiotracking was conducted in Belleek in April 2023. This method was deemed unsuitable for use in Derryclare due to the low trapping success and mountainous landscape. Eight squirrels were trapped in Belleek over a two day period in March 2023 for use in the radiotracking study. As only eight animals were required for this study, this trapping session was ceased once the required number of animals were trapped. Therefore, this trapping session is not included in density estimations, however, the individuals caught are included in all other analyses. Once the squirrels were trapped and processed, they were fitted with radiotracking collars (Advanced Telemetry Systems (ATS) at a frequency of 478- 479.99 MHz). Two female and six male adults were caught and radiotracked. Thirty fixes were recorded per animal consistent with other squirrel radiotracking studies (Kenward, 1987; Wauters & Dhondt, 1992). Fixes were recorded from dawn, with the starting individual varying every day. A minimum gap of three hours was left between each individual's fix to avoid auto correlation. A maximum of four fixes were taken per day. The fixes were recorded using Google maps. The radiotracking study lasted a total of two weeks, minimising the likelihood of an individual's home range shifting.

Fix locations were inputted into the analysis software Ranges 9, where home ranges were generated using minimum convex polygons (MCP). These MCPs represent the smallest

polygon that encompasses the 30 fixes for each individual, effectively delineating their home range. The core areas of these home ranges were identified by creating an incremental plot showing the percentage of fixes (Peeled MCPs) on the x-axis against the corresponding cumulative percentage of the home range revealed by each fix on the y-axis. By identifying the inflection point on this graph, we determined the percentage of the individual's home range that constituted their core range. The inflection point can usually be identified visually. However, if any doubt exists, a ratio test may be performed on possible inflection points. Divide the percentage of the range by its corresponding number of fixes and compare the ratios of the inflection points. The smaller ratio represents the true inflection point, as this number of fixes reveals the most concentrated area of use. In the example below (Figure 3.8), the ratio of the inflection point marked A, is smaller than the ratio of inflection point B. Therefore, point A, which indicates that 23% of the home range was revealed by 78% of fixes, is the true inflection point. The core range of this squirrel is contained within 23% of its home range. The percentage of the home range representing the core range was then input into Ranges 9 to generate a new MCP designating the core range of the individual.

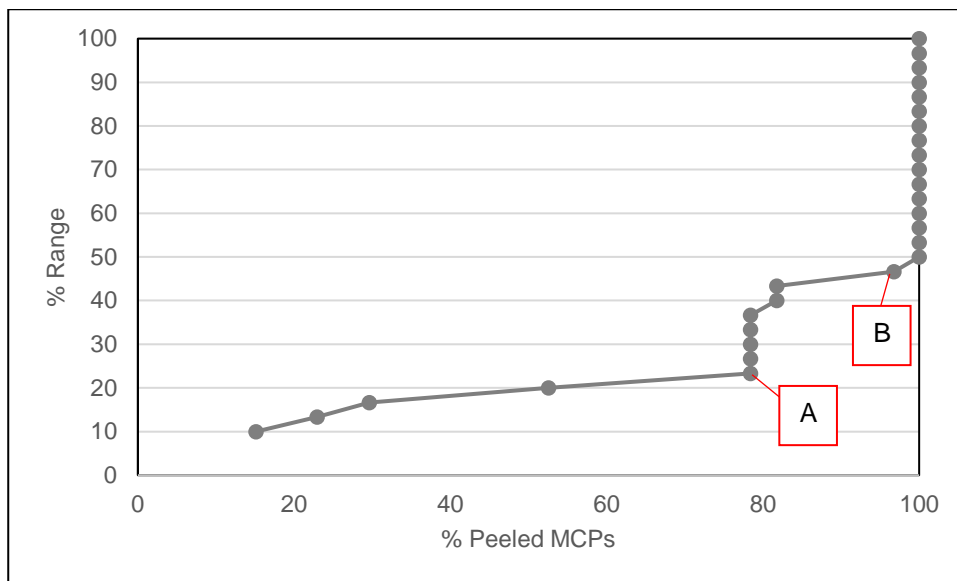


Figure 3.8 An example of an incremental plot showing percentage peeled MCPs and the corresponding percentage of the total home range. The true inflection point is point A, and is the point of the most concentrated range use data, as opposed to point B, which has a lower concentrated range use. In this example, the inflection point indicates that the core range occupies 23% of the home range.

As radiotracking was deemed unsuitable for use in Derryclare, home range estimates were derived using trapping data. This technique assumes that all traps visited by individuals are

within the home range of the individual. A minimum home range size was determined by identifying the midpoint of the traps used by an individual, and the distance from that midpoint to the furthest trap. This distance was then employed as a radius to generate a circular home range originating from that midpoint and incorporating all traps used by the individual. Unsuitable habitat such as immature woodland, rivers and urban fabric were excluded from the generated home ranges. In order to validate this technique, the trapping data of the radiotracked Belleek squirrels was examined for comparison. Only four of the radiotracked squirrels could be used in this analysis as they had been caught in more than one trap. Their estimated home ranges were calculated using the technique described here, and subsequently compared to their home range size determined by radiotracking. This allowed us to assess the accuracy and reliability of the trapping-based home range estimations. Home ranges were subsequently estimated using trap data for all other Belleek squirrels who had been caught in more than one trap. The estimated home ranges of the Derryclare squirrels were compared against the home ranges of the Belleek squirrels derived from the trap data and the home ranges of Belleek squirrels derived from the radiotracking data.

3.2.6 Mapping the spread of the translocated populations

Differing approaches were taken for mapping the spread of the translocated populations in Derryclare and Belleek woods. These differences in approach were necessitated by their contrasting remoteness and differences in the surrounding human population density. In Derryclare, the approach involved identifying habitable woodlands situated within a proximity of less than 2 kilometres from the woodland, as most juveniles are thought to disperse within 1km in fragmented habitats (Verbeylen et al., 1998; Wauters et al., 1994a). Four woodlands met this criterion, ranging in size from 5 hectares to 86 hectares (Figure 3.9). The investigations into squirrel presence within these woodlands were carried out in March 2021. The assessment of squirrel presence consisted of a search for feeding signs within a predetermined timeframe, determined by the size of the woodland. A guideline of one hour of searching per 20 hectares was allocated, with a minimum of 30 minutes allocated for the smallest woodland, spanning 5 hectares. In total, 166ha of nearby woodland were surveyed over a period of 8.5 hours.

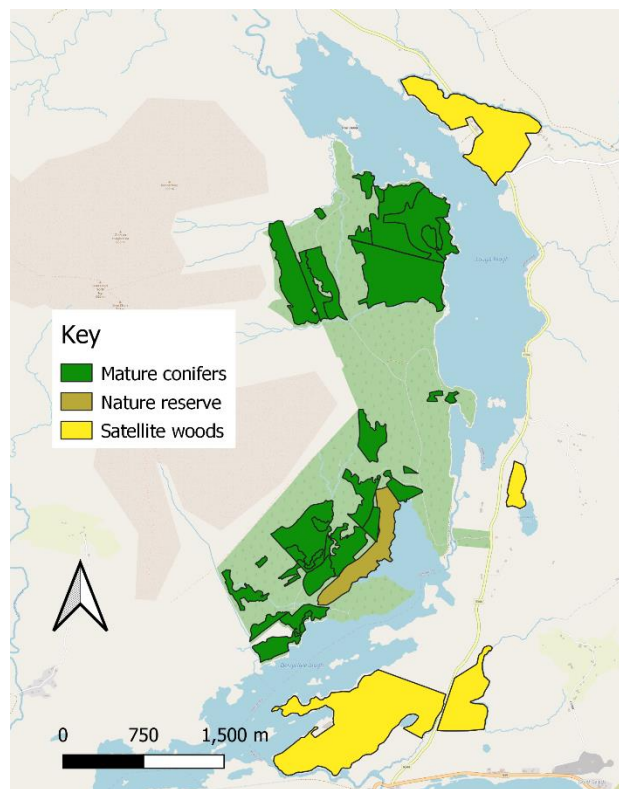


Figure 3.9 A map showing the satellite woods (yellow) within 2km of Derryclare.

In Belleek, a citizen science survey was implemented to map the expansion of the translocated population's range. Squirrels located in Ballina and the surrounding towns are assumed to have come from the Belleek population, as no squirrels were present in the area before the translocation (Carey et al., 2007). The Ballina Red Squirrel Survey was launched in March 2021 and concluded in January 2023. Participants were asked to submit red squirrel sightings in and around Ballina town, excluding Belleek woods. Participants were asked to provide the exact location and date of the sighting. Additionally, participants were asked to provide information on when they first began to see squirrels in this area and the date of their most recent sighting. This additional information enabled us to track the population's spread over time and accurately ascertain its current distribution. The survey primarily operated online, using a dedicated online form created on Typeform.com. Physical survey leaflets were also printed and distributed across various locations, including shops, community centres, schools, and libraries in Ballina, Crossmolina, Laherdaun and Foxford. These leaflets not only facilitated participants in submitting physical responses but also featured a QR code directing them to the online survey, a link to the survey's Facebook page, and the researcher's email address. Throughout its duration, the survey was promoted through multiple channels, including two radio interviews and their resulting newspaper articles, several school presentations at a local school, forest walks with

summer school camps, targeted posts in relevant Facebook groups of local communities, and direct communication with local residents.

3.2.7 Statistical analysis

Statistical analyses were conducted using IBM SPSS Statistics 27. Home and core range data were generated using Ranges 9.

3.3 Results

3.3.1 Non-invasive methods

Positive signs of squirrels were found in every stand in Derryclare that was surveyed using hairtubes, indicating that the red squirrel population is widespread within Derryclare woods. Squirrel usage of hairtubes was common, with only four hairtubes failing to record at least one squirrel over the duration of the project. The proportion of hairtubes visited by at least one squirrel per month varied between 0 and 0.45, with a mean proportion of 0.085 hairtubes visited per month. A Fisher's test determined that there was no significant difference in hairtube usage by season, month or year. However, hairtube usage did vary significantly depending on the region of the woodland. The southern region of the woods exhibited significantly more total positive IDs in the hairtubes, according to a Fisher's test (North; $n = 16$, South; $n = 25$, $p = 0.006$) (Figure 3.10).

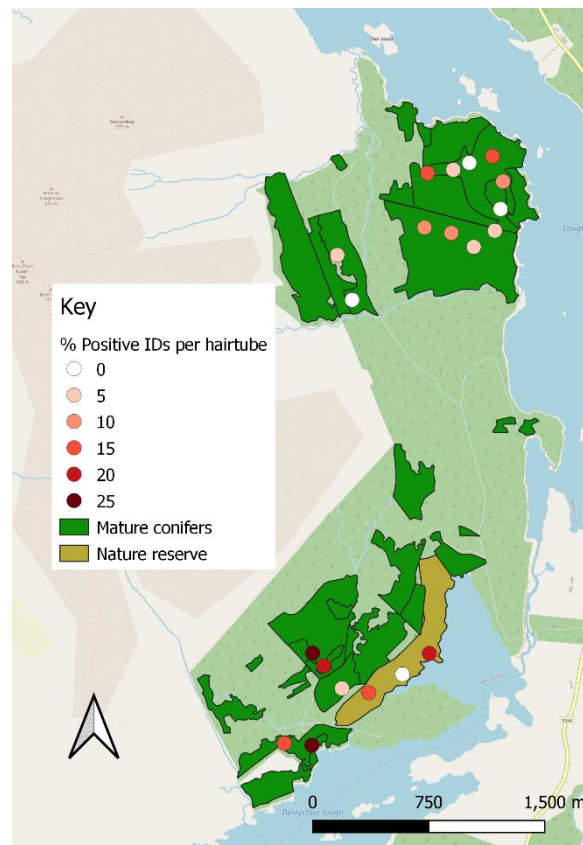


Figure 3.10 A map of Derryclare illustrating the squirrels' hairtube usage throughout the woods. The southern half of the woods recorded significantly more squirrel activity compared to the northern half.

Similarly, trail cameras found a greater squirrel presence in the southern half of the woods. Two cameras were placed in the northern half, and two were placed in the southern half (Figure 3.3). The northern cameras did not record any squirrel activity, while the southern cameras recorded a total of 37 squirrel visits.

The feeding survey confirmed the widespread presence of red squirrels in Derryclare, with at least one feeding sign discovered in every stand surveyed. Significantly more energy was consumed in the southern half of the woods ($\bar{x} = 46.14\text{kJ} \pm 27.03$ per transect) compared to the northern half ($\bar{x} = 7.08\text{kJ} \pm 6.78$ per transect), according to a Mann-Whitney U test ($U = 204.5$, $p = 0.008$) (Figure 3.11). This indicates a higher squirrel presence in the southern half, in line with the trail camera and hairtube results. Additionally, a higher energy content was found in the southern half of the woods ($\bar{x} = 1167\text{kJ} \pm 410.90$ per transect) compared to the northern half ($\bar{x} = 609.8\text{kJ} \pm 355.98$ per transect), although a Mann-Whitney U test revealed that this difference was not significant ($U = 176$, $p = 0.123$) (Figure

3.11). However, a significant moderate correlation was found between the energy available, and energy consumed per transect ($r^s = 0.554$, $p < 0.001$).

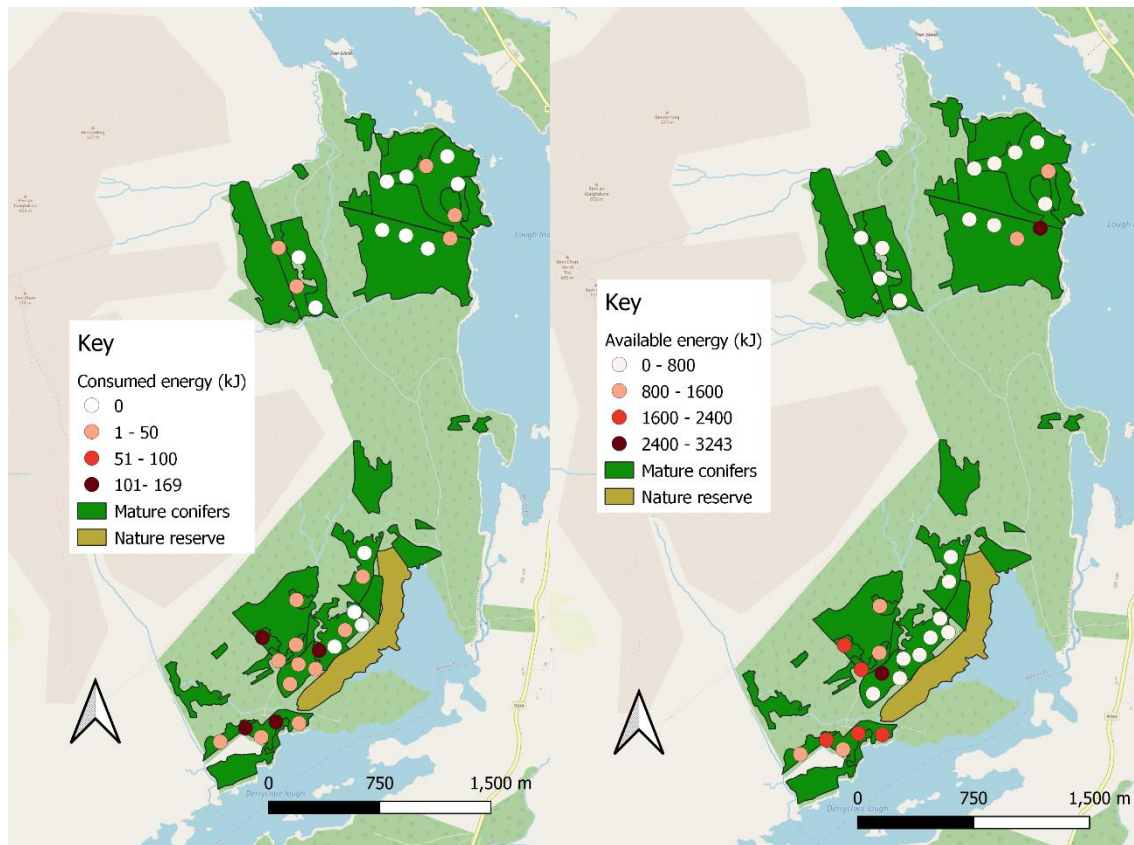


Figure 3.11 A map of Derryclare showing the amount of consumed energy per feeding transect (left) and the available energy per transect (right). Significantly more energy was consumed in the southern half of the woods. A higher average available energy was recorded for southern transects, although it was not found to be significantly different to the northern transect average.

No significant difference was found between the tree species composition area of the northern and southern regions, as determined by a chi square test ($\chi^2 = 1.93$, $df = 1$, $p = 0.16$). The regions also do not differ significantly in their age structure (Northern ha; $\bar{x} = 57$ years ± 4.48 , Southern ha; $\bar{x} = 52$ years ± 5.79) ($t(30) = 0.876$, $p = 0.388$).

Due to the higher number of squirrel signs detected in the southern half of Derryclare, live trapping efforts were concentrated in this area.

Signs of red squirrels were discovered throughout the woods via the hairtube and trail camera surveys in Belleek, indicating that their distribution is widespread throughout the

woods (Figure 3.12). The proportion of hairtubes visited per month varied between 0.4 and 0.6, with a mean of 0.52. The number of squirrel visits recorded on trail cameras varied from 8 – 56. Due to the observation that squirrels were widespread throughout Belleek, traps were not concentrated in any particular area.

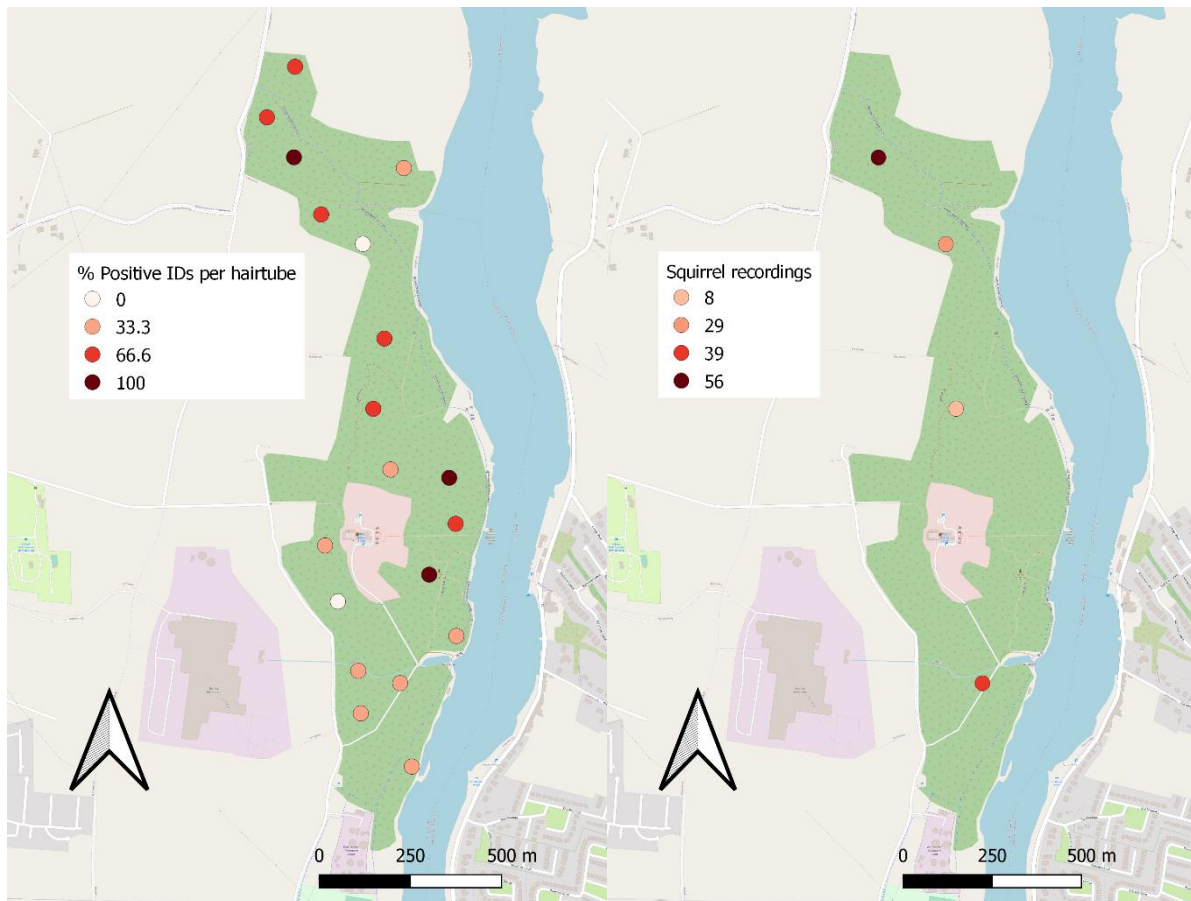


Figure 3.12 A map of Belleek illustrating the percentage of positive red squirrel IDs per hairtube (left) and the number of red squirrel recordings per camera (right). Signs of red squirrels are uniform throughout the woods.

3.3.2 Live Trapping

Red squirrels were captured a total of 375 times (Derryclare; 30, Belleek; 345) over 93 trapping days. A total of 82 individuals were trapped (Derryclare; 10, Belleek; 72). A total of 11 pine marten were captured unintentionally, all in Derryclare. The recapture number per individual squirrel ranged from 0 – 27. The majority of individuals were adults during their first capture ($n = 75$). Trapping success was higher in Belleek with a mean of $24.1 (\pm 4.1)$ trapping events per session, compared to Derryclare with a mean of $1.9 (\pm 1.1)$ trapping events per session. A mean of $15.2 (\pm 3.2)$ individuals were captured per month in Belleek,

compared to a mean of 1.3 (± 0.6) individuals per month in Derryclare. Table 3.2 presents an overview of the demographics of both populations.

	Derryclare			Belleek		
Study period	July 2020 - Jan 2023			Aug 2020 - Nov 2022		
	male	female	total	male	female	total
N	7	3	10	34	38	72
Trapping events	16			14		
Sex split (% male)	70%			47%		
Average body weight (g)	258.4 \pm 14.05			279.3 \pm 2.67		
Average shinbone length (mm)	65.5 \pm 1.28			66.1 \pm 0.75		
Average body index	3.94 \pm 0.22			4.24 \pm 0.04		

Table 3.2 A summary of the demographic data for squirrels in Derryclare and Belleek. Average body weights, shinbone lengths and body indices were calculated using each individual's mean value.

3.3.3 Population and density estimates

In Derryclare, hairtube usage data was used to calculate population density estimates. A maximum squirrel density of 0.01 squirrels/ha, and a mean density of 0.006 squirrels/ha was calculated using the proportion of hairtubes visited and the linear regression analysis detailed by Bertolino et al. (2009). When extrapolated to all mature woodland (202ha), an estimation of a maximum of 2.26 squirrels and a mean of 1.32 squirrels per month was calculated.

Population estimates based on the minimum number present (MNP), and the Lincoln index are displayed in figures 3.13 and 3.14 below, for Derryclare and Belleek, respectively. In Derryclare, a stable but very low density estimate may be seen. The MNP method estimates an average of 0.032 (± 0.011) squirrels per hectare (range = 0.013 – 0.075 squirrels/ha). When extrapolated to the mature area of the woodland the mean actual population estimation 6.5 (± 2.2) squirrels.

In Belleek, the highest density estimate was in the first trapping month in both estimates used, with the Lincoln estimate peaking at 1.78 squirrels per hectare, and the MNP estimating 0.66 squirrels per hectare. The lowest population density is estimated by the Lincoln density to be 0.14 squirrels per hectare and the MNP estimate to be 0.23 squirrels per hectare. The mean density estimated by the Lincoln index is 0.44 (± 0.16) squirrels per hectare and the MNP yields a mean density of 0.41 (± 0.08) squirrels per hectare. When

extrapolated to the total mature woodland, the mean actual population estimated by the MNP is 24.6 (\pm 4.8) squirrels and the Lincoln index estimates a mean of 26.4 (\pm 9.6) squirrels. Both estimates of Belleek squirrel density show a slight decline. Despite this, Belleek exhibited a consistently higher density of squirrels per hectare (\bar{x} = 0.41 squirrels/ha) compared to Derryclare (\bar{x} = 0.032 squirrels/ha) (Figure 3.15). The MNP estimates of both sites are used for comparison purposes.

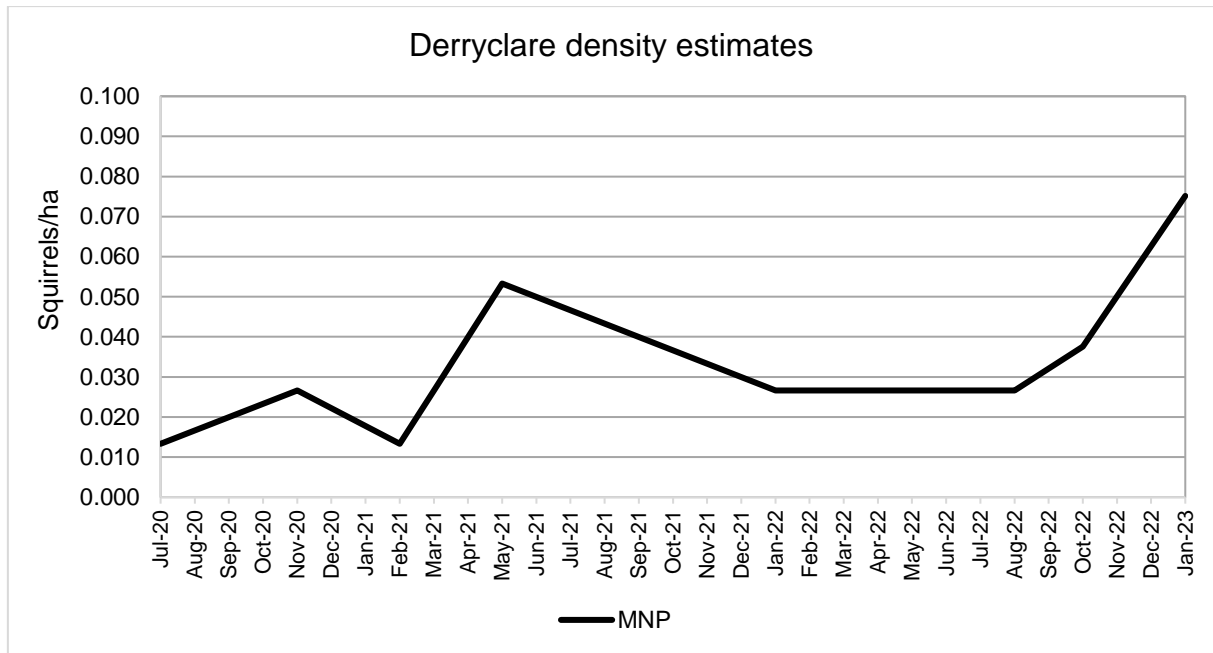


Figure 3.13 Squirrel density estimates for Derryclare based on the minimum number of individuals present.

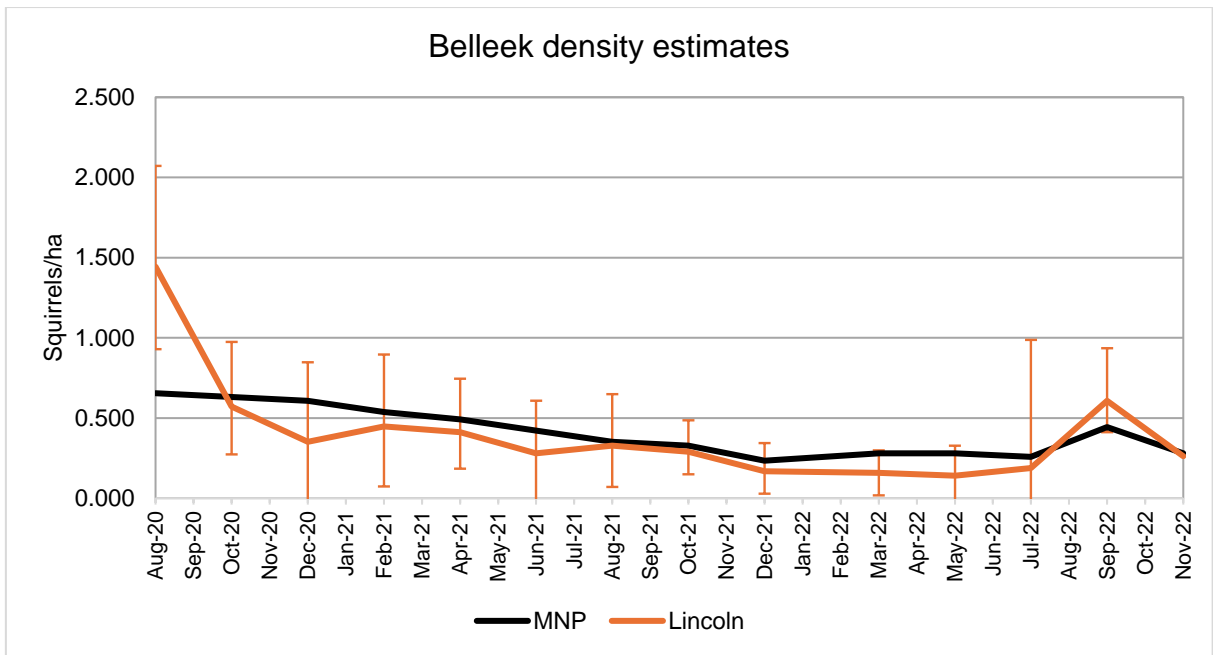


Figure 3.14 Squirrel density estimates for the Belleek population, based off two population estimates. Orange bars represent the standard error for the Lincoln population values. A particularly high density was estimated from the first trapping session with the Lincoln estimate.

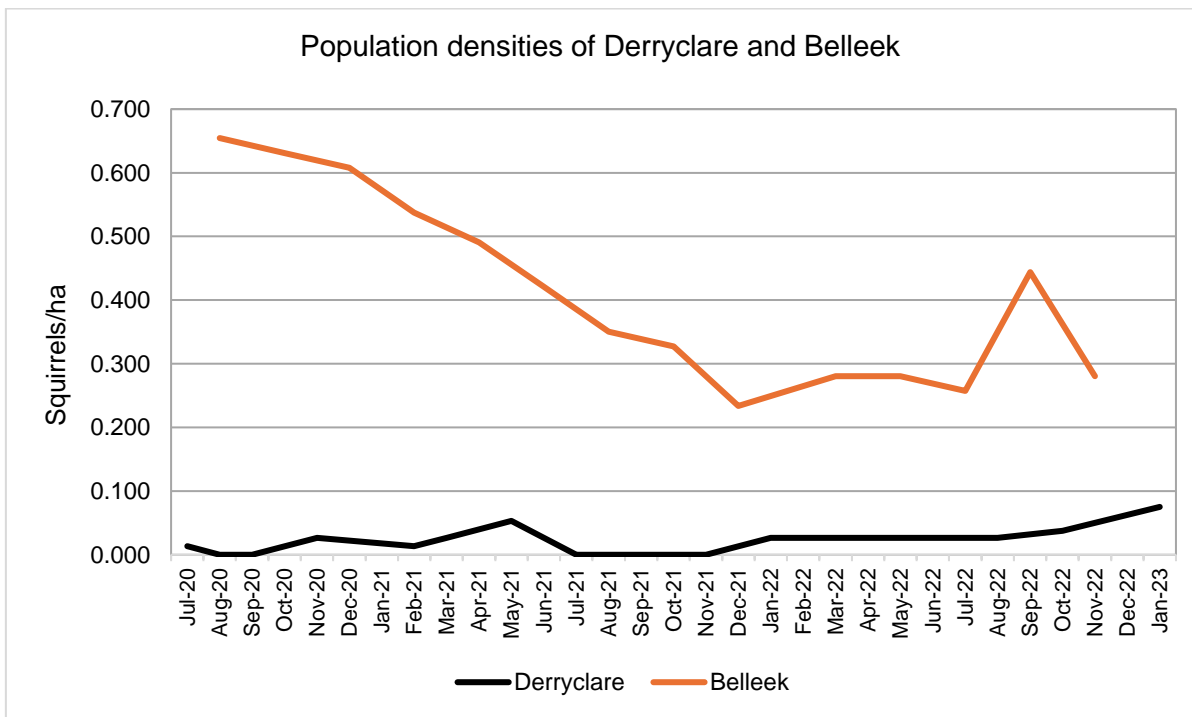


Figure 3.15 The MNP density estimates from both sites. This method was most suitable for estimating the Derryclare population due to its small size. A downward trend may be seen in the larger Belleek population, with an upswing in late 2022.

3.3.4 Breeding rates and recruitment

Breeding rates differed between the two sites, with only one female out of a total of three females observed to have had a litter in Derryclare, while 47% of females ($n = 17$) in Belleek successfully had litters. The number of new recruits in Belleek was consistently higher per session compared to Derryclare (Figure 3.16). Squirrels trapped during the first year of the project were considered to be new recruits to the population if they weighed less than the average recruit (Belleek; $\bar{x} = 267\text{g}$, Derryclare $\bar{x} = 260\text{g}$) caught in subsequent years. In Belleek, new recruits were trapped in 13 of the 14 trapping sessions. In Derryclare however, new recruits were only trapped in 6 of the 16 sessions. The highest number of new recruits were recorded in Belleek in September 2022 ($n = 9$), followed by the next highest number of recruits in August 2020 ($n = 7$). In contrast to Belleek, the highest number of recruits caught in Derryclare was 3, in January 2023. New recruits in Derryclare and Belleek did not differ significantly in their weight, shinbone length or body index.

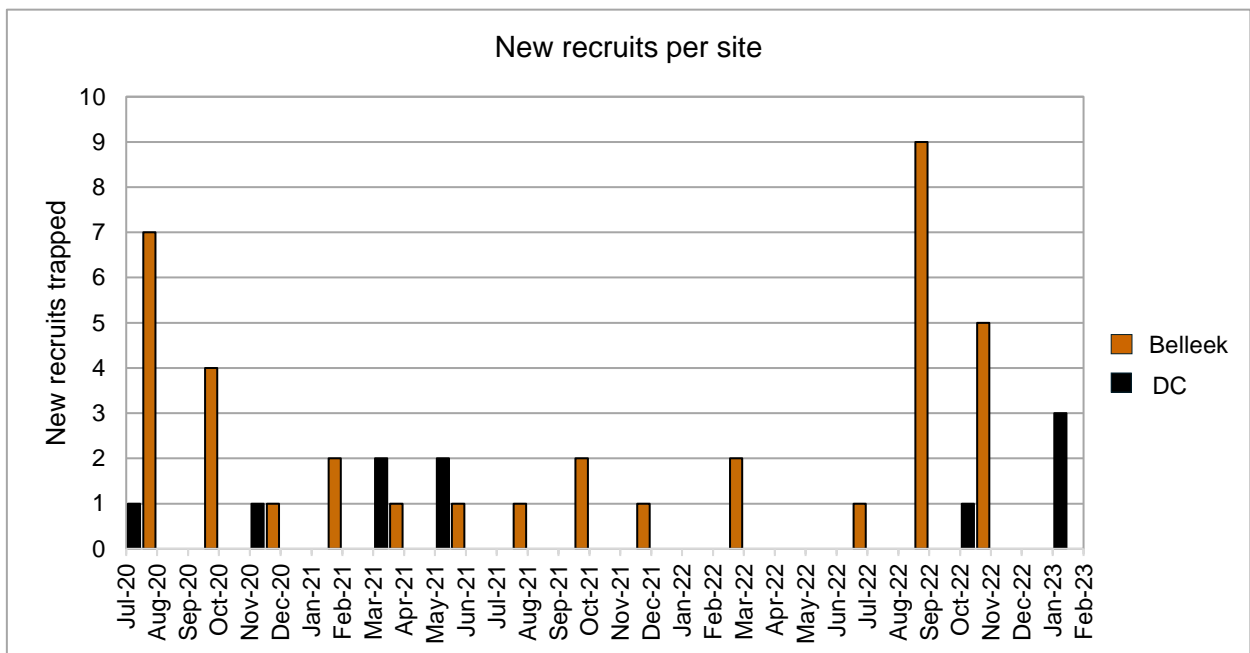


Figure 3.16 The number of new recruits trapped during each session at Derryclare and Belleek. A total of 10 individuals were trapped in Derryclare, compared to 72 individuals in Belleek.

Table 3.3 displays the estimated number of young born in both sites based on the number of lactating females and an average litter size of 3 young. This was then compared to the actual number of new recruits captured during that period. New recruits trapped in the months of January and February were included in the previous year's count as the breeding season has not yet begun at this time. As trapping began towards the end of the breeding

season of 2020 in both sites, the number of breeding females in 2020 reported below is likely an underestimation.

	Breeding season	Lactating females	Potential young	New recruits trapped
Derryclare	2020	0	0	2
	2021	1	3	4
	2022	2	6	4
Belleek	2020	4	12	14
	2021	16	48	6
	2022	13	39	17

Table 3.3 The number of lactating females, an estimate of the number of young produced and the number of new recruits captured per trapping year in both sites. Only one female produced young in Derryclare, compared to 17 females in Belleek.

A summary of the breeding data is presented in table 3.4.

Litters		Derryclare			Belleek		
		Spring	Summer	Total	Spring	Summer	Total
	2020	-	0	0	-	4	4
	2021	1	0	1	9	7	16
	2022	1	1	2	9	4	13
Total litters per female	0	2			21		
	1	-			8		
	2	-			5		
	3	1			1		
	4	-			3		
Mean recruits per month	0.6 (\pm 0.5)			2.6 (\pm 1.4)			

Table 3.4 A summary of the reproductive data for both Derryclare and Belleek.

3.3.5 Fitness

The mean overall weight of squirrels captured per month is displayed in table 3.5 below. Month significantly affected the weight of squirrels in Belleek, according to a one-way ANOVA ($F(14, 206) = 2.565, p = 0.002$). A post-hoc pairwise comparison revealed that the difference exists between the low weight observed in August 2020 and the heavier weights observed in April 2021, March 2022 and May 2022. Similarly, weight was also significantly affected by month in Derryclare, according to a one-way ANOVA ($F(10, 10) = 3.945, p =$

0.021). A post-hoc pairwise comparison was unsuitable due to the small sample size. All individuals were included once per month for this analysis.

Derryclare			Belleek		
Session	Overall weight (g)	N	Session	Overall weight (g)	N
Jul-20	176	1	Aug-20	276 ± 15.8	28
Aug-20	-	-	Oct-20	283.4 ± 20.9	25
Sep-20	-	-	Dec-20	297 ± 28.4	15
Nov-20	216 ± 43.1	2	Feb-21	292.8 ± 17.9	19
Feb-21	213.5 ± 3.5	1	Apr-21	304 ± 26.1	20
Mar-21	297.7 ± 20.2	2	Jun-21	301.8 ± 37.9	13
May-21	286.6 ± 27.3	4	Aug-21	293 ± 22.4	15
Jul-21	-	-	Oct-21	290.6 ± 17.1	12
Sep-21	-	-	Dec-21	290.4 ± 18.4	8
Nov-21	-	-	Mar-22	310.5 ± 34.8	10
Jan-22	276	1	May-22	312 ± 17.8	10
Mar-22	281 ± 7.1	1	Jul-22	300.4 ± 50.3	8
Jun-22	302.6 ± 30.1	2	Sep-22	286.6 ± 36.1	18
Aug-22	318.5 ± 17.7	1	Nov-22	278.5 ± 30.6	12
Oct-22	256	1	Mar-23	281 ± 23	8
Jan-23	267 ± 14.3	4			

Table 3.5 The mean weight of squirrels in Derryclare and Belleek per trapping session. Only one value was used per individual per month.

A two-way ANOVA determined that breeding status had a significant effect on the weight of females in both sites, but site and the combination of site and breeding status were not significant. Pregnant females and lactating females were found to be significantly heavier than non-pregnant females ($F(55, 2) = 4.716, p = 0.021$). Breeding status did not significantly affect the weight of males.

The average weight of each squirrel in Derryclare and Belleek were compared, with site and sex included as fixed variables. A two-way ANOVA revealed that site had a significant impact on the mean weight of the squirrels ($F(1, 78) = 4.944, p = 0.015$). Specifically, Belleek squirrels had a higher mean weight ($\bar{x} = 279.3g \pm 2.67$) compared to Derryclare

squirrels ($\bar{x} = 258.4\text{g} \pm 14.05$) (Figure 3.17). The effect of sex and the effect of the interaction between sex and site were not significant.

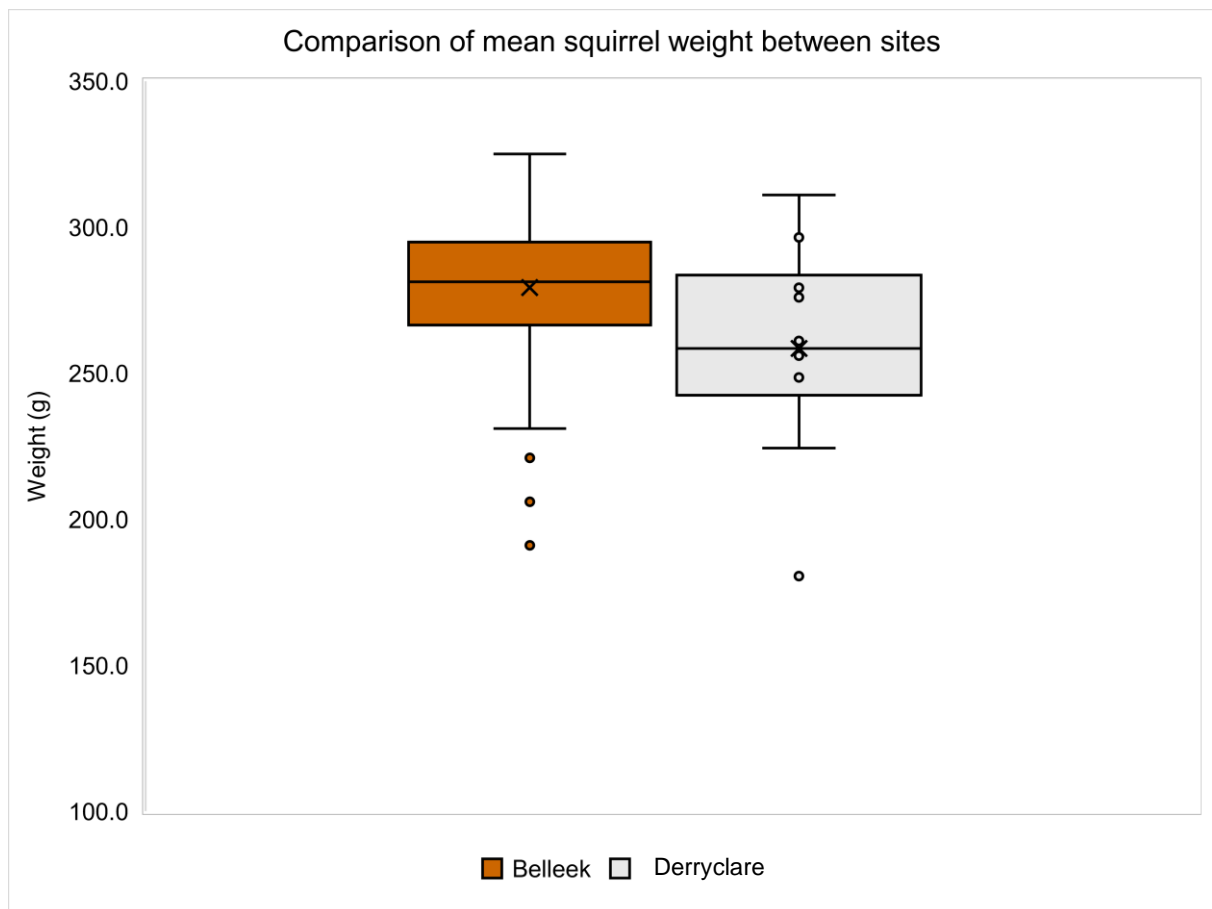


Figure 3.17 A boxplot comparing the weight of squirrels in Derryclare and Belleek. The mean weight of each individual was used, ensuring each squirrel is counted only once. Belleek squirrels were found to be significantly heavier.

Body weight was found to be significantly moderately correlated with shinbone length ($R^2 = 0.430$, $p < 0.001$). The average shinbone measurement per individual in Derryclare and Belleek were compared. No significant difference was found either between site or between sexes.

The average body index of each squirrel in Derryclare and Belleek were compared using a two-way ANOVA, with site and sex included as fixed variables. The body index of Belleek squirrels ($\bar{x} = 4.24 \pm 0.04$) was found to be significantly higher than that of Derryclare squirrels ($\bar{x} = 3.94 \pm 0.22$) ($F(1, 78) = 5.585$, $p = 0.021$). Sex and the interaction between site and sex had no effect on body condition. This indicates that Belleek squirrels are in a fitter body condition compared to Derryclare squirrels (Figure 3.18).

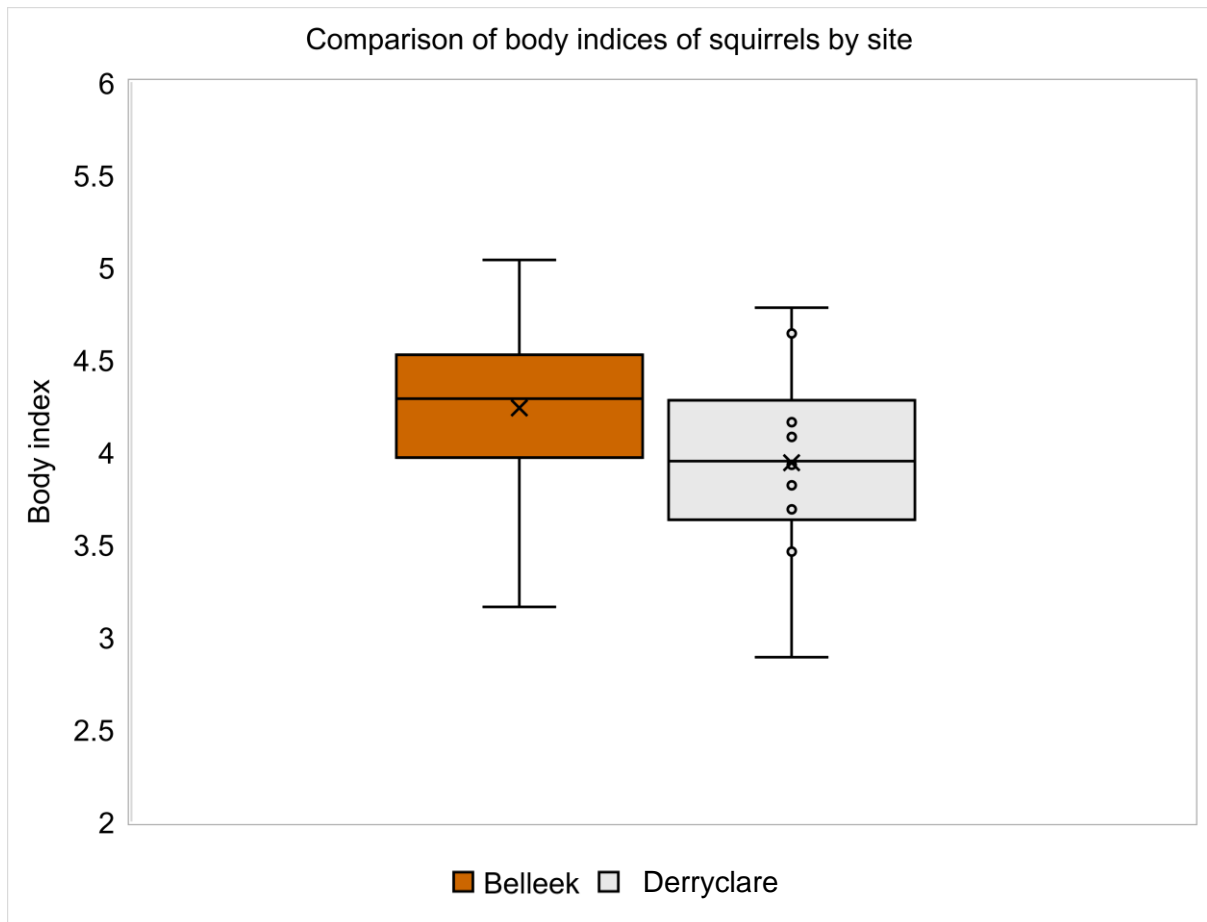


Figure 3.18 A boxplot comparing the mean body index of each individual in Derryclare and Belleek. Belleek squirrels were found to be significantly fitter.

3.3.6 Habitat use

Table 3.6 summarises the main findings of the radiotracking study. Six male and two female adults were radiotracked in Belleek. The average home range was found to be 4.02ha (\pm 1.34). Overlap between home ranges was common, with only one radiotracked squirrel not overlapping with the others (Figure 3.19). However, another squirrel was frequently seen within her home range (pers observation), and captured at the trap within her home range, indicating that overlap occurred with an uncollared squirrel. Core ranges, which indicate the areas squirrels use most intensively within their home range, did not overlap with the core range of any other squirrels (Figure 3.20). Seven out of eight squirrels incorporated traps into their home ranges, with individuals having an average of two traps each in their home range. Seven squirrels incorporated feeding stations into their home ranges, with one individual containing two feeding stations within his home range. Only three squirrel's core ranges contained a feeding station, and none contained a trap.

ID	Sex	HR area (ha)	CR area (ha)	% peeled MCPs	Squirrel overlap (HR)	% HR overlap	Area of HR overlap (ha)	Traps in HR	Feeding stations in HR	Traps in CR	Feeding stations in CR
825	F	2.39	1.27	92	0	0.00	0	1	1	0	1
874	M	3.00	1.07	77	3	27.04	0.81	3	0	0	0
864	M	3.58	2.26	84	5	95.46	3.42	1	1	0	0
915	F	2.80	1.88	99	5	83.09	2.33	3	1	0	1
955	M	4.62	0.92	73	5	99.83	4.61	2	1	0	0
845	M	8.49	1.95	78	6	84.52	7.18	3	2	0	0
965	M	3.41	2.28	95	5	60.67	2.07	1	1	0	1
945	M	3.85	1.54	84	3	31.44	1.21	2	1	0	0

Table 3.6 Home range, core range and overlap data for each radiotracked individual. The percentage peeled MCPs represents the proportion of time each individual spent within their core range. The number of squirrels each individual's home range (HR) overlapped with, and the area of that overlap are shown. Additionally, the number of traps and feeding stations within an individual's home range and core range are shown.

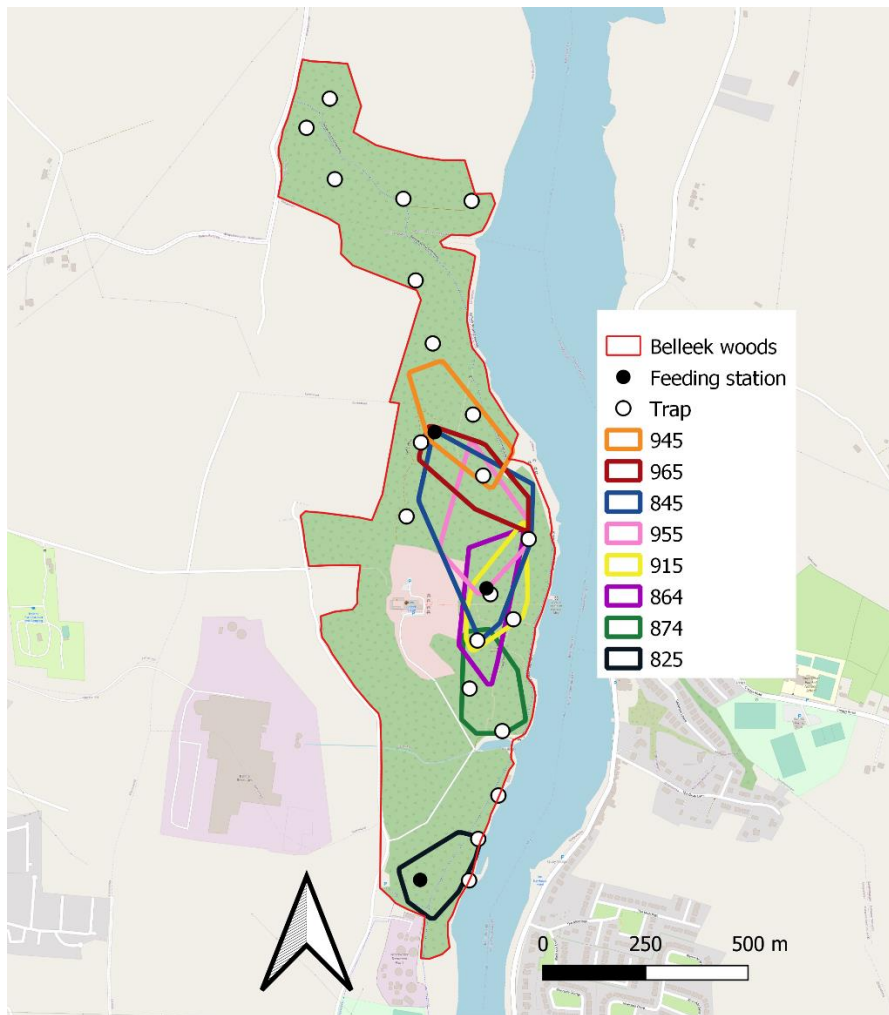


Figure 3.19 A map showing the home ranges of the radiotracked squirrels in Belleek. A strong overlap is visible in seven of the eight squirrel's home ranges. All home ranges overlap with traps, and seven of the eight overlap with feeding stations.

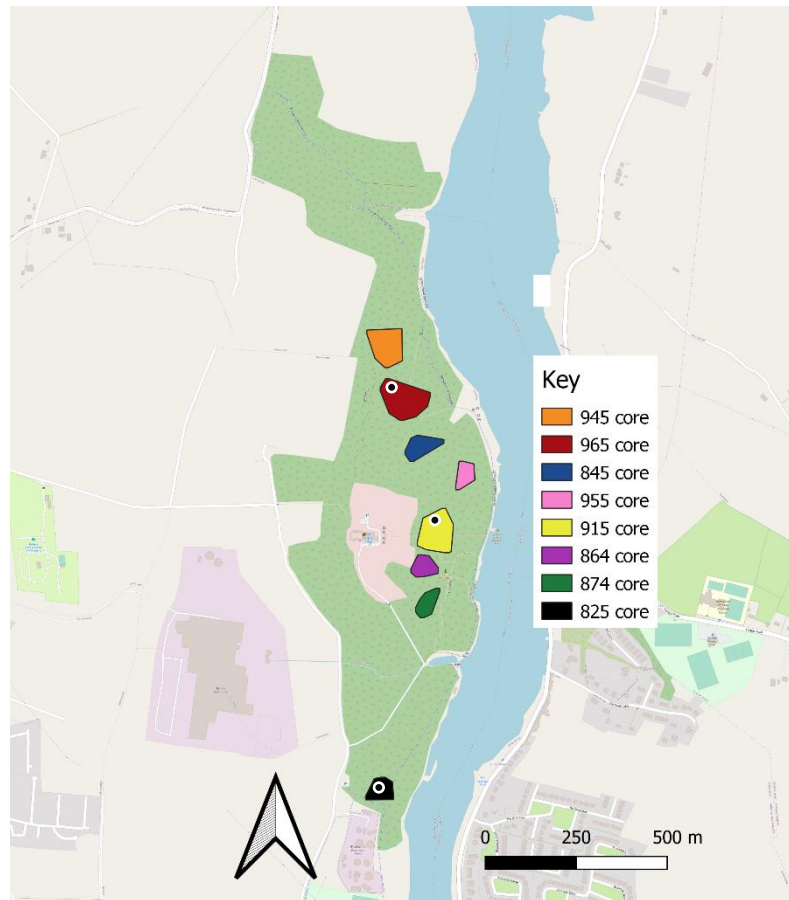


Figure 3.20 The core ranges of the radiotracked squirrels in Belleek. No overlaps in core areas were observed. Feeding stations (black dots) that were incorporated into core ranges are shown.

Trapping data was utilised to estimate the home ranges of the Belleek radiotracked squirrels. Four squirrels were only caught at one location and therefore could not be included in the analysis. The home ranges estimated from the trapping data were compared to that individual's actual home range, as determined by the radiotracking study (Table 3.7). A paired t-test indicated that the means of both groups were not significantly different ($t(3) = -0.316$, $p = 0.611$, $n = 4$), meaning that trapping data provided a reasonably accurate home range estimate for the population. Therefore, trapping data in Derryclare was used to estimate the home ranges of Derryclare squirrels.

<i>ID</i>	<i>HR (ha) by radiotracking</i>	<i>no. of traps</i>	<i>HR (ha) by traps</i>
825	2.39	3	2.7
874	3.00	1	-
864	3.58	1	-
915	2.80	4	4.3
955	4.62	1	-
845	8.49	2	5.4
965	3.41	1	-
945	3.85	2	1.3

Table 3.7 The home ranges of Belleek squirrels as determined by radiotracking, compared to their home ranges as determined by trapping data. The number of traps each individual was caught at throughout the study are noted. Squirrels who were only caught at one trap could not be used in the analysis. The mean home range of each group were found not to be significantly different.

Home ranges were estimated for seven Derryclare squirrels. Three individuals were only caught at one location each and therefore could not be included in the home range analysis. These home ranges were compared to the radiotracking-determined home ranges of Belleek squirrels using a Mann-Whitney U test. The estimated home range of squirrels in Derryclare ($\bar{x} = 19.61, \pm 15.39, n = 7$) was found to be significantly larger than Belleek home ranges that were determined through radiotracking ($\bar{x} = 4.02\text{ha}, \pm 1.93, n = 8$) ($U = 9, p = 0.029$). A summary of the results can be seen in table 8.

ID	Sex	Estimated home range (ha)
1	F	5.03
2	M	20.80
3	M	21.78
4	F	47.74
5	M	14.64
6	M	26.17
9	F	1.09

Table 3.8 The estimated home ranges for seven of the ten Derryclare individuals.

Six out of seven individual's home ranges overlapped with the nature reserve. There was no significant difference between the size of the home ranges of males and females. Six out of seven squirrel's home ranges overlapped with each other.

Home ranges were estimated for all Belleek squirrels who used more than one trap, using their trapping data. The estimated ranges of Derryclare squirrels were then compared to the estimated home ranges of all Belleek squirrels. Belleek squirrels were found to have significantly smaller home ranges compared to Derryclare squirrels, according to a Mann-

Whitney U test (Belleek; $\bar{x} = 8.02\text{ha}$, $n = 35$, Derryclare; $\bar{x} = 19.61\text{ha}$, $n = 9$, $U = 62$, $p = 0.041$).

3.3.7 Population spread

No signs of red squirrels were detected in the satellite woodlands surrounding Derryclare, indicating that no spread has occurred in recent years.

In Belleek, red squirrels were observed outside of Belleek woods in Ballina town and in neighbouring towns. A total of 136 red squirrel sightings were reported to the Ballina Red Squirrel Survey. Of these, 10 were omitted due to insufficient information and a further 10 were excluded as they reported sightings from within Belleek woods. Another 7 sightings were omitted as they reported sightings outside the range of study and were unlikely to represent squirrels from the Belleek population. A total of 109 sightings were included in the final survey, with the majority of responses originating from the online survey ($n = 93$), and others reported via social media ($n = 9$) and personal communications ($n = 6$). Only 1 sighting was reported via paper leaflet. Thirty responses did not provide information on when a squirrel was first spotted in the area of the sighting, but all other data from these submissions including the location and time of the sighting were included in the survey.

Red squirrel sightings were reported within a 21km radius of Belleek woods (Figure 3.21). The highest concentration of reports were located within Ballina town, with over a third of sightings ($n = 39$) reported within 5km of Belleek woods. Squirrel sightings to the east and north were uncommon, with the majority of reported sightings outside Ballina town originating from the west and south, as far as Crossmolina and Foxford, respectively. Figure 3.22 illustrates the spread of the population by showing the first instance a sighting occurred outside of Belleek woods. This figure also includes sightings reported by Waters (2012b) from the years immediately following the translocation. Squirrel sightings south of Ballina town were reported to have begun prior to 2018, with three submissions reporting sightings in Foxford and one submission reporting a sighting on the western side of Lough Conn during this period. Sightings to the west and southeast of Belleek woods began in 2020 (Figure 3.22). In 2022, the squirrels' distribution spanned a total distance of 738.5km^2 . Figure 3.23 depicts the most recent sighting of a squirrel in a particular location, allowing us to see where squirrels have become established. For example, one isolated sighting on the western side of Lough Conn has not been observed since 2020, meaning establishment is unlikely to have occurred in that area. Much of the range features sightings from 2022, and the volume of sightings suggests an established presence (Figure 3.22).

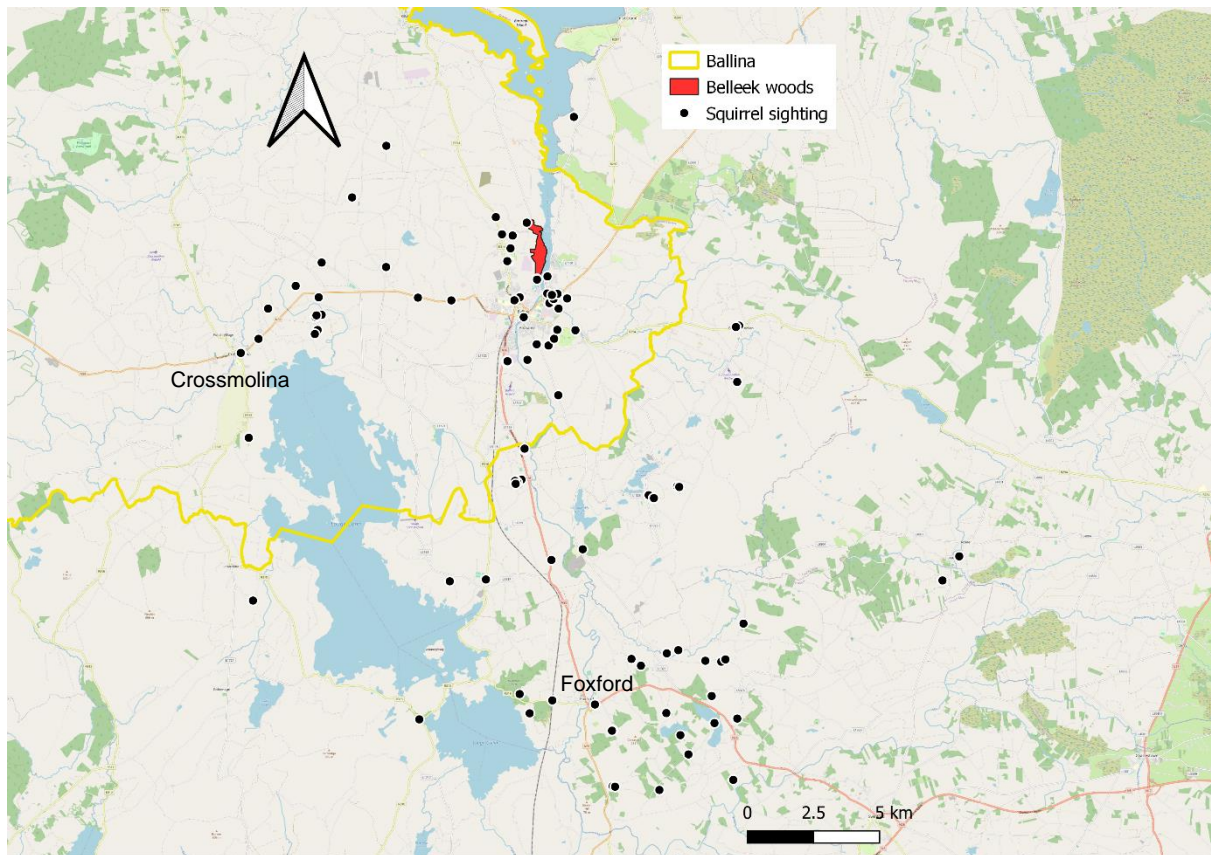


Figure 3.21 Red squirrel sightings (n = 109) reported to the Ballina Red Squirrel Survey. Sightings stretched as far west as Crossmolina (12km from Belleek woods) and as far south as Foxford (18km from Belleek woods).

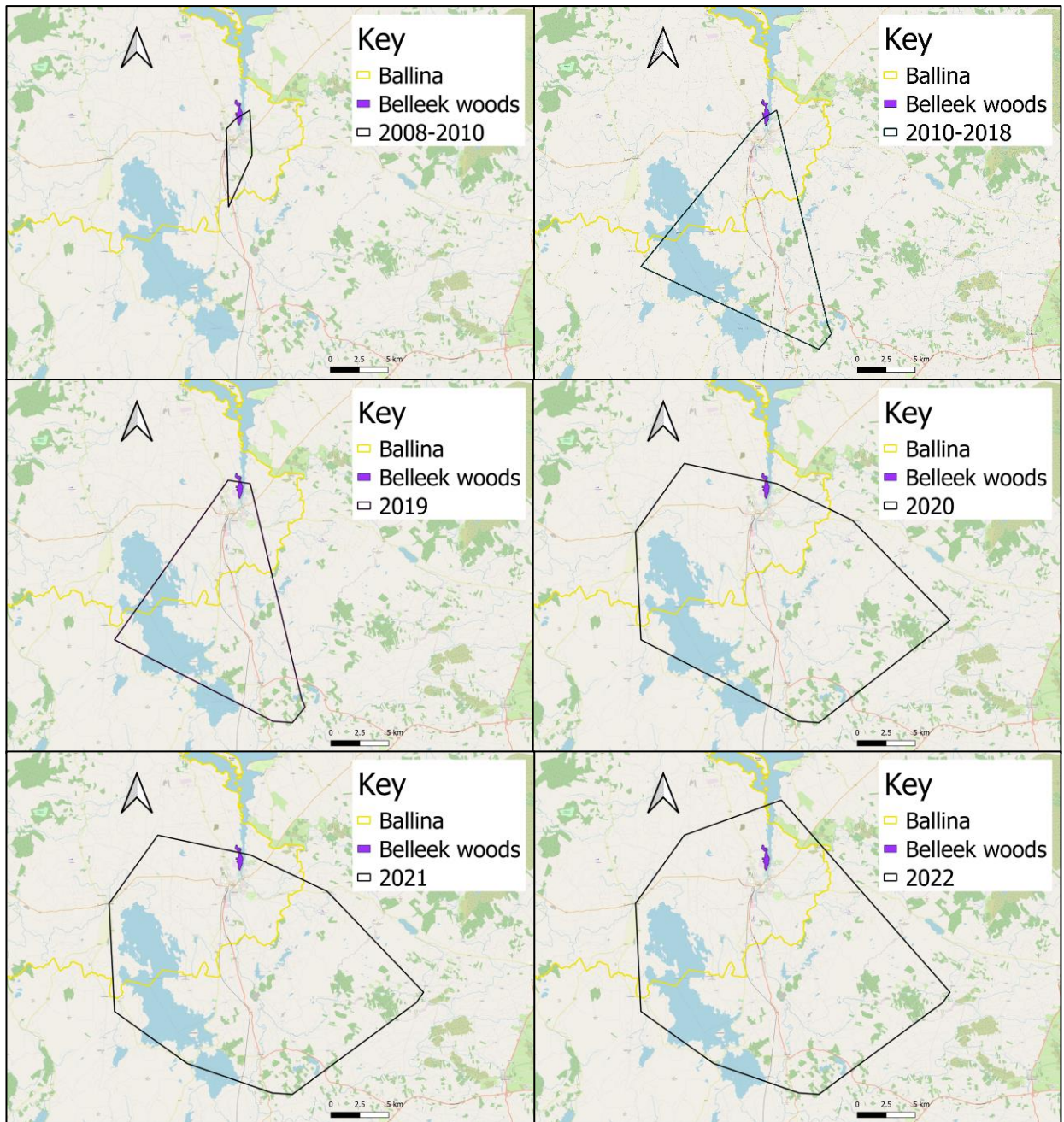


Figure 3.22 A map illustrating the spread of the squirrels from the translocation site of Belleek woods. Lines indicate the furthest areas reached by the red squirrel population during that year, according to first sighting reports. The oldest records (2008-2010) recorded by Waters (2012) show the initial spread immediately following the translocation. Between 2010 and 2018 the population's range expanded over 20km south of the woods. Further expansion to the southeast and west of the woods can be seen in 2020 and 2021. The population subsequently expanded north, with the first sightings occurring in this area in 2022.

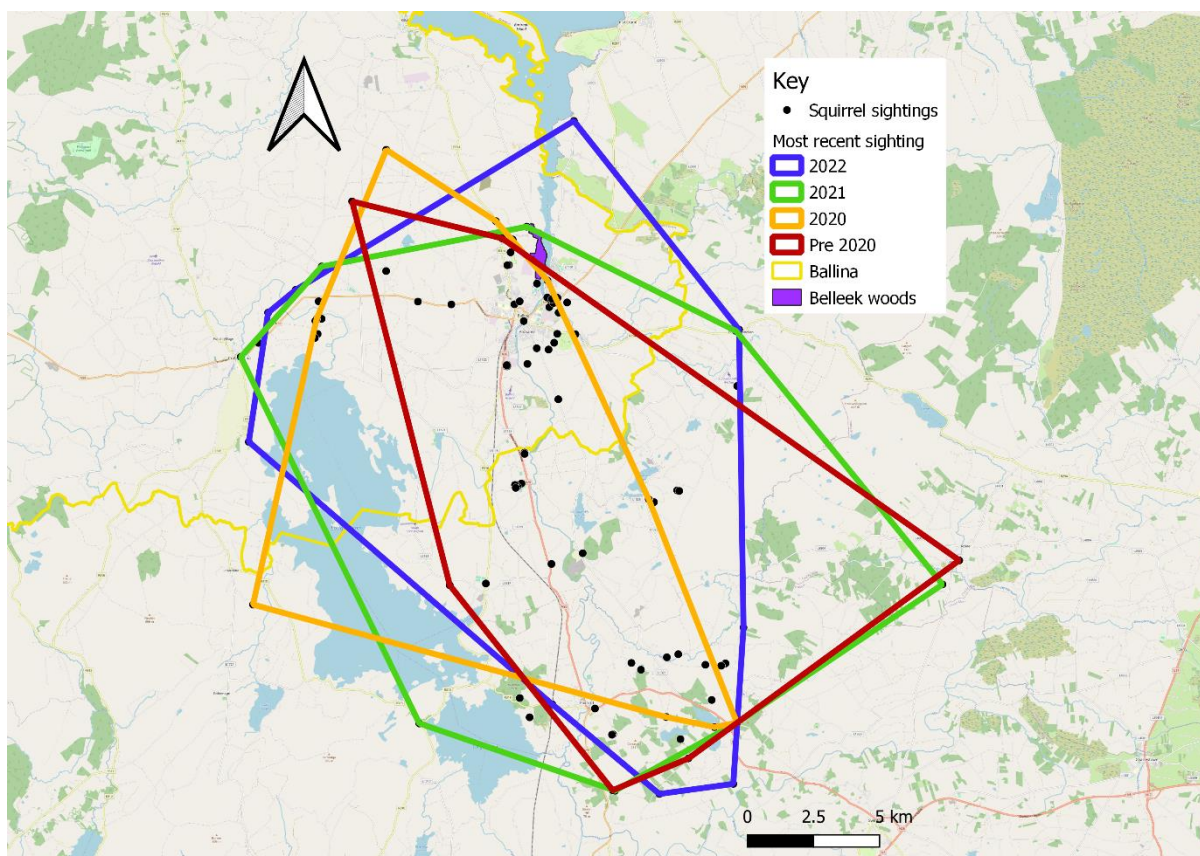


Figure 3.23 A map depicting the distribution of the population based on the year the most recent sighting was reported. Lines indicate the year in which squirrels were last reported in that location. Squirrels have been observed throughout the majority of their range in 2022, indicating a continued presence.

3.4 Discussion

The translocations at Derryclare and Belleek have resulted in contrasting outcomes. In Derryclare, the population have not transitioned into the regulation phase, whereas the Belleek population have successfully done so. The key characteristics of the regulation phase include a continued presence of the population and a stabilised density (IUCN/SSC, 2013). The continued presence of the population throughout Derryclare woodland was confirmed by all non-invasive and invasive techniques used in this study. The range expansion observed during the growth phase is still present in the Derryclare population, however, the population is no longer growing, but rather is declining. The live trapping maximum estimated density of 0.032 squirrels/ha represents a significant decline in the population over the last decade. The current study has revealed an eighteenfold decrease in the minimum estimated density compared to Waters' 2012 study (2012 = 0.24 squirrels/ha, 2023 = 0.013 squirrels/ha). During the aforementioned study, the woodland was estimated to be home to a peak population of 62 squirrels, while the current maximum estimate stands at only 15.15 individuals. To put this into context, the recorded density in

this study is considerably lower than the reported density of 0.28 squirrels/ha in a similar Irish coniferous woodland habitat (Reilly, 1997).

It is possible that our live trapping density estimation slightly overestimates the true population size in Derryclare. The trapping grid in this study was chosen due to the prevalence of squirrel signs detected via non-invasive methods. Population density has been found to be correlated with hairtube visits (Bertolino et al., 2009; Finnegan et al., 2007), trail camera sightings (Shannon et al., 2023) and feeding signs (Andr n & Lemnell, 1992), thus indicating that a greater number of squirrels occupy the southern half of the woods, where the highest concentration of these signs were recorded. This spatial distribution is consistent with the fact that woodland use by squirrels is influenced by food availability (Lurz et al., 1997; Wauters & Dhondt, 1992), with squirrels occurring in higher densities in patches of greater quality (Wauters et al., 2001), such as those in the southern half of the woods (Figure 3.11). Furthermore, supplementary food, such as the bait provided during trapping sessions, has been shown to attract squirrels from one area of a woodland to another (Starkey, 2019; Verbeylen et al., 2003), although the low frequency of the feeding may not have been sufficient to attract any individuals (Lurz, 1995). Due to this potentially unequal distribution of individuals throughout the woodland, an extrapolation of the density recorded in the trapping grid may overestimate the number of squirrels elsewhere in the woods.

On the other hand, there is a possibility that trap avoidance in Derryclare may have led to an underestimation of the actual population size, as individuals may have remained undetected in the woods. Rural populations have been shown to exhibit increased neophobia and reduced boldness compared to their urban counterparts (Biondi et al., 2020; McDonnell & Hahs, 2015), thus affecting their trap use. Additionally, the presence of the red squirrel's predator, the pine marten, in Derryclare may further impact the red squirrel population's trap use. During trapping sessions in Derryclare, pine marten scat was frequently observed in and on top of traps. Furthermore, pine marten were unintentionally trapped in Derryclare during the day eleven times throughout the study, indicating their frequent visits to the traps. Red squirrels have been shown to avoid feeders with the scent of pine marten scat for up to 48 hours after deposition (Twining et al., 2020, also see chapter 4). Small mammals have also demonstrated a reduced likelihood of entering traps if the previous occupant was of a different species (Brouard et al., 2015). This effect is likely to be exacerbated when the scent is that of a predator. Based on the hypothesis that pine marten primarily visited the traps at night to access leftover bait, the trapping methodology was modified during the final month of the study. In this session, no prebaiting was conducted, and all traps were cleared of bait at the end of every trapping day, thus removing

the food source for pine marten and hypothetically reducing the likelihood of their visits to the traps. During this session, four individual red squirrels were captured, including three new recruits, representing the highest number of recruits captured in a single Derryclare session. While this trapping success lends support to the hypothesis that pine marten presence acted as a deterrence for red squirrels visiting traps, conclusions cannot be drawn from only one trapping session. We recommend that future trapping studies consider the behaviour of both the study population and their interactions with other species when devising trapping methodology. The effects of uneven squirrel distribution as well as possible trap avoidance behaviour complicate density estimations in Derryclare, however, these effects are negligible in the broader context of the significant decline evident in this population.

In Derryclare, an additional density estimation calculated from hairtube usage data estimated a density of 0.006 squirrels per hectare. The model used to calculate this estimate had been validated through live trapping and was specifically recommended for application in low density coniferous woodlands (Bertolino et al., 2009), aligning with the Derryclare population. However, this method warrants a cautious approach as hairtube usage varies depending on various site and population characteristics. Woodland composition (Wauters & Dhondt, 1992), food availability (Wauters et al., 2001), predator presence (Twining et al., 2020a), and habituation to anthropogenic food sources (Krauze-Gryz et al., 2021) have all been shown to influence hairtube usage. Indeed, the average estimated number of squirrels present generated by this model (1.32 squirrels) is smaller than the average minimum number present as revealed by the live trapping (6.5 squirrels), meaning that it underestimated the actual population size and may not be appropriate for this population. Interestingly, the density estimate of 0.01 squirrels per hectare, or 2.02 squirrels overall, derived from the feeding survey (See chapter 2) similarly underestimated the actual population size. This discrepancy could be attributed to the non-uniform distribution of squirrels within the woods, influenced by their relatively low population. The resulting patchy dispersal of feeding signs may lead to inaccuracies in data extrapolation (Fewster et al., 2008), specifically resulting in an underestimated density in this scenario. Despite this underestimation, these methods provide further evidence of the decline of the Derryclare population.

This dramatic decline in density in Derryclare has revealed that the population have not entered the regulation phase of the translocation (IUCN/SSC, 2013). Instead, it may be experiencing a population collapse, characterised by a substantial and rapid population decline (Park & Allaby, 2007), possibly leading to a local extinction in the future. Small populations and isolated populations are particularly susceptible to extinction (Brito &

Fernandez, 2000; Reed, 2004), due to demographic and environmental stochasticity, natural catastrophes and genetic factors (Shaffer, 1981). The minimum viable population is one that can sustain itself and avoid extinction under these changing conditions. The minimum number of individuals required to create a viable population is difficult to accurately assess. For the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) a minimum viable population of 40 – 250 squirrels has been estimated. For the red squirrel, it has been estimated that at least 35 individuals are required to sustain a population in an unstable habitat, under the most optimistic breeding scenarios (Wood et al., 2007). The maximum population estimate of 15.15 individuals in Derryclare is less than half of this minimum viable population estimate, indicating that the Derryclare population size is below the viability threshold. It is therefore unlikely to persist in the long term.

In contrast to Derryclare, the Belleek population has successfully entered the regulation phase. Continued presence and a stabilised density are key characteristics of the regulation phase of a translocation (IUCN/SSC, 2013). Their continued presence is observed throughout the woodland, detected by trail cameras, hairtubes and live trapping. Additionally, the Belleek population has exhibited an increase in density since the 2012 monitoring project, but has since stopped increasing, indicating that carrying capacity has been met. Waters (2012a) reported the average Belleek population density as 0.31 squirrels per hectare, whereas our study recorded an average density of 0.41 squirrels per hectare. This density is comparable to the 0.39 squirrels/ha recorded in another mixed woodland Irish red squirrel population (Flaherty, 2016). However, it's worth noting that a fluctuation in the population was recorded over the course of the study. A gradual decline and subsequent upswing was observed over the three years of trapping, with minimum individual estimates declining from 40 squirrels in the first trapping month to 13 squirrels in the final trapping month. There are several possible explanations for this fluctuation in the population estimation. Predation (Kenward & Hodder, 1998), disease transmission (Rushton et al., 2006; Simpson et al., 2013b), habitat loss, and grey squirrel presence (O'Teangana et al., 2000) are all common causes of red squirrel population declines. However, in the case of Belleek, there is no evidence to suggest that these factors were responsible, particularly given the absence of the grey squirrel in the west of Ireland (Lawton et al., 2019) and the continuous food availability resulting from the supplementary feeding. It is well established that red squirrel populations are prone to population fluctuations, primarily driven by annual changes in seed crops (Andrén & Lemnell, 1992) and adverse weather conditions (Wauters & Dhondt, 1990b; Wauters & Dhondt, 1989) which may impact their survival. Additionally, density dependent factors, such as increased competition for resources when the population nears or exceeds carrying capacity can cause increased emigration, leading to

reduced recruitment rates (Wauters et al., 2004a). This overshoot and subsequent drop in population numbers often balances out, resulting in a stable density (Turchin & Taylor, 1992). It is therefore likely that the decline observed in Belleek may be a result of a natural population fluctuation, supported by the upswing in the population density recorded at the end of the study, and the overall health of the population.

The Belleek population's expansion beyond the woodland and their subsequent establishment in these areas further support the theory that the woodland has reached its carrying capacity. This stands in stark contrast to the Derryclare population who have not appeared to spread beyond the woods, indicating that carrying capacity was likely never met. The point at which recruitment within Belleek woods began to decline is unknown, however, sightings of squirrels outside the woods have been reported since 2008 (Waters, 2012b). While initial sightings likely represented individual dispersers, the present study found evidence of establishment outside the woods indicated by consistent sightings in these areas over multiple years, up to 2022. The range of the population has continuously increased since their original introduction (Figure 3.22), initially spreading south, before expanding in all other directions, most recently north of the woods. The far west of Ireland is lacking in naturally occurring red squirrel populations (Poole & Lawton, 2009), due to fragmentation and a shortage of suitable corridors (Flaherty & Lawton, 2019; Waters, 2012b). Therefore, the expansion of the Belleek population's range represents a significant step toward reestablishing these populations in currently unoccupied territories, a key aim of the translocation project. The failure of the Derryclare population to contribute to the expansion of the distribution of red squirrels in the west of Ireland further highlights how the translocation has not met its goals, and will likely never do so. Further research should focus on the Belleek population's continued expansion, considering potential movement corridors, barriers, and suitable settlement areas.

The reasons behind the contrasting outcomes of the two translocation projects are undoubtedly complex and multifactorial. However, a prominent distinction between the projects lies in the availability of food at each site. While the food availability in Belleek was not quantified, the presence of both broadleaf and coniferous food sources, combined with the constant supply of supplementary food provide a stable and abundant food source throughout the year (Lurz & Garson, 1998; Lurz et al., 1997; Wauters & Dhondt, 1987). This stands in contrast to the low energy availability observed in Derryclare (chapter 2). It is well established that food availability has a significant influence on red squirrel populations, impacting their abundance (Gurnell, 1983), density (Wauters et al., 2008; Wauters et al., 2001), space use (Lurz et al., 2000; Wauters & Dhondt, 1992), dispersal patterns (Lurz et al., 1997) and reproductive output (Boutin et al., 2006). In areas characterised by

heterogeneous patch quality, such as Derryclare (as depicted in Figure 3.11), red squirrels have been shown to establish their home ranges in patches of higher quality (Wauters et al., 2001). This pattern may be seen in Derryclare, where evidence of squirrel feeding is most abundant in areas with a higher food quality. Consequently, this heterogeneity in the habitat quality results in a patchy distribution of squirrels and overall decreased density when compared to the homogeneous food quality of mixed woodlands (Wauters et al., 2001). Mixed woodlands, such as Belleek, have been shown to be particularly suitable for red squirrel populations, enabling higher red squirrel densities (Cagnin et al., 2000; Lurz & Garson, 1997; Wauters et al., 2004a), due to their reliability as a food source (Gurnell, 1983; Lurz et al., 1995). Conversely, woodlands containing high proportions of Sitka spruce stands, such as Derryclare, are particularly unfavourable for red squirrels due to the low nutritional value of this tree species (Lurz et al., 2000) and the unreliability of its crop yield (Broome et al., 2007; Lurz et al., 1998). It is therefore likely that the poor habitat quality of Derryclare, resulting in an uneven and limited food supply, has played a significant role in the failure of the population to transition into the regulation phase. In addition, the disturbances to the Derryclare population have likely exacerbated this issue, further limiting the available food and interrupting population processes (chapter 2).

While the mixed woodland of Belleek provides a more stable and favourable habitat for red squirrels, long-term supplementary feeding undoubtedly played a pivotal role in the success of this translocation, by further increasing food availability. Supplementary feeding is commonly used in translocations to aid in population establishment by improving survival (Armstrong & Ewen, 2001) and site fidelity (Ebrahimi & Bull, 2012; Poole & Lawton, 2009). This positive effect was observed during the first year of the Derryclare translocation, after which time the additional feeding ceased (Poole & Lawton, 2009). The reduced daily activity (Beliniak et al., 2021) observed in squirrels benefitting from supplementary feeding suggest a decreased foraging effort, allowing them to allocate more energy towards reproduction. Indeed, red squirrel densities in habitats supported by supplementary feeding are significantly higher than their non-supplemented counterparts (Magris & Gurnell, 2002; Shuttleworth, 1996; Verbeylen et al., 2003). It's important to acknowledge, however, that supplementary feeding also carries potential drawbacks, including the potential for predator attraction, creating an overreliance on supplemental food (López-Bao et al., 2010), and disease transmission risks, notably squirrel pox from grey squirrels (Rushton et al., 2000). However, grey squirrels are not present in Belleek. The combined advantages of a favourable woodland habitat and the support provided by long-term supplementary feeding are likely a significant contributing factor to the success of the translocation in Belleek.

The distinct differences in habitat qualities are also apparent in the significant variations in body condition between the Derryclare and Belleek squirrel populations. It was observed that Belleek squirrels are in significantly better physical condition. Stable habitats of higher quality, such as mixed woodlands, allow for greater body masses (Wauters et al., 2007). Additionally, supplementary feeding, which is available in Belleek, results in greater and more stable body masses (Reher et al., 2016), enhancing their overall fitness (Ferrer et al., 2018; Wauters & Dhondt, 1989; Wauters et al., 2007). Body condition is closely linked to reproductive output (Wauters et al., 2001), with females in poor body condition being more likely to experience offspring losses (Lurz et al., 2005; Wauters & Dhondt, 1989). Poor body condition is also associated with increased susceptibility to disease and is an indicator of overall poor health and reduced food intake (LaRose et al., 2010). The body condition of squirrels in both Belleek and Derryclare has not shown significant changes since their last recorded assessments during the growth phase (Waters, 2012a). The body weights of both populations fall below the average red squirrel body weight recorded in many studies in Britain and Ireland, ranging from 302g to 357g (Cartmel, 1997; Holm, 1990; Lurz, 1995; Magris & Gurnell, 2002; Reilly, 1997; Shuttleworth, 1996; Simpson et al., 2013b). However, the average Belleek body weight corresponds to the weights recorded by Tittensor (1977), Tonkin (1983) and Flaherty (2016) in healthy populations. The average weight of Derryclare squirrels aligns with the average weight of a population of British squirrels infected with the adenovirus disease (Martínez-Jiménez et al., 2011). It is suggested that the suboptimal quality of the woodland has adversely impacted the condition of the Derryclare population to the extent that their weight is comparable to squirrels in a diseased population.

The disparity in food availability between the two sites is further highlighted by the difference in home range sizes displayed by the two populations. Home range size has been shown to increase with decreasing food abundance (Lurz et al., 1997), as squirrels must travel greater distances to gather enough food to meet their energy requirements. Our findings align with this pattern. The ranges of Derryclare squirrels were significantly larger than those of Belleek squirrels, although it's important to note that the estimations calculated using trapping data are approximate. The method used to estimate home ranges using trapping data may overestimate their sizes by not accounting for shifts in home ranges that occur over time in response to food availability (Lurz et al., 1997; Wauters et al., 1995) and local densities (Wauters & Dhondt, 1992; Wauters et al., 1995). On the other hand, this method may underestimate their ranges if individuals have low trapping success, as observed in Derryclare, or if their range extends beyond the trapping grid (Hayne, 1949; Socias-Martínez et al., 2023). This is unlikely to apply to the Belleek population, as the trapping grid covers the entire woodland. Despite these limitations, trapping data has been used to

accurately estimate home range sizes in a study by Socias-Martínez et al. (2023) and in the current study with the Belleek radiotracked squirrels. The relatively small home ranges observed in Belleek align with the home ranges of red squirrels in high quality habitats (Halliwell, 1997; Wauters & Dhondt, 1986; Wauters & Dhondt, 1992). The larger home ranges estimated in Derryclare are more consistent with populations found in patchy and fragmented coniferous woodlands (Andrén & Delin, 1994) and poor quality coniferous woodlands (Lurz, 1995).

The high degree of overlap among home ranges in Belleek (average of 4 overlapping home ranges per individual) is characteristic of a population in a high quality habitat (Lurz et al., 2005) and is comparable to the overlap observed in other food-abundant habitats (Wauters & Dhondt, 1992). However, the home ranges recorded here are relatively small compared to other squirrel populations in mixed habitats (Lorusso, 1999; Pierro et al., 2008; Wauters & Dhondt, 1992), possibly due to the abundant food supply. The average home range in Belleek is comparable to the average home range of 2.72 squirrels/ha observed in an Irish red squirrel population located in a native broadleaf habitat (Emma Roberts, Unpublished data). The two females in this study had the smallest observed home ranges, although no significant conclusions could be drawn from this information due to the small female sample size. However, it is well established that male red squirrels have larger home ranges than females (Andrén & Delin, 1994; Lurz et al., 2000; Wauters & Dhondt, 1992). While home ranges of red squirrels exhibit extensive overlap, they tend to maintain distinct core areas. In Belleek, no overlap was observed among core areas, although it remains possible that these core areas overlapped with other untracked squirrels. Home range overlap with feeding stations was common, and core range overlap with feeding stations was observed in three individuals. Individuals have been shown to alter their home ranges in woods containing supplementary feeding stations (Reher et al., 2016; Starkey, 2019), with heavier individual's home ranges located closer to the feeding station. Squirrels may also shift their home ranges in response to poor breeding conditions, with female range shifts being directly related to food abundance (Wauters et al., 1995). Additionally, home ranges have been observed to change depending on the season (Lurz et al., 1997) and year (Wauters & Dhondt, 1992). It was expected that home ranges determined via trapping data would be significantly larger than those determined through radiotracking, as these data were collected over several seasons or even years. However, no significant difference was found, indicating that home ranges did not shift significantly in size throughout the duration of the project. For example, one female (ID 825) was caught from the first trapping session to the last on 25 occasions. During this time, she used a total of three traps, resulting in a home range estimate that exceeded her radiotracking-determined range by only 0.31

hectares. It is likely that the high food availability in Belleek, boosted by her use of a feeding station, negated the need for her to shift her home range.

In conclusion, the contrasting outcomes at Derryclare and Belleek have highlighted the complexities and challenges of translocation projects, underscoring the role of food availability, rather than woodland size, as a determinant of the success of red squirrel reintroductions. Therefore, it is highly recommended that future red squirrel translocations be carried out in regions characterised by abundant and high-quality food resources, with less of an emphasis placed on the size of the site. Where feasible, the implementation of long-term supplementary feeding is recommended in order to bolster population growth by supporting higher densities, heavier squirrels, and increased reproductive success. However, it is essential to carefully consider the associated risks, especially in the presence of grey squirrels. This study highlights the advantages and utility of non-invasive monitoring techniques in determining squirrel distribution, with a caution on using them for density estimates. This study also suggests that trapping data may be used to aid the determination of home ranges, although further validation of this technique is required. Furthermore, this study highlights the immense value of engaging the public in conservation efforts, both in their participation in the citizen science survey and their dedication to the provision of supplementary food. We therefore believe that strong partnerships with local communities significantly enhance both the monitoring capabilities and the potential outcome of translocation projects, and we encourage future projects to utilise this asset. We hope these recommendations will provide useful insights for future red squirrel translocation projects.

4 Assessing the behaviour of the two translocated populations

4.1 Introduction

Animal personality is defined as consistent differences in an individual's behaviour that remain stable over time and/or across situations (Réale et al. 2007) (See Glossary). Personalities are commonly measured by the expression of specific behavioural traits such as boldness (risk-taking behaviour), exploration (response to novelty), activity, sociability (responses to conspecifics) and aggressiveness (Réale et al., 2007; Sih et al., 2004). These traits are measured by the expression of one or more behaviours. Over the past two decades, the study of animal personality has gained significant attention (Réale et al., 2010; Réale et al., 2007; Wolf & Weissing, 2010), with consistent and repeatable inter-individual behavioural differences observed across a variety of taxa (Conrad et al., 2011; Freeman & Gosling, 2010; Gosling, 2001; McCully & Rose, 2023; Rodríguez-Prieto et al., 2011). Animal personalities have been shown to influence various aspects of population ecology including space use (Aliperti et al., 2021), dispersal (Cooper et al., 2017), translocation success (Mason, 2010) parasite load (Santicchia et al., 2019a), disease transmission (Hawley et al., 2011), invasion rates (Fogarty et al., 2011) and responses to novel environments (Perals et al., 2017) among other ecological processes. Furthermore, animal personality has been shown to have a direct impact on individual fitness and survivorship by influencing predator interactions (Belgrad & Griffen, 2016), foraging success (Toscano et al., 2016), social status (McCully & Rose, 2023) and reproductive output (Both et al., 2005). Given the relevance of these processes to conservation and management strategies, it is crucial to consider the profound impact of animal personality on both individual animals and the population as a whole.

Glossary

Term	Definition
Behaviour	An action exhibited by an animal
Behavioural syndrome	Correlated behaviours at the population level
Behavioural trait	A consistent aspect of an individual's personality, measured by the expression of one or more behaviours
Personality	A combination of traits in an individual that remain consistent over time and across situations

Behavioural traits in animals represent specific aspects of their personality and are measured by the repeatable expression of one or more behaviours e.g. the trait of sociability

may be measured by their willingness to approach a conspecific. Traits are shaped by both intrinsic and extrinsic factors. Intrinsic factors that influence traits include an individual's sex (Koszalka et al., 2023), age (Sudakov et al., 2021), breeding status (Edwards et al., 2016), body condition (Seltmann et al., 2012), size (Sih et al., 2015) and weight (Bachman, 1993). For example, in many species males are observed to display higher levels of aggression compared to their female counterparts, a difference that can be further magnified by their age and reproductive status (Knell, 2009). In socially hierarchical species, an individual's weight, body condition and body size often correlate with their social status (Wauters & Dhondt, 1989). For example, in grey squirrels (*Sciurus carolinensis*) heavier, physically fitter and larger squirrels are often the most dominant and display higher levels of boldness, thus affecting their overall fitness and reproductive output (Santicchia et al., 2019a). Genetics also play a role in behaviour, with animals often inheriting the traits of their parents (Dochtermann et al., 2015). External factors that may affect the expression of traits include seasonal variations (Eccard & Herde, 2013), habitat quality (Wauters & Dhondt, 1992) and population density (Korpela et al., 2011), mostly due to the effect of these factors on resource availability and social dynamics. For example, red squirrels (*Sciurus vulgaris*) living in low-density populations have been found to be more active and aggressive than their high-density counterparts (Haigh et al., 2017). The complex interplay between these intrinsic and extrinsic factors prompts the expression of a combination of behavioural traits in an individual, which collectively define their individual personality.

Behavioural traits that are correlated with each other at the population level across multiple contexts are known as a behavioural syndrome (Sih et al., 2004). Within a population, individuals may exhibit varying levels of specific traits (e.g. aggression, sociability, exploration etc.) which can fluctuate but generally maintain a consistent rank order (Sih et al., 2004). These traits are typically correlated with factors that impact an individual's fitness such as foraging effort, reproductive success, or survivorship. The expression of behavioural syndromes varies depending on the environment and species, reflecting a combination of traits that optimise fitness for that particular species in a specific environment (Penke et al., 2007). For instance, more aggressive individuals may have increased fitness in competitive situations, but may be less suited to situations that do not favour aggression (e.g. parental care). The environmental characteristics that can influence the expression of a behavioural syndrome include the presence of predators and their hunting style (Belgrad & Griffen, 2016; Bell & Sih, 2007), the quality of the habitat (Santicchia et al., 2018), population density (Haigh et al., 2017) and the degree of urbanisation (Uchida et al., 2020). For example, in red squirrels boldness has been shown to enhance survivorship in a poor-quality, fluctuating habitat, while boldness decreases

survival chances in a high-quality stable habitat (Santicchia et al., 2018). Within their respective environments, animals may adopt different behavioural styles, prioritising reproductive output over survivorship or vice versa (Wolf et al., 2007). However, the success of different syndromes is not solely determined by the environment; it can also be influenced by the sex of the individual (Han et al., 2015) and can vary over time as the environment changes and selection pressures shift (Weiss & Adams, 2013). For example, in blue tits it was found that fast-exploring females and slow-exploring males had higher survivorship in poor crop years, while the opposite was true in good crop years (Dingemanse et al., 2004). Such fluctuations in the environment contribute to maintaining behavioural variation in a population, ultimately enhancing productivity and decreasing vulnerability (Wolf & Weissing, 2012).

Urbanisation presents unique challenges and opportunities for animal populations, and commonly results in significant changes in the behaviour of urban animals (Lowry et al., 2013; Miranda et al., 2013). Urban environments expose animals to a multitude of novel stressors and hazards, including light and noise pollution, road traffic, and a constant human presence (Partecke et al., 2006). However, they also offer potential advantages such as readily available anthropogenic food sources and a reduced presence of native predators (Shannon et al., 2014). In order to exploit these opportunities, urban animals must adapt their behaviour. Animals in urban areas have been widely reported to display increased boldness, exploration and aggression, while displaying decreased neophobia compared to their rural counterparts (Lowry et al., 2013). This behavioural combination is commonly referred to as an urban syndrome (Lowry et al., 2013; Miranda et al., 2013). However, this effect has been shown to be species specific (Birnie-Gauvin et al., 2016). It has been suggested that both behavioural plasticity and microevolution are responsible for these behavioural shifts (Miranda, 2017; Miranda et al., 2013). Urban red squirrels have been shown to behave differently compared to rural populations, inhabiting smaller home ranges (Krauze-Gryz et al., 2021), exhibiting lower stress levels during trapping sessions and making a greater number of mobbing calls directed towards humans (Uchida et al., 2020). However, it has been suggested that urbanisation may not necessarily alter red squirrels' core personalities, but rather they display flexible human-related behaviours as a result of increased exposure and habituation to human presence (Uchida et al., 2020).

The open field test (OFT) and mirror image simulation (MIS) test are commonly employed in behavioural ecology to directly assess an individual's behavioural traits. The OFT evaluates an animal's response to novelty, and typically measures activity, exploration and stress levels (Svendsen & Armitage, 1973; Walsh & Cummins, 1976). In contrast, the mirror image simulation (MIS) test measures an individual's reaction to a conspecific, indicating

sociability or avoidance traits (Mazzamuto et al., 2019; Svendsen & Armitage, 1973). These tests have been employed across various taxa including amphibians (Carlson & Langkilde, 2013), fish (Toms et al., 2010), birds (Funghi et al., 2015), and have been well established in the study of personality in sciurids (Haigh et al., 2017; Mazzamuto et al., 2019; Santicchia et al., 2020; Uchida et al., 2020). One critique of these tests is that they measure various behaviours simultaneously, making it challenging to extract and interpret individual traits (Carter et al., 2013). However, since multiple traits are usually expressed in the wild concurrently, the measures obtained from the OFT and MIS test offer ecologically relevant insights, revealing behavioural syndromes rather than isolated traits (Koski, 2014; Sih et al., 2004). Live trapping is commonly used to observe and assess the traits of tree squirrels (Boon et al., 2007; Goldstein, 2014; Haigh et al., 2017). Breath rates recorded during these sessions indicate the stress level of the individual (Haigh et al., 2017). The time spent struggling to escape from the trapping process serves as a measure of their flight response (Hernández et al., 2018). Boldness is commonly measured as the willingness of an animal to re-enter a trap and is established in the literature as being directly linked to their trappability (Le Coeur et al., 2015; Réale et al., 2007; Santicchia et al., 2020). The number of traps used by an individual represents its propensity for exploration (Santicchia et al., 2019a; Santicchia et al., 2020). Additionally, the vocalisations and handling response of squirrels reveal insights into their underlying temperaments (Diggins, 2021; Tinkle, 2016).

The red squirrel translocation sites of Derryclare and Belleek differ in many significant ways. Firstly, in terms of composition and structure, Derryclare is a remote commercial woodland spanning 202 hectares, characterized by an approximately equal mix of Sitka spruce and lodgepole pine stands. Additionally, a 13-hectare broadleaf nature reserve is located in the southern half of the woods. In contrast, Belleek is a recreational park situated in the town of Ballina, consisting of 60 hectares of mixed broadleaf and conifer woodland. Food availability also varies between the two sites. The food availability in Derryclare is patchy, and this is reflected in the uneven distribution of red squirrels, who are primarily found in the southern half of the woods (See chapter 3). The current density of squirrels in the woods is 0.032 squirrels per hectare. Belleek, on the other hand, has widespread food availability, supported by eight feeding stations spread throughout the woods, resulting in the equal distribution of red squirrels at a density of 0.41 squirrels per hectare (See chapter 3). Human activity in Derryclare is almost non-existent, with the exception of occasional visitors to the nature reserve. The commercial stands, however, are not accessible to walkers. Belleek, in contrast, contains a network of forest pathways, a castle, picnic locations and a duck pond. It is a popular destination for walkers, joggers, and cyclists year-round. The presence of predators is low in Belleek, with no recorded instances of pine marten being captured in

live traps, whereas Derryclare has seen 11 accidental pine marten trapping events. Finally, disturbance is relatively common in Derryclare, with routine felling operations occurring every few years and a major fire in 2011 destroying mature woodland (See chapter 2). In Belleek, disturbance to the habitat structure is infrequent, with only occasional, isolated maintenance works taking place.

Our primary research question centres on identifying the behavioural syndromes present in each site, if any, and the effect of various extrinsic and intrinsic factors on the expression of these syndromes. We will record and analyse the following behaviours shown during live trapping sessions (3 consecutive days of trapping): aggression vocalisations, trap use diversity, trappability, breath rate, alarm vocalisations, and struggle rate in each individual. The repeatability of these six behaviours, and the correlations between them at each site will be investigated. We hypothesise that the observed behaviours are repeatable, indicating the behavioural traits of aggressiveness, exploration, boldness, stress response, alarm response and flight response, respectively. Furthermore, we will explore how these traits influence survival and reproductive success, uncovering the ways in which different traits confer advantages depending on the environmental context and sex of the individual. We hypothesise that different syndromes will confer different advantages in the two sites. In particular, we expect Belleek squirrels to exhibit an urban syndrome characterised by higher levels of boldness and aggression, as well as showing increased habituation to humans. Further investigation into the behaviours and traits of the Belleek squirrels will be conducted using an OFT and MIS test. Again, we expect the behaviours shown in these tests to be repeatable, representing behavioural traits. We will investigate correlations between these traits and the traits recorded in the live trapping sessions at the population level, revealing behavioural syndromes. The relationships between the recorded behaviours, the sex of the individual, their morphological characteristics, and ecological context will provide valuable insights into the complexities of animal behaviour within distinct environments.

4.2 Methodology

4.2.1 Study site

A description of the Derryclare study site can be found in chapter 2. Belleek woodland is described in chapter 3.

4.2.2 Live Trapping Behavioural Tests

See chapter 3 for a detailed description of the live trapping schedule and procedure. Throughout the live trapping process, four behaviours were assessed: struggle rate, alarm vocalizations, aggression vocalizations, and breath rate. Struggle rate was recorded once

the squirrel had been transferred from the trap to the hessian sack. The struggle rate was determined by recording the number of seconds, within a thirty-second test period, during which the squirrel actively attempted to free itself from the sack. This struggle behaviour consisted of actions like running around the sack and forcefully pushing against it. Aggression calls, characterised by growling sounds, were counted from the moment the squirrel was transferred to the handling cone, until it was released. Similarly, alarm calls, characterised by loud, high pitched vocalisations, were also counted during this same period. Breath rate was measured once all other data had been gathered. Breath rate was calculated as the number of breaths taken by the individual within a 10 second interval, with the assistance of a stopwatch.

The number of times a squirrel had been caught was recorded during each trapping event, in order to assess any effects of repeated exposure to the trapping process on their observed behaviours. If a squirrel was caught more than once, the mean value of their observed behaviours were utilised in the analysis. Additionally, survivorship was calculated for squirrels who were caught more than once, utilising their first and final trapping events. The breeding status of each individual was recorded during processing. When analysing the effect of breeding status on their behaviours, the mean values of each individual per breeding category was used. Similarly, mean values of each individual per season were used to detect the influence of season on their behaviour (Winter = Nov - Jan, Spring = Feb - April, Summer = May - July, Autumn = August – Oct). This ensured that every individual was only included once for each breeding status and season they experienced. Variables including age, sex, shinbone length and weight were also recorded. Shinbone length was used as a measure of the size of the individual, with larger animals having longer shinbones (Finnegan et al., 2009). The mean values per individual were utilised when the variable was continuous. Body index was calculated as a measure of fitness, by dividing the body weight by the shinbone length (Wirsing et al., 2002) (See chapter 3 for more details on the processing procedure).

Two additional behaviours were recorded during the live trapping sessions, resulting in a total of six live trapping behaviours. The site at which an individual was captured and the number of captures it experienced in a session were recorded to determine trap diversity indices and trappability, respectively. Values were only calculated for individuals who were caught more than once, and mean individual values were utilised for the analyses. Trappability (TB), which is an indication of boldness (Le Coeur et al., 2015; Réale et al., 2007; Santicchia et al., 2020), was calculated as the ratio of the number of times an individual was trapped during a session to the number of days in a session. Trap diversity (TD), which indicates exploration (Boyer et al., 2010; Réale et al., 2007; Santicchia et al.,

2020) was measured as the number of traps in which an individual was caught per session, divided by the total number of available traps at that site (in both sites, $n = 20$). These indices were calculated for every session an individual was present in the woods. When calculating the amount of time an individual remained in the woods, we utilised the time span from their first capture to their last capture.

The behaviours recorded during the live trapping sessions and the traits that they measure are outlined in table 4.1.

Trait	Behaviour	Citation
Aggression	The number of aggression vocalisations (growls) made during processing	Kondo and Watanabe (2009)
Alarm response	The number of alarm calls (loud, high pitched vocalisations) made during processing	Diggins (2021)
Boldness	An individual's trappability (number of times trapped) per session	Le Coeur et al. (2015), Réale et al. (2007), Santicchia et al. (2020)
Exploration	An individual's trap diversity index (traps visited/traps available) per session	Boyer et al. (2010), Réale et al. (2007)
Flight response	The amount of time spent struggling (actively trying to free itself) from the hessian sack within a 30 second timeframe	Hernández et al. (2018)
Stress response	The number of breaths taken by an individual within a 10 second time frame	Haigh et al. (2017)

Table 4.1 An ethogram outlining the various behaviours recorded during the live trapping sessions and the traits that they represent.

4.2.3 OFT and MIS tests

Open field tests (OFT) were conducted to assess squirrels' reactions to a novel environment, while mirror image simulation (MIS) tests were used to evaluate their sociability and avoidance behaviours. Both tests were only carried out in Belleek, due to the low capture success in Derryclare. These tests were carried out over five trapping sessions between March 2022 and November 2022. To minimise stress and habituation to the test, OFT and MIS tests were conducted only once per trapping session. These tests were performed immediately following the live trapping processing stage and involved all squirrels who were captured on the day of testing.

Upon being processed, squirrels were placed in a large white plastic box with dimensions of 62L x 57W x 76H cm (Figure 4.1). The box featured a small circular hole at the bottom

of one of the sides, into which a handling cone was slotted. This hole could be opened and closed with a small hinged wooden door located inside the box that could be controlled from outside the box via a pulley string. The lid of the box consisted of a removable plastic panel that was lightweight yet sturdy. Two wooden planks were fit to the underside of the ends of the lid to prevent it from slipping when in place. The lid had two holes cut out of it: one for the camera mounted on the lid for observational purposes, and another to allow the panel blocking the mirror from view to lift, thus revealing the mirror. The camera was equipped with a wide-angle lens to ensure a view of the entire interior of the box. The mirror measuring 56 x 25cm, was located on one of the narrower sides of the box. A panel made of robust white plastic was attached to a metal rod, which could be lifted to unblock the view of the mirror. Both the mirror and the panel were held in place by grooved wooden planks which were fixed to the sides of the box. These grooves acted as guides for panel to be lifted and lowered into place. Once lifted, the panel could be secured in the open test position using a stop pin inserted into the metal rod above the lid, preventing it from falling and covering the mirror. The floor of the box was divided into four quadrats with two pieces of tape, to allow for squirrel movement to be more accurately assessed by counting the number of lines they crossed during the test.

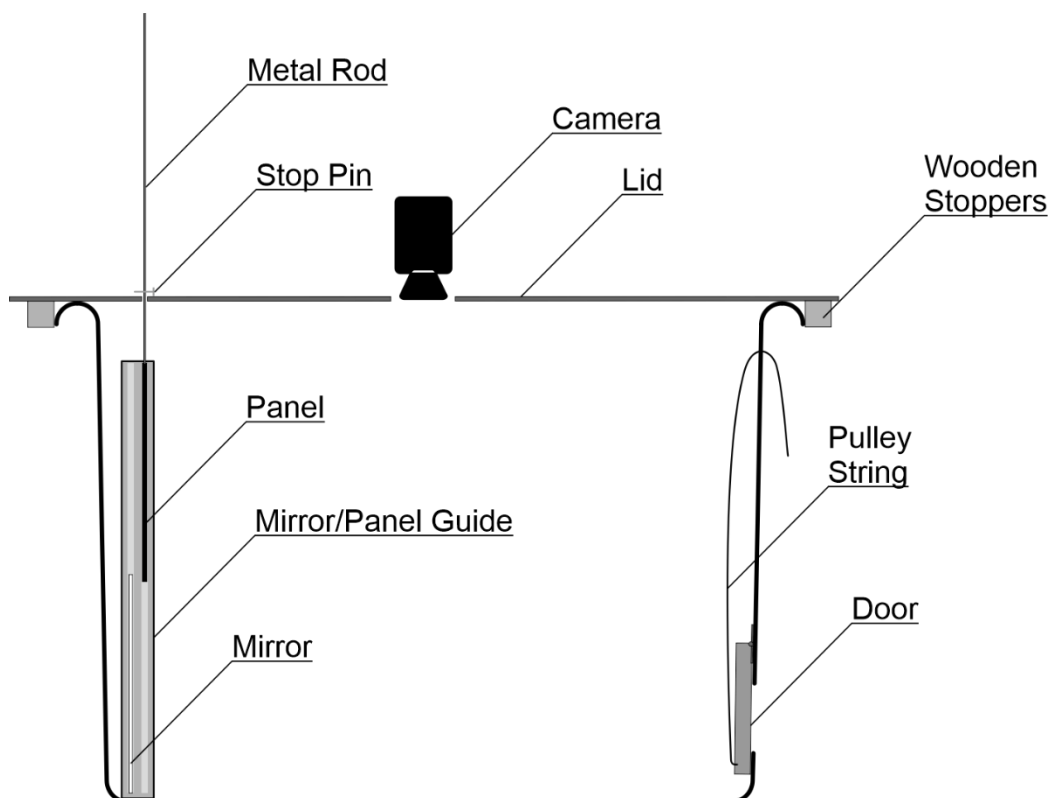


Figure 4.1 A cross section view of the OFT and MIS box, showing the mirror in its open test position, having been revealed by the sliding panel.

The squirrel was considered to have begun the OFT once it fully backed out of the handling cone and the small wooden door was closed, preventing escape. The squirrel was filmed for the entire test duration of 3 minutes. After this point the mirror was revealed, and the MIS test began. This test was filmed for 3 minutes. These test durations were chosen based on previous research indicating that extending the recording time beyond 3 minutes did not significantly affect the outcomes of a MIS test (Mazzamuto et al., 2019). To ensure cleanliness and minimize potential scent cues, the box was wiped down with 70% ethanol between tests.

Recordings were analysed using BORIS software (Friard & Gamba, 2016), which allowed us to record the duration an individual spent exhibiting each behaviour. During the OFT, all behaviours were recorded. During the MIS test however, only behaviours related to the squirrel's sociability/avoidance response were recorded, as this is the primary focus of the test (Mazzamuto et al., 2019; Svendsen & Armitage, 1973). Sociable and avoidant behaviours were identified based on an expert-based method, which relies on the researcher's previous knowledge of the species behaviour, and has been validated for use with red squirrels (Mazzamuto et al., 2019). Behavioural classifications were modified from Santicchia et al. (2020) and are outlined below (Table 4.2).

Test	Behaviour	Description of behaviour	Trait
OFT	Locomotion	Walk, run, head moving	
	Sniff	Sniffing the edges of the box	
	Climb	Standing on hind legs against a wall, front leg/s on wall	
	Immobile	No movement	
	Escape	All paws off the ground in a jump/escape attempt	
	Groom	Self-grooming	
	N Lines	The number of lines a squirrel crossed during the test	
MIS	Locomotion	Walk, run, head moving	Other
	Groom	Grooming	
	Sniff	Sniffing the edges of the box	
	Immobility in back half	No movement, squirrel is in back half, furthest from mirror	Avoidance
	Climb	Standing on hind legs against a wall, front leg/s on wall	
	Escape	All paws off the ground in a jump/escape attempt	
	Front immobile	No movement, squirrel is in front half, closest to mirror	Sociability
Approach	Squirrel is approaching the mirror slowly		

Table 4.2 The behaviours recorded in the OFT and MIS tests, adapted from Santicchia et al. (2020). A description of each behaviour is given, along with the trait it represents. As we were only testing for the sociability/avoidance behaviour during the MIS test, all other behaviours are not considered.

Locomotion and the number of lines crossed by the squirrel were considered to measure different aspects of an animal's behaviour. The count of lines crossed indicates how extensively the squirrel moved around the given space, whereas locomotion offered a general indication of movement, and allowed us to quantify both activity and immobility. For instance, a squirrel who actively scanned their environment from one corner of the box was showing different behaviour to one who was running around the four corners of the box. External factors have been found to influence these behaviours differently, with the number of lines crossed, but not locomotion, being affected by seasonal variations, in a study by Uchida (2019).

4.2.4 Data analysis – trapping behaviours

The relationships between the six trapping behaviours: struggle rate, breath rate, aggression vocalisations, alarm calls, trappability and the diversity of traps visited, and non-behavioural variables were investigated. Non-behavioural variables consisted of intrinsic factors including body index, weight, shinbone length, sex and breeding status as well as extrinsic factors including the season and site (Belleek or Derryclare) in which they were caught. Using data gathered from all instances when they were captured, we determined the mean values for struggle, breath, aggression, and alarm for each individual. Mean values for trappability and trap diversity indices were derived from values calculated per individual per session. The mean values of all six behaviours were used to compare the behaviour between the two study sites, as well as between the sexes.

The effect of sex and site on the occurrence of aggression and alarm behaviour was investigated with a Fisher's test. When comparing struggle rate, breath rate and trappability by sex and by site, a t-test was used to investigate significant differences, and mean values are reported, with 95% confidence intervals. The distribution of aggression and alarm vocalisations as well as trap diversity indices was found not to be normal and therefore a Mann-Whitney U test was used for comparison purposes and the median values are reported. Subsequently, the sample was split for both vocalisation behaviours into those who vocalised and those who didn't. The mean number of vocalisations made by those who did vocalise were compared between the sexes and sites, to assess the level of their aggression and alarm behaviour. A t-test was used for this purpose and mean values are reported. When investigating the effect of season and breeding status on the six trapping behaviours, a one-way ANOVA or Kruskal Wallis test was used, depending on the distribution of the data. Bivariate correlations were used to investigate the relationship between the behaviours and continuous intrinsic variables. Additionally, correlations between the different behaviours themselves were assessed, to identify behavioural syndromes.

Survivorship was calculated for individuals in both sites using their presence data. All individuals from the first trapping year (Derryclare; July to November 2020, Belleek; August to December 2020) were considered present in all months from their first to their last visit. The longest time a squirrel was considered present in the woods but was untrapped was 6 months. Therefore, any individuals whose final trapping session was within 6 months of the end of the study were not included in the survivorship calculations. Their endpoint (death or dispersal) cannot be identified because the study ended. In Derryclare the same method was used, although a 9 month period was the longest time in which a squirrel was not trapped and therefore, those caught within 9 months of the end of the project were not included. Reproductive output was determined by the number of litters each female produced, indicated by a pregnant or lactating breeding status during the trapping sessions.

The relationship between the number of times a squirrel had been captured and its behaviour was investigated. A linear regression analysis was used to determine if there was a correlation between the total number of times a squirrel was trapped and its mean behavioural values. Subsequently, a Generalised Linear Mixed Model (GLMM) was used to investigate whether the trapping process itself affected an individual's behaviour. Sex, site, season and trapping event (as experienced by the squirrel) were used as fixed variables, with the identity of the squirrel included as a random variable.

The first capture events for all individuals were analysed to determine if there was a difference in morphology or behaviours between those who were subsequently recaptured, and those who never returned. Continuous data for the two groups, both behavioural and non-behavioural, were compared using a t-test and Mann-Whitney U test, depending on the distribution of the data. Additionally, a Fisher's test was used to determine the relationship between discrete values and their recapture status.

The repeatability of struggle rates, breath rates, aggression vocalisations, alarm calls was assessed using data from every squirrel capture. The repeatability of trappability and trap diversity indices were assessed using only squirrels who returned to the traps, using their mean values per session. These data were analysed using Linear Mixed Models (LMM) and Generalised Linear Mixed Models (GLMM), depending on the distribution of the data. Struggle rate was square root transformed to normalise its distribution. This variable along with breath rate, trappability and trap diversity indices were assessed with an LMM. To address negative values, a transformation was applied to aggression and alarm behaviours by adding 1 to all values. Subsequently, the transformed data were analysed using a GLMM with a gamma distribution. Fixed variables for all analyses included sex, season, breeding status and trapping session. The individual's identity was used as the random variable

which allowed us to explore the individual variation not accounted for by the fixed effects. The repeatability, represented by the Intraclass Correlation Coefficient (ICC), was calculated as the ratio of the random variance to the overall variance. The goodness of fit of the model, as indicated by the -2 Log Likelihood (-2LL) value, was compared to the goodness of fit of the null model, i.e. without ID included as a random variable. The model is deemed to fit better than the null model if its -2LL value is smaller. The likelihood ratio test (LRT) shows the differences between these values, and is used to test the significance of the repeatability. The significance of the LRT was determined by comparing the statistic to the critical value at one degree of freedom and a significance level of 0.05. The results from these tests indicated whether a behaviour was repeatable, the strength of the repeatability and whether it was statistically significant.

4.2.5 Data analysis – OFT/MIS behaviours

Mean values for the behaviours recorded during the OFT and MIS were calculated for each individual, ensuring that every individual was only included once in the subsequent analyses. To reduce the number of behavioural variables recorded in the OFT and to identify underlying patterns, we conducted a Principal Component Analysis (PCA). A Varimax rotation was applied to enhance interpretability of the extracted components (Kaiser, 1958). Components with an eigenvalue greater than 1 were retained (Norman & Streiner, 2008). A variable was deemed to exhibit significant loading on a component if its loading coefficient exceeded 0.4 or was below -0.4 (Ferrari et al., 2013). Component scores were generated for each individual representing how well their behaviour fits with that component. For the MIS test, the cumulative percentage of time spent displaying sociable and avoidant behaviours, as determined through the expert based method (Table 4.2) were used as the individual's sociability and avoidance scores. These scores as well as the component scores were subsequently compared to each other as well as the other behavioural and the morphological data of the squirrel. A bivariate correlation was used to identify patterns between the scores and continuous data, while a t-test and Mann-Whitney U test were used to identify significant relationships between the scores and discrete data. The mean morphological and behavioural values for each individual were utilised in these analyses.

All statistical analyses were performed using IBM SPSS Statistics, version 27.

4.3 Results

4.3.1 Trapping

In total, 82 individuals were caught across both sites (Belleek; 72, Derryclare; 10), in 375 trapping events. The mean capture frequency for Belleek squirrels was 4.8 times (95% C.I. = [3.32, 6.28]), with the number of recaptures per individual varying from 0 – 27. In Derryclare, the mean number of trapping events per individual was 3 (95% C.I. = [1.3, 4.7]), with recaptures varying from 0 – 10. In Belleek, an equal number of males and females were caught (males; 36, females; 36). In Derryclare, 7 males and 3 females were captured. Return rates varied between the two sites, although not significantly, with 50% of Belleek squirrels ($n = 36$, male = 17, female = 19), and 70% of Derryclare squirrels ($n = 7$, male = 4, female = 3) caught more than once.

Behaviours were compared between sites, as well as between sexes (Table 4.3). Site did not influence the likelihood of an individual either exhibiting or not exhibiting an aggression or alarm vocalisation. Overall, females were not more likely to make aggressive vocalisations, but did make significantly more aggression vocalisations compared to males ($U = 1083$, $n = 83$, $p = 0.021$). This pattern was also seen in Belleek, with females displaying a higher number of aggression vocalisations ($U = 871.5$, $n = 72$, $p = 0.01$), but was not observed in Derryclare. Sex had no influence on alarm behaviour in Belleek or Derryclare. Site had no effect on struggle or breath rates. However, males had significantly higher breath rates than females overall ($t(80) = 2.719$, $n = 72$, $p = 0.008$). This relationship was also observed in Belleek ($t(70) = 2.408$, $n = 72$, $p = 0.019$), although no significant difference was observed in Derryclare. Males were found to be significantly more trappable than females when both sites were combined ($t(4) = 2.492$, $n = 43$, $p = 0.017$), and no difference in trappability existed between the two sites. Site and sex had no effect on the variety of traps an individual visited.

	Belleek				Derryclare				Combined			
	n	All	Male	Female	n	All	Male	Female	n	All	Male	Female
Individuals who exhibited aggression	72	49	22	27	10	6	4	2	82	55	26	29
Median aggression vocalisations	72	2.75	1	5	10	0.55	0.4	0.7	82	2	1	4
Mean aggression vocalisations	49	5.31 ± 0.96	3.82 ± 1.12	6.53 ± 1.33	6	3.6 ± 2.57	4.85 ± 4.63	1.1 ± 0.2	55	5.13 ± 0.87	3.98 ± 1.34	6.16 ± 1.15
Individuals who made alarm calls	72	17	7	10	10	0	-	-	82	17	7	10
Median alarm vocalisations	72	0	0	0	10	-	-	-	82	0	0	0
Mean alarm vocalisations	17	1.4 ± 0.66	1.65 ± 1.19	1.28 ± 0.79	0	-	-	-	17	1.4 ± 0.66	1.65 ± 1.19	1.28 ± 0.79
Mean struggle rate (per 30 sec)	72	6.83 ± 0.64	7.24 ± 1	6.42 ± 0.81	10	8.5 ± 1.48	9.41 ± 1.4	6.37 ± 2.63	82	7.04 ± 0.6	7.6 ± 0.89	6.42 ± 0.77
Mean breath rate (per 10 sec)	72	28.88 ± 1.14	30.22 ± 1.73	27.52 ± 1.36	10	29.56 ± 2.76	30.63 ± 2.52	27.07 ± 7.3	82	28.95 ± 1.05	30.29 ± 1.5	27.48 ± 1.34
Mean trappability	36	0.59 ± 0.08	0.66 ± 0.12	0.52 ± 0.09	7	0.64 ± 0.29	0.72 ± 0.41	0.54 ± 0.45	43	0.60 ± 0.08	0.69 ± 0.12	0.50 ± 0.09
Median trap diversity	36	0.15	0.15	0.15	7	0.1	0.125	0.1	43	0.17	0.18	0.16

Table 4.3 A comparison of the behavioural traits of squirrels in Belleek and Derryclare recorded during live trapping sessions, with 95% confidence intervals shown. The mean number of aggression and alarm vocalisations made during processing were calculated only for those who demonstrated those behaviours. Trappability (captures per session) and trap diversity indices (traps visited/traps available) were only calculated for those who were trapped more than once. Significant findings are indicated in bold.

Struggle rate was significantly affected by season ($F(3, 199) = 7.225, p < 0.001$), with a post hoc pairwise comparison revealing that squirrels in spring struggled for longer than those in winter ($p = 0.002, 95\% \text{ C.I.} = [0.88, 5]$) and squirrels in autumn struggle for longer than those in summer ($p = 0.48, 95\% \text{ C.I.} = [0.01, 4.1]$) and winter ($p = 0.001, 95\% \text{ C.I.} = [0.92, 4.69]$). No other behaviour was affected by season. The breeding status of squirrels did not have a significant effect on any of their behaviours.

Several correlations between behavioural and physical variables were identified in both sites and both sexes. In Belleek, squirrels with higher body indices made more aggression

vocalisations ($R = 0.305$, $n = 72$, $p = 0.009$) and had lower breath rates ($R = -0.247$, $n = 72$, $p = 0.037$). Individuals who made more aggression vocalisations also struggled less ($R = -0.398$, $n = 72$, $p = 0.001$). Larger females were found to be more trappable ($R = 0.472$, $n = 19$, $p = 0.041$). For males, the opposite was found, with larger males being less trappable ($R = -0.532$, $n = 17$, $p = 0.028$). Aggression vocalisations and struggle rates were significantly negatively correlated in both Belleek females ($R = -0.341$, $n = 36$, $p = 0.042$) and Belleek males ($R = -0.451$, $n = 36$, $p = 0.006$). Males in Belleek who made more aggression vocalisations were also found to have higher body indices ($R = 0.389$, $n = 36$, $p = 0.019$).

In Derryclare, larger squirrels had higher breath rates ($R = 0.888$, $n = 10$, $p = 0.001$). No syndromes were observed in females, although the sample size was very small ($n = 3$). Larger males in Derryclare were found to have higher breath rates ($R = 0.882$, $n = 7$, $p = 0.009$), while more trappable males had lower breath rates ($R = 1.000$, $n = 4$, $p < 0.001$).

Relationships between survivorship and an individual's traits were investigated. In Belleek, 29 individuals were included in the analysis including all those caught in the first year of the study and those whose final trapping appearance occurred 6 months before the end of the study. In Derryclare, 5 of the 10 individuals were included in the analysis, including those whose final trapping appearance occurred 9 months before the end of the study.

In Belleek, there were significant correlations found between the survivorship of an individual and their weight, struggle rate, breath rate and trappability. Females who remained in the woodland longer struggled less ($R = -0.560$, $n = 14$, $p = 0.037$) and had higher breath rates ($R = 0.655$, $n = 14$, $p = 0.011$). Males who remained in the woodland longer were lighter ($R = -0.571$, $n = 15$, $p = 0.026$) and more aggressive ($R = 0.666$, $n = 15$, $p = 0.007$). Overall, squirrels in Belleek who remained in the woodland the longest struggled less ($R = -0.408$, $n = 29$, $p = 0.028$). There was no difference in the survivorship of males and females. In Derryclare, no correlations were found between the survivorship of squirrels and their behaviours. Trappability of the Derryclare squirrels was lowest in those who remained in the woods the longest, although not significantly so ($R = -0.539$, $n = 5$, $p = 0.349$) (Figure 4.2). Sex had no effect on survivorship.

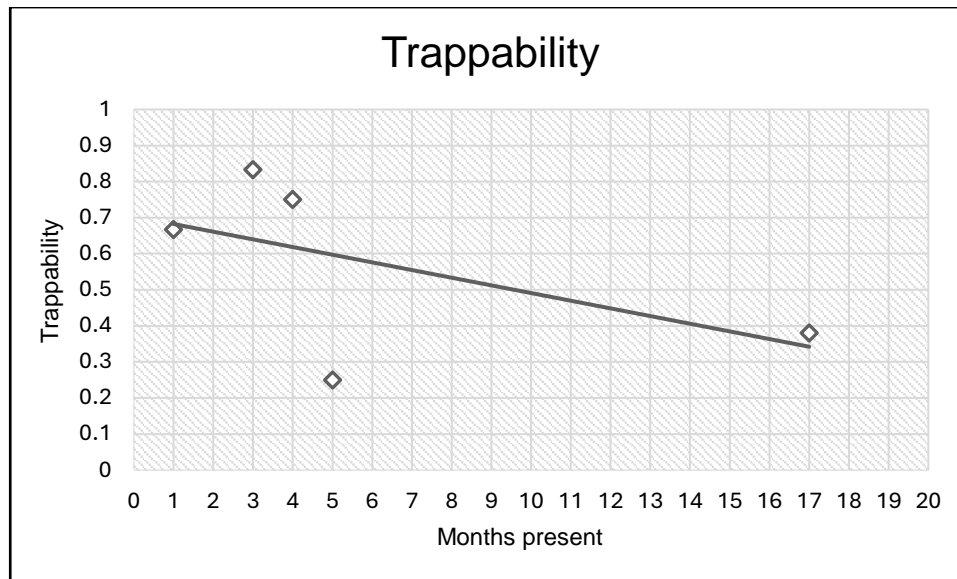


Figure 4.2 The trappability of Derryclare squirrels ($n = 5$) plotted against the number of months they were present in the woods. Only squirrels who had been caught in the first year or who's final trapping event was at least nine months from the end of the study were included in the analysis.

In Belleek, increased reproductive output was significantly positively correlated with body index ($R = 0.466$, $n = 36$, $p = 0.004$) and negatively correlated with struggle rate ($R = -0.398$, $n = 36$, $p = 0.016$). Squirrels who produced at least one litter made significantly more alarm calls compared to those who did not breed ($U = 243.5$, $n = 36$, $p = 0.005$). In Derryclare, no significant correlations were found, and no differences existed between females who bred and those who didn't.

While there was no significant difference between the total number of times an individual was captured in Belleek or Derryclare, squirrels who returned to the traps in Belleek were subsequently caught a greater number of times (median = 3, range = 2 – 10) than those who returned to the traps in Derryclare (median = 5, range = 2 – 28) ($U = 186.5$, $n = 43$, $p = 0.045$). Sex had no effect on trappability or the total number of times an individual was captured in either site.

A GLMM accounting for individual variability found that the increased exposure to the trapping process influenced struggle rate in Belleek ($p < 0.001$), but not in Derryclare. Aggression vocalising in Belleek, but not Derryclare, was also influenced by the number of trapping events a squirrel experienced ($p = 0.016$). Both males and females in Belleek struggled less ($R = -0.465$, $p < 0.001$) with repeated trapping events, while only males increased the number of aggression vocalisations in response to multiple trapping events ($R = 0.828$, $n = 36$, $p < 0.001$) (Figure 4.3). There was no significant relationship between

alarm vocalisations, breath rate, trappability or trap diversity indices. Increased exposure to the trapping process did not affect behaviour in Derryclare.

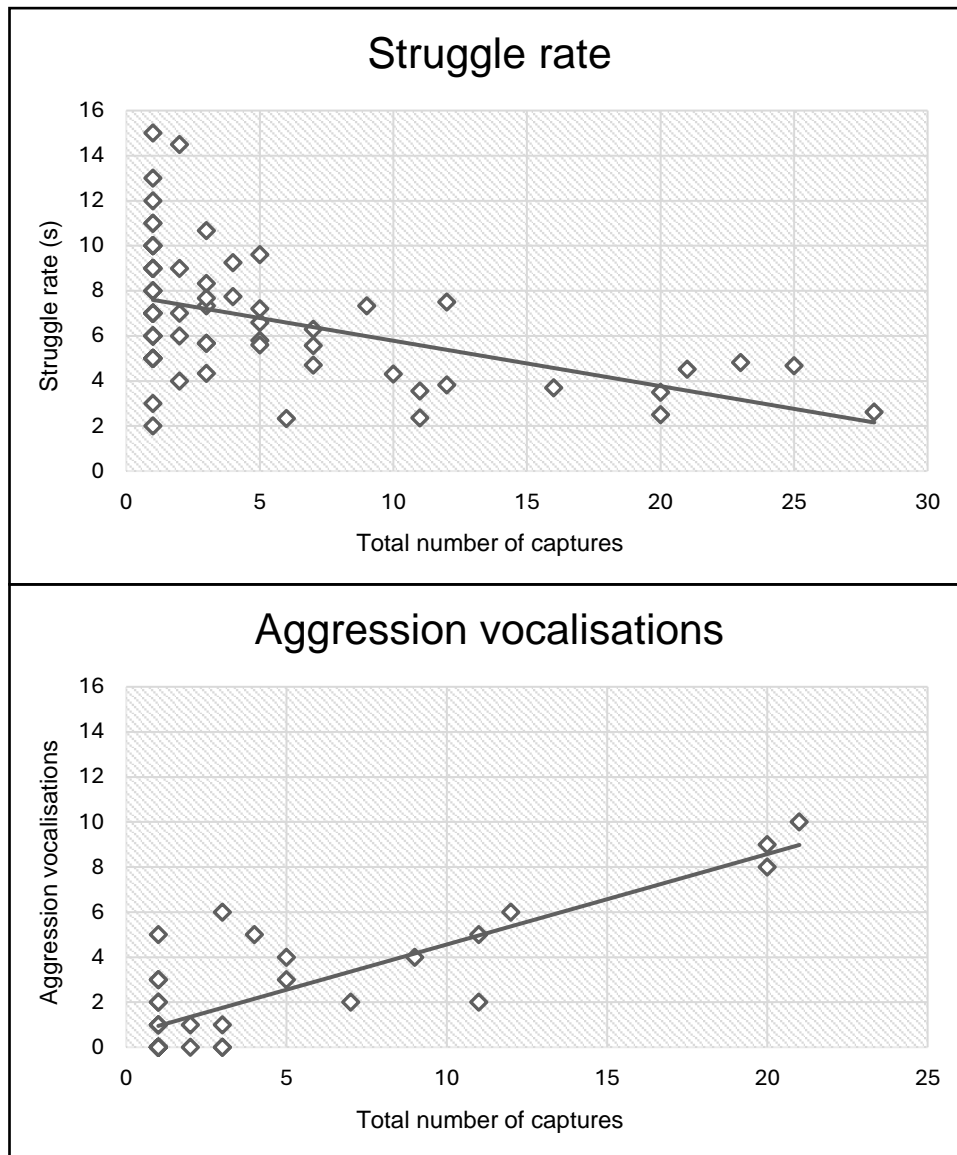


Figure 4.3 The mean struggle rate for each individual in Belleek ($n = 72$), and the mean aggression vocalisations of males in Belleek ($n = 36$) plotted against the total number of times the individual was captured. The more frequently an individual was trapped, the less they struggled. As the frequency of trapping events increased, males produced a greater number of aggressive vocalisations.

The first visits of each individual were analysed separately to determine if those who subsequently returned to a trap ($n = 43$) and those who were never trapped again ($n = 39$) displayed differences in their morphological characteristics or behaviour. It was found that the weight of squirrels who never returned to a trap ($\bar{x} = 265.6$, 95% C.I. = [257.8, 273.4]) was significantly lower than those who were captured more than once ($\bar{x} = 275.7$, 95% C.I.

= [268.2, 283.2]) ($t(80) = 2.182$, $n = 82$, $p = 0.032$). Similarly, the body index of those who did not return ($\bar{x} = 4$, 95% C.I. = [3.91, 4.09]) was lower than those who did ($\bar{x} = 4.22$, 95% C.I. = [4.11, 4.33]) ($t(80) = 2.623$, $n = 82$, $p = 0.010$). Belleek squirrels who returned to the traps were significantly more likely to make an alarm call on their first visit ($p = 0.042$), although no difference existed between the Derryclare squirrels, or when both sites were combined. Struggle rates in Derryclare ($\bar{x} = 10.6$, 95% C.I. = [8.1, 13.1]) were significantly higher than struggle rates in Belleek ($\bar{x} = 8.1$, 95% C.I. = [7.3, 8.9]) during their first trapping experience ($t(80) = 2.133$, $n = 82$, $p = 0.036$). No other behavioural differences existed between the first visits of squirrels in the two sites. The season in which the individual was caught, the sex of the individual, the site in which they were caught, the trap, their breeding status and shinbone length all had no significant effect on whether they were recaptured.

The relationship between the number of recaptures an individual experienced and their behaviour during their first trapping event was investigated to see if their future susceptibility to trapping was indicated by their initial behaviour, before habituation to the trapping process occurred. No correlations were found.

The repeatability of struggle rate, breath rate, aggression vocalisations, alarm calls, trappability and trap diversity indices were investigated using LMMs and GLMMs. We found significant moderate repeatabilities for breath rate and aggression calls, as well as significant weak repeatabilities of struggle rate and trappability (Table 4.4). Both alarm calls and trap diversity were not found to be repeatable. The fit of the alarm calls null model, as indicated by the “-2LL value without ID” in Table 4.4, was greater than the fit of the model with ID included as a random variable, meaning that the behaviour of alarm calling was not repeatable. The variance within the trap diversity data was too small for any random effects to be picked up.

Behaviour	n	Repeatability	-2LL value	-2LL value without ID	LRT	df	p
Struggle rate	375	0.16	846.31	873.6	27.29	1	0.012
Breath rate	375	0.35	2176.36	2207.03	30.67	1	0.01
Aggression vocalisations	375	0.34	939.02	2058.15	1119.13	1	<0.001
Alarm calls	375	0.08	927.78	745.26	-	-	-
Trappability	214	0.22	91.933	114.541	22.608	1	0.014

Table 4.4 The repeatability of five of the trapping behaviours. Struggle rate, breath rate, aggression vocalisations were all found to be significantly repeatable. Alarm calls and trap diversity were not found to be repeatable.

4.3.2 OFT & MIS Tests

A total of 28 OFT and MIS tests were performed on 17 individuals (male; 7, female; 10) over 5 trapping sessions. Five individuals were tested more than once (median = 4, range = 2 – 4), and 12 individuals were only tested once. Of the 17 individuals who were tested, 12 of these were caught in a trap more than once, meaning that they have been assigned trappability and trap diversity indices. Grooming was omitted from the analyses due to the low occurrence of this behaviour (0.003% of total recorded time).

A principal component analysis (PCA) identified 2 OFT components. The two OFT components explain 34.92% and 27.48% of the variance respectively (62.41% of the overall variance). OFT1 is characterised by its positive associations with locomotion and number of lines crossed. This component is categorised as activity/inactivity. OFT2 is characterized by an inverse relationship with sniffing, and positive associations with climb and escape. This component is categorised as proactivity/reactivity (Table 4.5).

Behaviour	OFT1	OFT2
Locomotion	0.835	-0.082
Sniffing	-0.093	-0.660
Climb	-0.172	0.695
Escape	0.180	0.752
N Lines	0.908	0.192

Table 4.5 The results of the Open Field Test PCA. Two components were identified and have been identified as activity/inactivity (OFT1) and proactivity/reactivity (OFT2). Variables contributing significantly to each component are highlighted in bold.

Two traits were identified from the MIS test using an expert based approach: sociability and avoidance. A visual inspection of the data revealed two clusters of data indicating that squirrels display a bimodal behavioural pattern, with individuals tending to only show sociability or avoidance, not both (Figure 4.4).

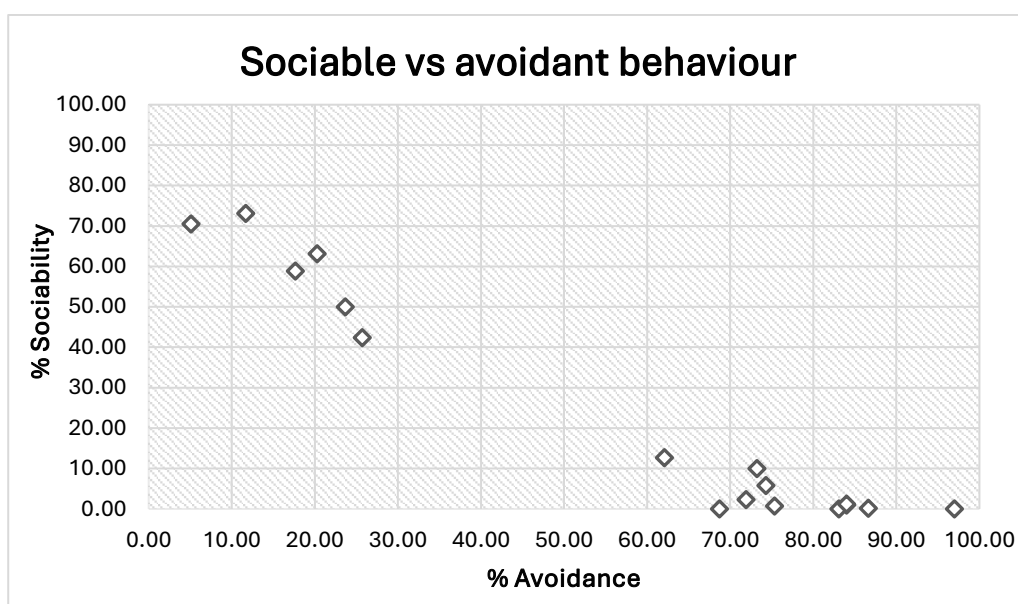


Figure 4.4 A scatter plot showing the percentage time each individual ($n = 17$) spent displaying sociable and avoidant behaviours. A clear distinction can be seen between the two groups, indicating that squirrels may be sociable or avoidant, but not both.

Active squirrels, as indicated by a high OFT1 score, were found to be less trappable, an indication of shyness ($R = -0.647$, $n = 12$, $p = 0.016$). Proactivity, or a high OFT2 score, was found to have a negative correlation with avoidance ($R = -0.535$, $n = 17$, $p = 0.027$), and conversely, a positive correlation with sociability ($R = 0.517$, $n = 17$, $p = 0.033$). No correlations were found between these components and other behavioural or physical traits of individuals. The number of times an individual experienced the test, and the individual's sex had no effect on the expression of any of the four observed behaviours.

According to an LMM which accounted for individual variation, sociability increased with habituation to the test ($p = 0.009$), but there was no significant effect on avoidance. No other behaviours were affected by repeated exposure to the test.

4.4 Discussion

We found the existence of repeatable personality traits in red squirrels that were correlated with each other, giving rise to behavioural syndromes. Contrary to expectations, Belleek and Derryclare squirrels did not differ significantly in their traits, despite their differing environments and pressures. We initially anticipated that Belleek squirrels, located in the town of Ballina, Co. Mayo would display an 'urban syndrome', characterised by increased aggression and boldness (Lowry et al., 2013; Miranda, 2017). However, no significant differences were found between the expression of these traits in Belleek and Derryclare. This finding aligns with a similar observation in urban and rural red squirrels in Japan, where the two populations differed only in their stress responses and human-related behaviours (Uchida et al., 2020). They hypothesise that the innate personalities of red squirrels remain unaffected by urbanisation. Instead, increased human presence leads to an increase in human-related behaviours such as mobbing calls directed at humans, and a reduced flight distance. Only one significant behavioural difference was noted between our two study populations; Derryclare squirrels exhibited a greater flight response on their first visit, compared to Belleek squirrels on their first visit. Belleek squirrels, having become accustomed to human presence, have a low risk perception of humans (Uchida et al., 2019), and may be able to assess the level of risk more accurately and respond accordingly. It is also possible that the lack of behavioural differences between the two sites is not caused by similar personalities, but rather a lack of data from Derryclare.

Poor trapping success in Derryclare resulted in data collection from only 10 individuals, who were trapped a total of 30 times. Interestingly, Derryclare squirrels were not less likely to return to a trap after their first capture, and the trappability per session of those who did return was comparable to those in Belleek. However, the recapture frequency of those in Derryclare was lower than those in Belleek, meaning that individuals in Belleek were

recaptured a greater number of times compared to Derryclare squirrels. The discrepancy in total trap events per individual likely stems from Derryclare squirrels having a shorter life span, as individuals who did not return to the traps are presumed to have died. It appears that the low number of individuals detected through trapping may be due to the undetectability of squirrels who never interacted with a trap, or simply due to the small population number. Since other non-invasive techniques in Derryclare have estimated a similarly low population number (see chapter 3), it is probable that most, if not all, of the squirrels in the trapping grid were captured at some point. Therefore, further behavioural insights would require longer study periods, rather than a change in trapping methodology.

Despite the limited data available, one behavioural syndrome was observed in Derryclare. Larger males exhibited higher stress levels and shyer behaviour, as evidenced by their trappability. This finding was unexpected as typically, dominance, which may be indicated in squirrels by larger body sizes, heavier weights or greater fitness (higher body indices) (Wauters & Dhondt, 1989) is associated with boldness (Moiron et al., 2020; Santicchia et al., 2019b) and lower stress responses (Haigh et al., 2017). However, the correlation between shyness and higher stress levels has also been observed in red squirrels (Uchida et al., 2020), and in other species such as great tits (*Parus major*) (Carere & Van Oers, 2004) and ground squirrels (*Urocitellus richardsonii*) (Clary et al., 2014). While there was no significant effect of behaviour on their survival, it is suggested by the correlation between survival and trappability that shy, subordinate squirrels live longer in Derryclare (Figure 4.2). Shyness is considered an advantageous trait in environments with high predation risk (Carrete et al., 2016; Møller, 2008; Smith & Blumstein, 2008), as bold animals are more likely to take risks and encounter predators (Bamber et al., 2020). However, further data on the behaviour of Derryclare squirrels is necessary to validate this finding.

In Belleek, dominant males were found to exhibit greater levels of aggression, lower stress, a decreased flight response, and reduced boldness. Additionally, the OFT and MIS test revealed that this cohort were also more active. In contrast, subordinate males were less aggressive, had a greater flight response, demonstrated more inactivity, stress, and greater boldness. This suite of correlated behaviours has been observed in red squirrels in several studies. For example, aggression has also been found to negatively correlate with stress levels (Haigh et al., 2017), in line with our results. Activity has also been found to correlate with dominance in red squirrels (Santicchia et al., 2019b). However, boldness has been found to be positively correlated with this suite of dominant behaviours across a variety of taxa (Koolhaas et al., 1999; Lowry et al., 2013; Merrick & Koprowski, 2017a; Tamin et al., 2023), including in squirrels (Boon et al., 2008; Santicchia et al., 2019b). It was therefore unexpected that less dominant and less aggressive males displayed higher levels of

boldness in this study, and the reasons for this unexpected pattern are explored further below.

The expression of this behavioural syndrome had implications for the survival of males, with subordinate males living longer and displaying higher levels of aggression the longer they lived. The correlation between aggression and survivorship is likely to be a plastic habituation response, influenced by increased exposure to the trapping process (Figure 4.3) and does not reflect the underlying personality of the squirrel. Therefore, in Belleek males who were subordinate, less aggressive, less stressed, less active, had a decreased flight response, and were bolder, tended to have longer lifespans. Their lower aggression levels, possibly made it less likely that they would engage in fights (Diggins, 2021), thus reducing their mortality risk. While this study did not record any effects on reproduction due to the difficulty of tracking reproductive output in males through live trapping, it is well-established that dominant and aggressive males typically have higher mating success (Lee, 2001; Wauters & Dhondt, 1989; Wauters et al., 1990). This may indicate that this cohort prioritised reproduction over longevity.

Females in Belleek displayed higher levels of aggression and were less stressed compared to males overall. Despite these differences, female squirrels in Belleek exhibited a similar syndrome to that of males, albeit with a reversal in the correlation with boldness, consistent with previous research (Boon et al., 2007; Santicchia et al., 2019b). Larger females, and therefore likely dominant females, displayed higher levels of aggression, were less stressed, had a decreased flight response, and in contrast to males, were bolder. According to the OFT, this cohort were also more active. In contrast, subordinate females were shy, less aggressive, more stressed, less active, and had a greater flight response. Survival was highest in the latter group, mirroring the finding in males. Dominant females, as expected, displayed higher reproductive success, which is a well-established pattern in the literature (Lurz et al., 2005; Wauters & Dhondt, 1989). However, survival was lower among this group. Here we can see a clear trade off in life history strategies, with smaller, shyer females prioritising longevity, while larger, bolder females prioritise reproduction. The trade-off between reproduction and longevity is an established concept in nature (Badyaev & Ghalambor, 2001; Biro & Stamps, 2008) and has been documented in the American red squirrel (*Tamiasciurus hudsonicus*) (Descamps et al., 2006; McAdam et al., 2007). It has also been suggested to exist in red squirrel populations (Rodrigues et al., 2010; Santicchia et al., 2018). This trade-off may be influenced by the individual's body condition, as previous research has suggested that an individual's morphology can partly control their life history strategy (McAdam et al., 2007), implying that the behaviours that make up an individual's personality may be influenced by their physical characteristics.

The question remains; why is boldness advantageous for the longevity of males in the woodland, but detrimental for females? Given that boldness is well established to be correlated with increased aggression, dominance and lower stress rates (Haigh et al., 2017; Moiron et al., 2020; Santicchia et al., 2019b), as seen in Belleek females, its reversed relationship with these traits in Belleek males likely confers a unique advantage. Boldness has been observed to be advantageous in low predator, or predator free urban environments, such as Belleek (Carrete et al., 2016; Møller, 2008). The ability of an animal to adapt to human environments without suffering chronic stress plays a crucial role in overall fitness (Lowry et al., 2013). Additionally, bold animals are more inclined to interact with humans and human-made objects, such as traps and feeding stations, potentially granting them access to a wider array of anthropogenic food sources (Charles et al., 2022; Greenberg & Holekamp, 2017). On the other hand, shy animals may be less likely to utilise these manmade objects. In Belleek, supplementary feeding is provided at feeding stations. It is possible that the greater longevity of subordinate and bold males is influenced by their willingness to access this food source, while dominant males rely more heavily on the less stable natural food resources. In this case, boldness would allow subordinate males to exploit anthropogenic food resources in a competitive high density environment while avoiding conflict due to their low aggression tendencies.

Alternatively, boldness may represent an adaptation in subordinate males aimed at increasing their reproductive success. Subordinate male red squirrels have been known to “sneak past” the leading, dominant male in mating chases whilst he is occupied in chasing away another subordinate (Wauters et al., 1990). These smaller males would not otherwise gain access to the female, due to their inability to compete effectively with the leading male. Hence, they must rely on their boldness to enhance their prospects of reproducing. This potentially explains why boldness is linked with subordination in male squirrels but not in females, who do not engage in competition for access to males. Nonetheless, the intricate relationship between male survival, boldness, and the various intrinsic and extrinsic factors present at Belleek and within individual squirrels warrants further investigation. Monitoring the feeding habits and reproductive success of individual males could offer a more comprehensive understanding of this relationship.

A shift was noted in the expression of three traits with increased exposure to the trapping process: flight response, aggression, and sociability. Each behaviour shifted in one direction, with individuals displaying a decreased flight response, and increased aggression and sociability. This habituation to the trapping was only observed in Belleek. Habituation can complicate the detection of behavioural syndromes, as not all behaviours within a syndrome shift simultaneously with increased trapping (Carter et al., 2012). However, the

rate of habituation among individuals remains consistent and does not affect their ranking in the expression of behaviour (Carter et al., 2012; Ensminger & Westneat, 2012; Martin & Réale, 2008). In our study, individuals who remained in the woods the longest displayed increased aggression and a decreased flight response. However, these patterns were not evident during their initial visit, indicating that they are a result of habituation rather than innate personality traits.

Habituation is usually characterised by the decrease in strength of a response (Hinde, 1970), with animals tending to expend less energy reacting to human presence (Doran-Sheehy et al., 2007; Hansen & Aanes, 2015). However, in the current study, aggression in males was found to increase over time. It is possible that squirrels learned that there was no mortality risk associated with the trapping process, and therefore little risk in engaging in aggressive behaviour in an attempt to escape. Red squirrels are known to display aggression when the risk of engaging in a fight is low, as seen in males displaying aggression towards more subordinate males, but not more dominant ones (Wauters & Dhondt, 1989). The squirrels in the current study may perceive the risk as low after surviving multiple trapping events, leading them to choose to display aggression as an escape strategy. This behaviour has anecdotally been observed to be very effective, with instances of squirrels displaying highly aggressive behaviour, involving biting, leading to their premature release from the trapping process. This response was not observed in Derryclare. It is possible that habituation may occur at a slower rate in Derryclare due to their unfamiliarity with humans, a phenomenon observed in chimpanzee populations with varying degrees of familiarity with humans (Samuni et al., 2014). However, returning individuals at Derryclare experienced fewer trapping events than those at Belleek, making it likely that habituation was not detected as it may not have yet occurred.

Squirrels who never returned to the traps were found to be smaller and less fit than those who did. Their lack of recaptures could be attributed to several potential factors, including dispersal, mortality, or remaining undetected in the woods. Given that juveniles and subadults are typically smaller than adults (Wauters et al., 2007), and that younger squirrels exhibit higher dispersal rates (Wauters et al., 2010) it is possible that many of the non-returners were younger than those who returned, making dispersal a likely explanation for their lack of recaptures. Larger dispersal distances are associated with high squirrel densities due to an increased competition for resources (Wauters et al., 1994b). Belleek sustains a relatively high density population (See chapter 3), meaning that smaller, less fit squirrels are more likely to be displaced (Wauters & Dhondt, 1992). A poor body condition is associated with increased mortality (LaRose et al., 2010; Shuttleworth et al., 2015), which may also help to explain the lack of recaptures in this less fit cohort of squirrels.

Alternatively, it is possible that non-returners simply remained in the woods without revisiting a trap. A study on Uinta ground squirrels (*Citellus armatus*) revealed that the perceived balance between punishment (trapping) and reward (bait) influenced an animal's likelihood of being recaptured (Balph, 1968). It was expected that a negative trapping response would be reflected in a greater stress response of the animal (Romero, 2004), but this was not the case. Interestingly, increased alarm calling was observed in squirrels who subsequently did return to the trap. Rather than correlating with stress levels, alarm calling in the Belleek population was found to be linked to the reproductive success of females. Schwagmeyer (1980) found that alarm calling in the thirteen-lined ground squirrel, (*Spermophilus tridecemlineatus*) is used to signal to genetic relatives about the presence of danger. Therefore, it is likely that alarm calls were made by females to their offspring, indicating that these females were established in the woods and unlikely to disperse to a new habitat (Wauters et al., 1995), thereby increasing their recapture probability. The absence of other behavioural differences between the returners and non-returners indicates that either there were additional unmeasured behaviours at play, or that the likelihood of returning to a trap was not determined by the personality of the squirrel, but rather by another factor such as dispersal or death.

In conclusion, this study sheds light on the complex interplay between red squirrel behaviour, an individual's traits, and their environment. We have observed distinct behavioural syndromes among males and females, which most notably differed in their boldness levels. The expression of these syndromes have implications for the survival of both sexes, and the reproductive success of females, suggesting the existence of a trade-off in life-history strategies. This finding may have implications for conservation management as it influences population dynamics. Habituation to trapping processes has provided insight into the adaptability of these squirrels, as well as underscoring the importance of considering the impact of repeated trapping on behaviour expression and syndrome detection. The differences in recapture rates raise questions about the factors controlling squirrel trap use, and whether unmeasured behaviours could explain why some squirrels never return to a trap. This study provides valuable insights into red squirrel behaviour, particularly in an environment with a high human presence, and that it contributes to the broader understanding of wildlife behaviour and the dynamic interplay between individual traits and habitat dynamics.

5 Investigating the antipredator response of the red squirrel

5.1 Introduction

Animals in the wild face constant danger from a wide range of threats. One of the biggest threats an animal faces is that of a predator. Antipredator adaptations are traits that evolve through natural selection in the prey species to assist in their defence against a predator (Aguiar et al., 2023; Dugatkin, 2008). Some of these adaptations result in permanent antipredator responses that include but are not limited to changes in morphology (Cairns et al., 2020), physiology (Ruxton et al., 2019) and life history (Brodersen et al., 2015; Sih et al., 2010). Antipredator adaptations may also be expressed temporarily, such as changes in behaviour (Barnard, 2012). Plasticity in antipredator traits allows the animal to minimize the costs of expressing this trait, by not employing them when there is a low risk of predation (Agrawal, 2001). The recent presence of a predator can trigger a predator response sequence that allows for the expression of an antipredator trait (Kelley & Magurran, 2003). First, the prey detects the recent presence of the predator, then it recognises the threat and assesses the level of danger, and lastly it displays the appropriate antipredator response. If the prey fails in any of these steps, it will be at a greater risk of predation.

The first step in the antipredator response sequence is to detect the presence of a predator. Prey that experience a greater proportional fitness loss if attacked will detect the predation risk earlier than prey who would experience a lower proportional fitness loss (Sheriff et al., 2020). Predator detection is often facilitated by the cue of a predator. Cues may be chemical (Kats & Dill, 1998), visual (Blumstein et al., 2000), mechanical (Castellanos & Barbosa, 2006; Djemai et al., 2001; Virant-Doberlet et al., 2019), and/or auditory (Jayne et al., 2015; Pollack, 2016; Yack et al., 2020). Chemical cues include odours left by a predator, often through sources such as skin, fur, faeces, urine and gland secretions (Apfelbach et al., 2005). These olfactory cues may be left inadvertently by the predator or deliberately for communication (Wyatt, 2010). For example, mammalian predators such as the pine marten (*Martes martes*) often use urine, faeces, and anal scent glands to “mark” their territory. The use of scent marking means that olfactory cues are key indicators of the level of risk for the prey of mammalian predators (Banks et al., 2014). Olfactory cues are especially important for mammalian prey such as the red squirrel (*Sciurus vulgaris*), who rely heavily on scent detection and identification in other activities such as foraging and communication (Banks et al., 2014; Lledo et al., 2005). Olfactory cues may also be left without physical secretion by the predator (Apfelbach et al., 2005).

Once the prey has detected the recent presence of the predator, it must then recognise the threat and assess the danger of the situation. The recognition of a predator can be both learned (Hudson et al., 2017; Kelley & Magurran, 2003; Wyatt, 2010) and innate as a result of coevolution (Binz et al., 2014; Carthey & Banks, 2016; Dugatkin, 2008; Kemprij et al., 2020; Tariel et al., 2020). The level of risk can be determined using additional information revealed by the cue. Not only does the cue reveal the location of the predator at an earlier point in time, but the age or “freshness” can reveal how long ago it was left by the predator (Bytheway et al., 2013). Cues can also reveal the direction in which the potential predator was travelling (Steck, 2012). All of this information can be used by the prey to assess the likelihood of predation and react accordingly. The subsequent reaction to the predator’s recent presence is the final stage of the antipredator response sequence (Kelley & Magurran, 2003).

The detection of a predator generates a trade-off for the prey whereby the prey must weigh the cost of the perceived risk of predation against the benefits of opportunities such as mating or feeding (Siepielski et al., 2016). This trade-off is often expressed as a behavioural change in the prey animal. Behavioural responses are specific to the prey/predator relationship but generally involve reduced activity (Siegal et al., 2022; Van Buskirk & Yurewicz, 1998; Van Duren & Videler, 1996), increased refuge use i.e., hiding (Stauffer & Semlitsch, 1993), fleeing (Kats & Dill, 1998; Lingle & Pellis, 2002; Randler, 2006), and altering their habitat use (Dickman, 1992; Stoddart, 1982). For olfactory cues, the behavioural change will also vary depending on the freshness of the scent. Prey have been shown to reduce foraging behaviour when the predator’s scent is fresh, increase it as the predation risk drops, and stop responding once the cue has aged (Bytheway et al., 2013; Koivisto & Pusenius, 2003).

The red squirrel and the pine marten are both native to Ireland and share an evolutionary history (Moffat, 1937; Montgomery et al., 2014; O’Sullivan, 1983; O’Mahony et al., 2006). A simulation of pine marten presence, achieved through a mixture of scat and water, has been shown to affect the behaviour of the red squirrel (Twining et al., 2020a). Red squirrels reacted to the cue by reducing the number of visits to the feeder, reducing the time spent feeding, and increasing the time spent vigilant. Conversely, the invasive grey squirrel (*Sciurus carolinensis*) shows a lack of an antipredator response in the presence of a pine marten cue (Twining et al., 2020a). This predator naiveté, coupled with the resurgence of the pine marten, has led to the decline of the grey squirrel population in Ireland (Lawton et al., 2015a; Lawton et al., 2019; Sheehy & Lawton, 2014; Sheehy et al., 2018). Interestingly, the recovery of the pine marten has not had the same impact on red squirrel populations, despite it being the natural predator of this species (Lawton et al.,

2015a). Sheehy et al. (2018) has hypothesised that this coexistence is possible because the red squirrel is able to avoid the pine marten due to its inherent antipredator response, which the grey squirrel lacks.

The aim of this project was to investigate and analyse the antipredator behavioural adaptations of red squirrels in response to recent pine marten presence. While Twining et al. (2020) simulated the presence of pine marten by using a scat/water mixture, this study sought to investigate whether red squirrels could detect and react to the recent presence of a pine marten. Trail cameras were used to record red squirrel and pine marten visits to a feeder, and subsequently, the behavioural changes of red squirrels were analysed. It was hypothesised that red squirrels would detect the recent presence of a pine marten and display antipredator responses such as decreased activity, decreased feeding and increased vigilance. Additionally, it was hypothesised that these responses would become less pronounced with time since the pine marten visit, until normal behaviour was resumed.

5.2 Methodology

Data were collected from January 2020 to May 2021 at two sites in the west of Ireland. Red squirrels and pine martens were present at both sites. Derryclare woods (570ha) in Connemara is a commercial forest consisting mainly of lodgepole pine (*Pinus contorta*) and Sitka spruce (*Picea sitchensis*) stands. It also contains a small (12ha) broadleaf stand, consisting mainly of oak (*Quercus petraea*), ash (*Fraxinus excelsior*), birch (*Betula* sp.), and hazel (*Corylus avellana*). The second site, Belleek woods in Ballina, Co. Mayo (61ha), is a public park with a mix of broadleaf, mainly beech (*Fagus sylvatica*), and conifer trees, mainly Norway spruce (*Picea abies*). Sampling in Belleek lasted from February 2020 to September 2020 and Derryclare data were collected from January 2020 to May 2021. The number of videos recorded in Derryclare was much lower than in Belleek, so the duration of the study was extended at Derryclare.

Bushnell NatureView HD and Browning trail cameras were used to capture pine marten and red squirrel visits to feeders. The video length was set at 30 seconds. Two designs of feeders were used: hairtubes and feeding stations. Hairtubes consisted of 30cm long 65mm x 65mm square PVC pipes secured to trees between chest and head height. The feeding stations consisted of a rectangular box (L20cm x W15cm x H15cm) with a hinged lid and a small platform on which the animal could stand. Bait for the feeders consisted of hazelnuts and peanuts, and was refilled intermittently from once every few days to once every two months. Four cameras were deployed in each site, at least 150m apart, giving a total of eight cameras. Trail cameras were secured to a tree within 6m of the feeder.

During every visit to a site the camera batteries and memory cards were changed. The locations of cameras were moved between feeders throughout the project, to increase range and number of individuals monitored.

Behaviour was analysed using BORIS behavioural software (Friard & Gamba, 2016). For red squirrels, we recorded and analysed the following variables: the time and date of the visit, the visit duration (i.e., the length of time the squirrel spent in frame during the video), whether or not bait was available, the number of days since bait had been topped up, whether or not the squirrel was visiting within 48hrs of a pine marten, and if so, the number of minutes between the visits, and whether or not the pine marten left a scent via scent marking, urinating or defecating (henceforth referred to as marking), and the number of seconds the squirrel spent feeding, showing vigilance and sniffing.

Red squirrels usually feed in a hunched posture with the squirrel using its front limbs to hold the food to its mouth, while chewing. At times red squirrels feed in a quadrupedal stance with the head lowered to the food, also while chewing. Sniffing was normally conducted by the red squirrels with their heads lowered to the feeder. Vigilance was recorded when the red squirrels were completely immobile, or any time the red squirrel was immobile but flicking its tail. This behaviour, known as tail flagging, is considered to be an alarm response (Partan et al., 2009).

A Spearman rank test was used to analyse the relationship between the time since a pine marten visit and the behaviour shown by the squirrel. Based on the results from the Spearman rank test and the identification of natural breaks in the data, the dataset was subsequently divided into three time groupings – those that visited the feeder between 0-8 hours of a pine marten visit, those that visited between 8-48 hours of a pine marten visit, and those that visited more than 48 hours after a pine marten visit. Those that visited more than 48 hours after a pine marten visit were considered to be the control group, as the effect of the recent presence of the pine marten had dissipated.

Both the visit durations and behavioural factors (feeding, vigilance and sniffing) were measured in seconds, and were analysed by their time groupings (i.e., 0-8 hours, 8-48 hours, 48+ hours after a pine marten visit). The visit durations and the behaviours were tested for normality, and all were found to not have a normal distribution. A Spearman rank test was used to determine if a correlation existed between the behavioural factors and the time since a pine marten visit, as well as possible confounding factors such as the number of days since the bait was refilled and the time of the visit. A Fisher's exact test was used to determine if an association existed between the behaviour and the time grouping in which the visit occurred. The visit durations, and the behaviours sniffing and

feeding were tested only for visits during which bait was available, in order to remove food availability as a factor. The distributions of red squirrel visit durations and all three behaviours were found to be similar across the three time groupings. A Kruskal Wallis test, with a post-hoc pairwise comparison was used to test the differences between the means of all behaviours across the time groupings.

Red squirrel visits that were within 48 hours of a pine marten were further divided into two categories: visits following a marking occurrence, and visits where no marking had occurred. A Kruskal Wallis test was used to determine if the marking had a significant effect on the mean length of the squirrels' visits, and the mean time spent feeding, showing vigilance, and sniffing.

Analyses were performed using IBM SPSS Statistics 27.

5.3 Results

A total of 544 squirrel visits to feeders were recorded (Belleek = 507, Derryclare = 37), with a total of 8,797 seconds of red squirrel presence. A total of 226 pine marten visits were recorded (Belleek = 81, Derryclare = 145). Pine marten were recorded marking in 14 videos. In the other 212 videos, pine marten were recorded feeding and exploring the feeders, without marking. Squirrel visits were recorded within 48 hours of all 14 instances of marking. In the 8 hours following a pine marten visit 59 squirrel visits were recorded, 157 squirrel visits were recorded between 8-48 hours of a pine marten, and 328 squirrels were recorded more than 48 hours after a pine marten. The high rate of squirrel visits in the first 8 hours likely reflects the attraction of the food, which was frequently visited by pine marten on the day of topping up.

Squirrels usually visited the feeders from dawn to just before dusk, with the earliest and latest recordings occurring in the summer months. Pine marten mostly visited the feeders at night, but also occasionally during daylight hours. Pine marten activity overlapped with squirrel activity in the mornings for all months, but this overlap is more pronounced in some months, with some pine marten recordings occurring as late in the day as 12:58pm (see Figures 5.1 and 5.2).

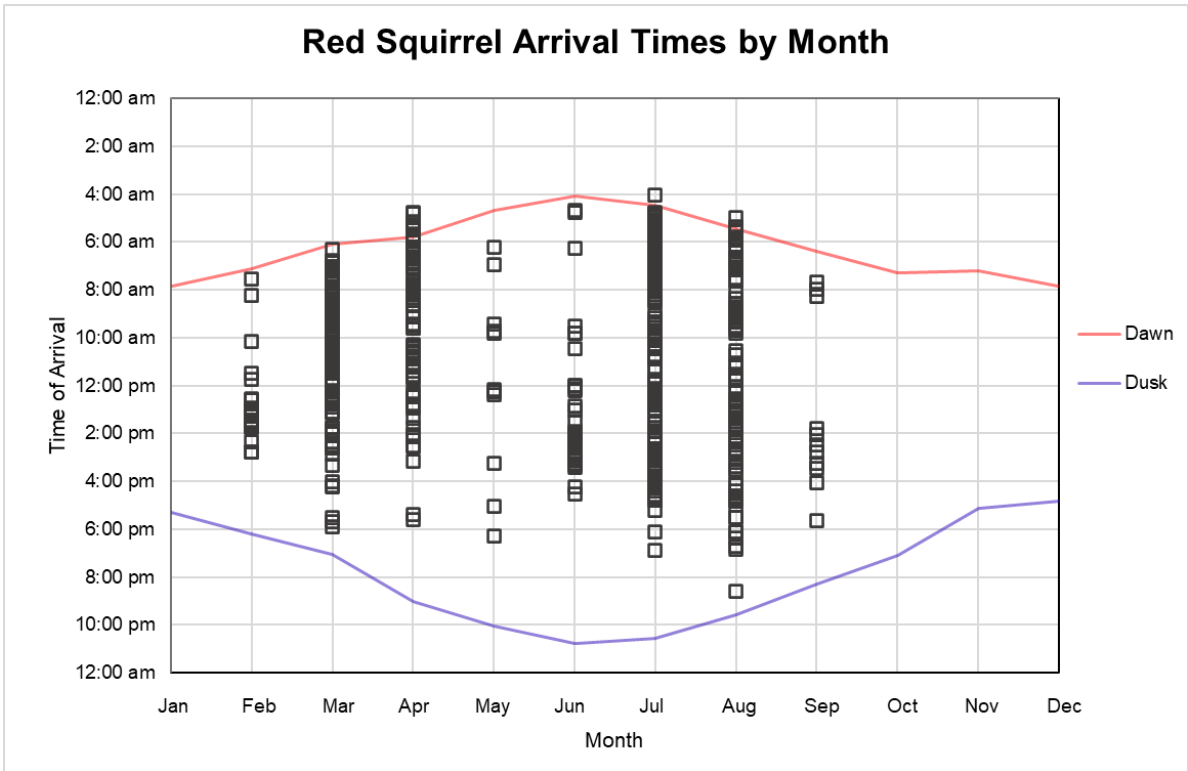


Figure 5.1 Red squirrel arrival times recorded at a feeder in the months of February - September.

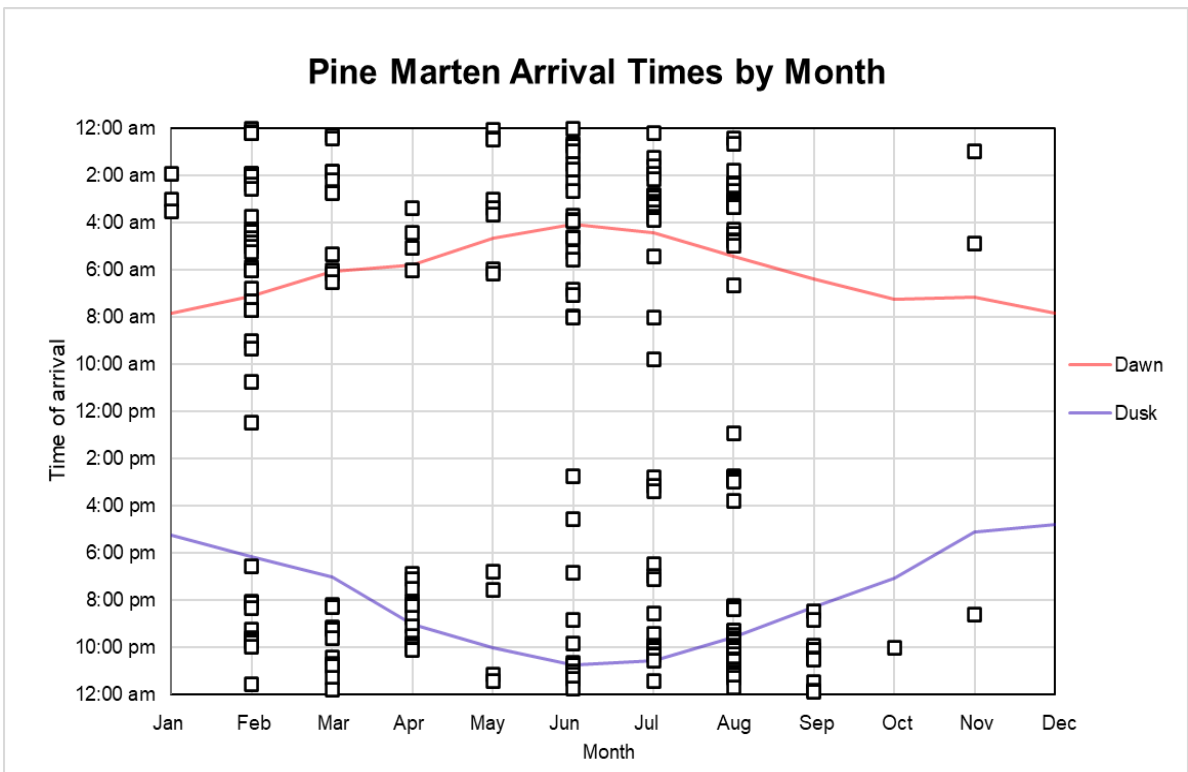


Figure 5.2 Pine marten recorded arrival times at a feeder in the months of January - November.

No significant correlations were found between the duration of the visits, the length of time spent exhibiting tested behaviours and the number of days since the bait was refilled, or the time of day. A marking occurrence was only found to have a significant effect on the length of time spent sniffing.

The relationship between sniffing and the time since a pine marten visit occurred was examined ($n = 213$). A Fisher's exact test revealed a statistically significant association between the number of squirrels sniffing and the time grouping of the visit ($p = 0.018$).

The percentage of squirrels sniffing 0-8 hours after a pine marten visit (84.62%, $n=26$) was significantly higher than for either 8-48 hours (54.79%, $n = 117$) or more than 48 hours (58.12%, $n = 73$) from a pine marten visit ($p = 0.018$) (Figure 5.3).

A Spearman rank test revealed a non-significant weak negative correlation ($r_s = -0.055$, $p = 0.211$) between sniffing duration and time since a pine marten visit.

However, when sniffing duration was analysed by time grouping it was found that red squirrels spent a significantly longer time sniffing in the 0-8hr interval ($\mu = 7.711$, $SD = 7.475$) compared to those visiting between 8-48hrs ($\mu = 2.795$, $SD = 4.677$) or those visiting over 48hrs after a pine marten ($\mu = 3.318$, $SD = 5.347$) (Figure 5.4), as indicated by a Kruskal Wallis test ($H(2) = 15.528$, $p < 0.001$). A post-hoc pairwise comparison revealed significant differences between those visiting in the 0-8hrs interval and all those that came after (0-8hrs and 8-48hrs: $p < 0.001$, 0-8hrs and 48hrs+: $p < 0.001$).

Squirrels visiting within 48 hours of a marking occurrence sniffed significantly longer ($n = 14$) than those visiting within 48 hours of a pine marten visit without marking ($n = 202$) ($H(1) = 4.508$, $p = 0.034$). However, the difference in sniffing duration between 0-8hrs and 8-48hrs after marking was not significant ($H(1) = 2.706$, $p = 0.1$), likely due to the small sample size in the former (0-8hrs: $n = 2$, 8-48hrs: $n = 12$).

There was no significant correlation between the length of time spent at a feeder and the time since a pine marten visit ($r_s = -0.060$, $p = 0.193$). The length of each squirrel's visit did not alter significantly across the three time intervals, as revealed by a Kruskal Wallis test ($H(2) = 1.961$, $p = 0.375$) (0-8hrs: $\mu = 23.162$, $SD = 7.459$, 8-48hrs: $\mu = 20.152$, $SD = 8.607$, 48hrs+: $\mu = 21.896$, $SD = 8.658$) (Figure 5.4).

The percentage of red squirrels exhibiting vigilance was significantly higher during the time grouping closest to the pine marten visit and decreased with time (0-8hrs: 79.66%, $n = 59$, 8-48hrs: 69.43%, $n = 157$, 48hrs+: 48.17%, $n = 327$, $p = <0.001$) (Figure 5.3).

There was a significant moderate negative correlation between the time spent exhibiting vigilance and the time since a pine marten visit ($r_s = -0.307$, $p < 0.001$, $n = 544$).

The decrease in vigilance duration could also be seen when vigilance was analysed by time grouping. Squirrels visiting between 0-8hrs spent the most time being vigilant ($\mu = 3.586$, $SD = 4.364$), those between 8-48hrs spent less time ($\mu = 2.269$, $SD = 3.322$) and those visiting after 48hrs spent the least time being vigilant ($\mu = 1.52$, $SD = 3.098$) (Figure 5.4). This difference in means was revealed to be statistically significant by a Kruskal Wallis test ($H(2) = 39.478$, $p < 0.001$). A post-hoc pairwise comparison showed that significant differences existed between the means of all three groups (0-8hrs and 8-48hrs: $p = 0.016$, 8-48hrs and 48hrs+: $p < 0.001$, 0-8hrs and 48hrs+: $p < 0.001$).

The percentage of squirrels who fed increased with increasing time from the pine marten visit (0-8hrs: 26.92%, $n = 26$, 8-48hrs: 61.64%, $n = 73$, 48hrs+: 79.49%, $n = 117$) (Figures 5.3 and 5.5). A Fisher's test revealed this association to be statistically significant ($p < 0.001$).

A Spearman rank test revealed a significant positive correlation ($r_s = 0.245$, $p < 0.001$) between the length of time spent feeding and the time since a pine marten visit.

When analysed by time grouping, the time spent feeding was found to increase with time from a pine marten visit (0-8hrs: $\mu = 2.438$, $SD = 5.846$, 8-48hrs: $\mu = 6.389$, $SD = 8.197$, 48hrs+: $\mu = 8.126$, $SD = 8.963$) (Figure 5.4). A Kruskal Wallis test revealed that this difference was statistically significant ($H(2) = 20.165$, $p < 0.001$). A post hoc pairwise comparison revealed that there was a statistically significant difference between the means of all three groups (0-8hrs and 8-48hrs: $p = 0.005$, 0-8hrs and 48hrs+: $p < 0.001$, 8-48hrs and 48hrs+: $p = 0.041$).

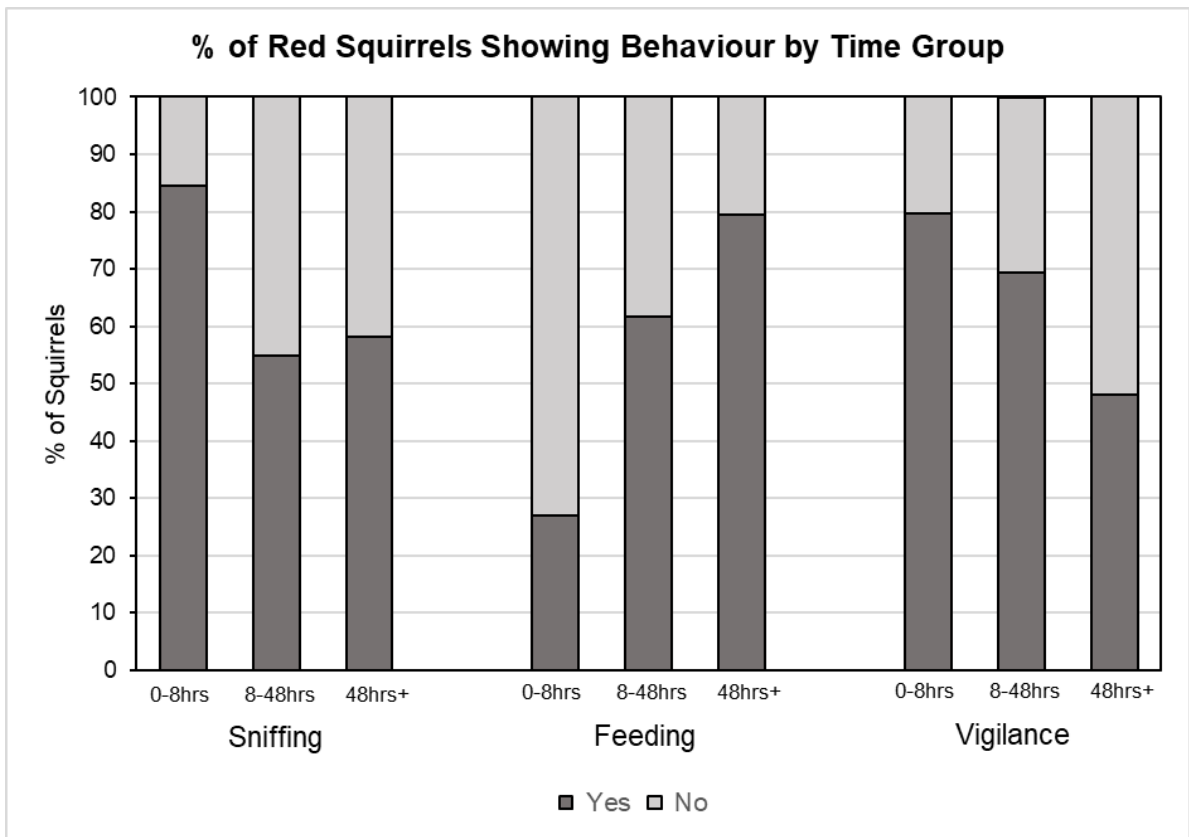


Figure 5.3 The percentage of red squirrels displaying various behaviours by their temporal proximity to the pine marten visit.

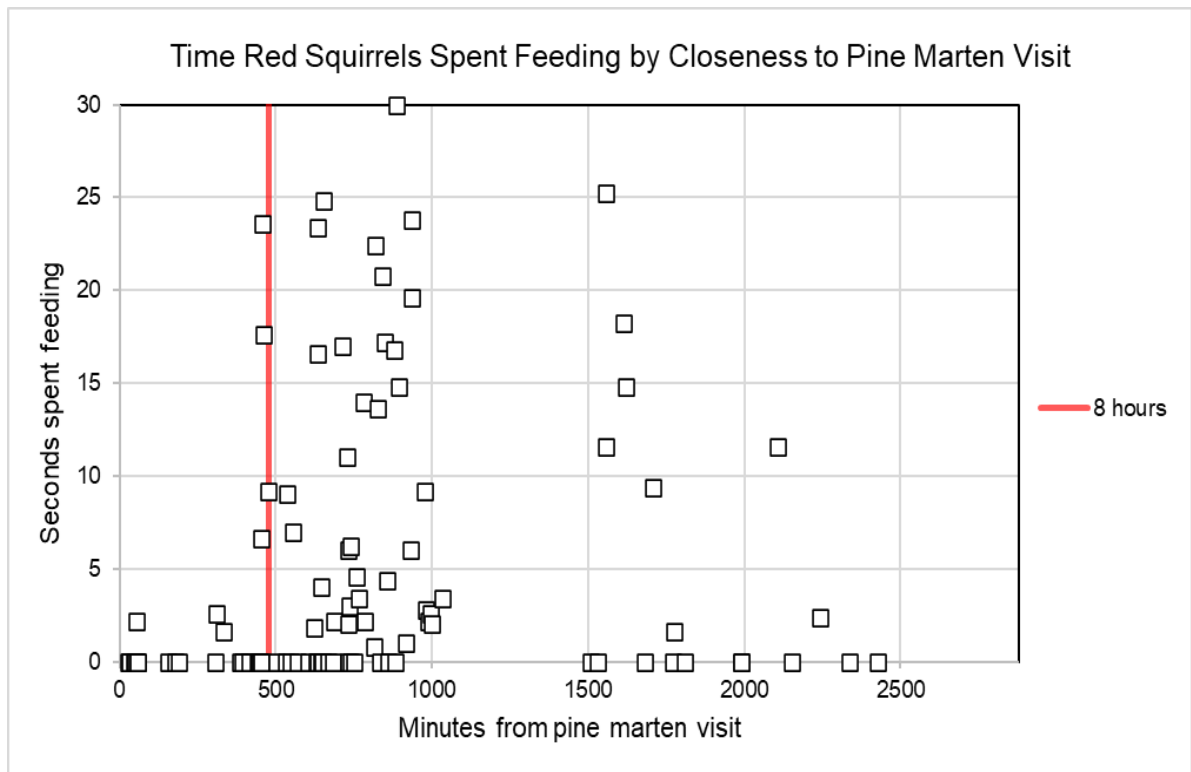


Figure 5.4 The number of seconds each red squirrel spent feeding on visits when bait was available, plotted by the number of minutes since the most recent pine marten visit.

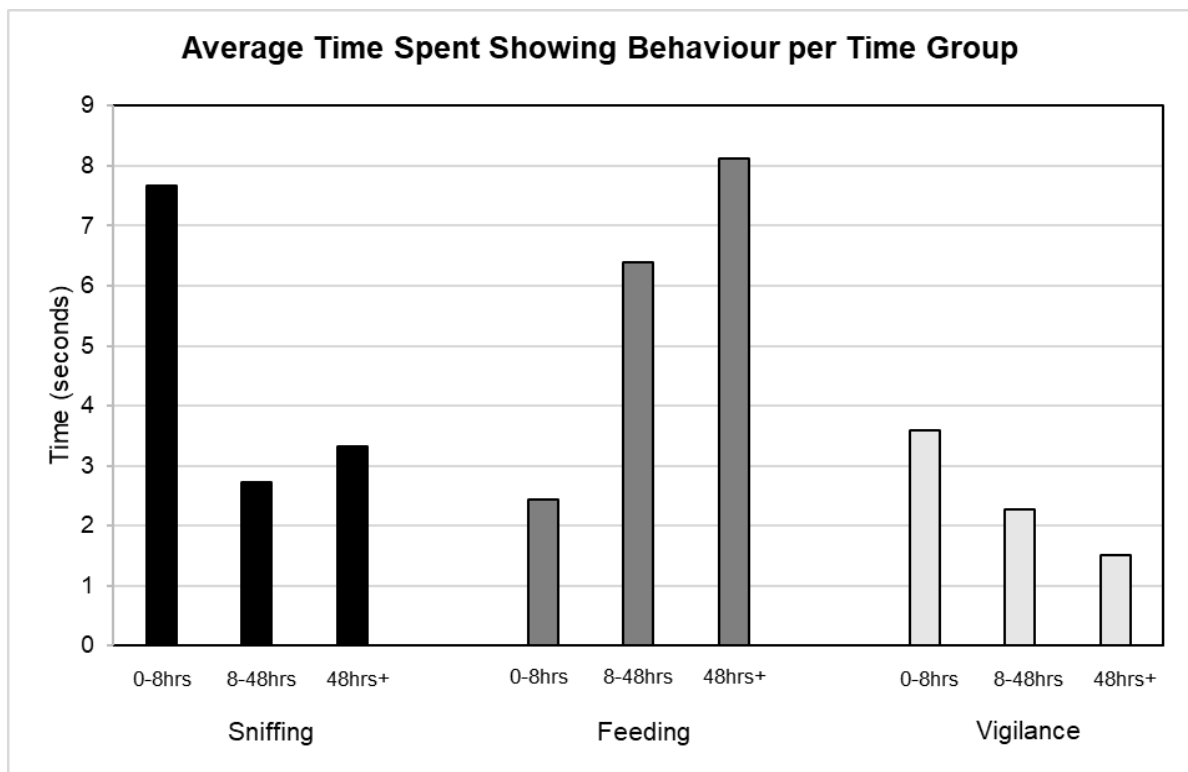


Figure 5.5 The length of time red squirrels spent displaying various behaviours by their temporal proximity to the pine marten visit.

5.4 Discussion

Red squirrels alter their behaviour in response to recent pine marten presence. Following a pine marten visit to a feeder, red squirrels displayed a typical antipredator response, exhibiting increased vigilance, decreased feeding and increased sniffing. This increase in sniffing, but not the other responses, was even more pronounced in visits following a pine marten that marked the feeder during its visit. There was no difference in the duration of the red squirrels' visits to a feeder, meaning red squirrels did not display a flight reaction in response to recent pine marten presence.

Red squirrel and pine marten activity patterns overlapped during daylight hours in some months, particularly in the summer (Figures 5.1 and 5.2). It was found that the pine marten was active during daylight hours for some of the year, which is in line with the literature (Zalewski, 2001; Zielinski et al., 1983).

The first two stages in the antipredator response sequence involve detection, followed by recognition and assessment (Kelley & Magurran, 2003). On visits when bait was present, red squirrels visiting within 8 hours of a pine marten sniffed more frequently, and for longer. Studies have indicated that animals spend more time sniffing in the presence of

their predator's cue when compared to controls (Carthey & Blumstein, 2018b; Dell'Omo & Alleva, 1994; Kepecs et al., 2006). It is therefore likely that the increased sniffing is an indication that the red squirrels detected and recognised the recent presence of their native predator.

This increase in time spent sniffing is especially pronounced in squirrel visits that followed a marking occurrence. This is likely because the scent of the pine marten is stronger, prompting the squirrels to sniff for longer to investigate the cue. However, marking occurrences did not affect visit duration, vigilance or feeding behaviours, indicating that while the scent might be more potent, the perceived level of risk has not increased. The perceived level of risk may therefore only be linked with the age of the cue, and not the source of the cue.

Markings may also have occurred in close proximity to the feeders but were not recorded because the pine marten was out of frame.

The increase in sniffing, even when not following a marking occurrence, demonstrates that red squirrels are able to detect the recent presence of a pine marten hours after their visit. This level of sensitivity to the natural cue of a pine marten gives red squirrels a greater insight into their recent activity, without relying on less frequent markings such as scats or urine.

Upon recognising the scent of a predator, the prey will display an antipredator reaction, such as fleeing (Kats & Dill, 1998; Lingle & Pellis, 2002; Randler, 2006). However, for visits when bait was present, no difference was found in the duration of the visits made in the first 8 hours, the subsequent 40 hours, or any time thereafter. Recent pine marten presence was predicted to elicit a flight response from the red squirrels, resulting in the visits immediately following a pine marten visit being the shortest, in keeping with the literature (Twining et al., 2020a). However, this was not the case. A flight response, if it were to occur, would be expected to happen immediately after the threat is recognised (Yilmaz & Meister, 2013). Therefore, a video length of 30 seconds is adequate to record a flight response. The absence of a flight response indicates that the red squirrels chose continued foraging over fleeing. This may be because the perceived predation risk is low, based on the strength of the cue (Sundell et al., 2004). Another possible response following the recognition of a predator's cue is avoidance (Apfelbach et al., 2005; Kats & Dill, 1998; Stoddart, 1982). However, the number of red squirrel visits recorded following a pine marten visit suggests that red squirrels did not show an avoidance response.

In the absence of a flight response, other common antipredator responses such as a trade-off between increased vigilance and decreased feeding may be expressed

(Bachman, 1993; Bednarz, 2021; Carthey & Banks, 2016; Mazza et al., 2019). In the 48 hours following a pine marten visit, red squirrels displayed vigilance more frequently, and were vigilant for longer. This increase in vigilance was even more pronounced in the first 8 hours and was least evident after 48 hours. The inverse was seen in feeding behaviour. Squirrels fed least often and for the shortest amount of time in the first 8 hours, more often and for longer in the following 40 hours, and most often and for the longest after 48 hours. These results show that red squirrels do display an antipredator reaction in response to a natural pine marten cue, in the form of increased vigilance and decreased feeding, rather than flight.

The effect of a predator's presence on antipredator behaviours diminishes over time as the cue ages and the perceived risk of predation decreases (Bytheway et al., 2013; Lima & Bednekoff, 1999). This diminishment can be seen clearly in this study as sniffing and vigilance decrease and feeding increases with time since the pine marten visit. The starkest response was seen in the first 8 hours following a pine marten visit, particularly in feeding behaviour. Red squirrels fed extremely rarely in the 8 hours following a pine marten visit, despite the availability of bait (Figure 5.5). All behavioural antipredator responses subsequently weakened beyond this 8-hour mark, with feeding and vigilance responses continuing to weaken beyond the 48-hour mark. This weakening of the red squirrel antipredator response over 48 hours from pine marten presence is in line with previous research (Twining et al., 2020a). The current study's results indicate that red squirrels can evaluate the cost-benefit relationship of displaying antipredator responses and react accordingly.

The grey squirrel does not have a shared evolutionary history with the pine marten and has shown a lack of an antipredator response to the danger associated with the simulated cue of the pine marten (Twining et al., 2020a). This is hypothesised to be one of the factors contributing to the grey squirrel's decline in Ireland and Scotland (Sheehy et al., 2018; Twining et al., 2020a). The antipredator behaviours displayed by the red squirrel in this study are a product of their coevolution with the pine marten. Their recognition of recent pine marten presence as a potential threat, as demonstrated by the increase in sniffing, triggers a response where they become more vigilant and reduce their feeding activity. In doing so, they allocate more time to investigate the perceived threat, thereby reducing the risk of predation. These data support the hypothesis that the red squirrel's antipredator response has allowed for the red squirrel population recovery, despite the resurgence of their native predator, in direct contrast to the grey squirrel decline (Sheehy et al., 2018; Twining et al., 2020a). Additionally, these data demonstrate that red squirrels can detect recent pine marten presence, in the absence of scent marking, defecating, and

urinating. The red squirrel's behavioural adaptations and sensitivity to a natural pine marten cue help to explain the conflicting outcomes of two squirrel species in the presence of a shared predator.

6 General Discussion

6.1 Overview of translocations at Derryclare and Belleek

Investigations into the translocations at Derryclare and Belleek have highlighted the complexities and challenges of undertaking such projects. We have uncovered contrasting outcomes for the two projects, which we suggest can be attributed to the differences in their habitats as well as the changes within these habitats since their initial introductions. The population at Derryclare have failed to enter the regulation phase, and appears to be experiencing a population crash. Despite their widespread distribution throughout the woods, the density of the population is extremely low, with an estimated total of 6.5 squirrels present in the woods, based on the minimum number present estimations from the live trapping study (see section 3.3.3). Such a small number of individuals likely falls below the minimum threshold required to sustain a viable population (Wood et al., 2007), casting doubt on the population's ability to recover. The individuals themselves are underweight compared to the average weight of other red squirrel populations in Ireland and Britain (Cartmel, 1997; Holm, 1990; Lurz, 1995; Magris & Gurnell, 2002; Reilly, 1997; Shuttleworth, 1996; Simpson et al., 2013b). This diminished weight has tangible repercussions on their reproductive output, as observed through the notably low reproductive success in Derryclare, with only one female displaying signs of breeding. While Derryclare squirrels were not less likely to be recaptured, the number of times they returned to the trap was low, indicating that they could no longer be recaptured either because they dispersed or died. The combination of low fitness levels within the population and the low density of squirrel signs beyond the trapping grid suggests the latter explanation. Moreover, the absence of any indications of population spread beyond the woods implies that carrying capacity was never reached in Derryclare. Red squirrel distribution is primarily influenced by food availability (Lurz et al., 2000), with squirrels occupying areas of greater quality (Wauters et al., 2001). The lack of successful dispersal to nearby woodlands suggests that these woodlands are of similar or poorer quality than Derryclare, thus limiting their potential expansion. Given that an expanded red squirrel range in the west of Ireland was one of the main aims of this translocation, the quality of the surrounding habitat may be a contributing factor to this project's lack of success.

The behaviour exhibited by the Derryclare population did not differ significantly from that of the healthy Belleek population, with the exception of a greater flight response during their first trapping experience, likely due to their unfamiliarity with humans. However, their home ranges were estimated to be significantly larger than those observed in Belleek. This discrepancy further suggests that the habitat quality in Derryclare is suboptimal,

necessitating extended foraging distances to meet energy requirements (Lurz et al., 1997). The low quality of the habitat was further revealed through the results of the feeding survey, revealing a patchy distribution of food with the highest quality found in the southern half of the woods. The potential carrying capacity of the woods has declined dramatically since the introduction of the squirrels in 2005, primarily due to habitat loss and a deterioration of habitat quality. Felling activities and a significant forest fire have contributed greatly to this diminishment in available habitat. Furthermore, these disturbances may have impacted the population directly by disrupting key population processes and indirectly exacerbating fragmentation within the woods. Additionally, the composition of the woodland has shifted, and continues to shift, towards the greater inclusion of Sitka spruce. This shift is unfavourable for the population, as Sitka spruce is less nutritious (Lurz et al., 2000), less stable (Broome et al., 2007) and less preferred (Lurz et al., 1998) for red squirrels. It is likely that the poor habitat quality, combined with the effects of habitat loss and disturbances have collectively resulted in the ultimate failure of this translocation.

In contrast, the Belleek population was found to have successfully entered the final stage of a translocation process; the regulation stage. These squirrels have not only maintained a widespread presence and a stabilised density within the woods, but have also demonstrated a substantial range expansion into neighbouring towns and villages. While the density of the population was found to fluctuate, an average of 0.41 squirrels per hectare, or 24.6 squirrels in total, was recorded, which is comparable to other healthy red squirrel populations (Cagnin et al., 2000; Flaherty, 2016), and higher than the density last recorded for the Belleek population during their growth phase. This plateaued density, coupled with a significant range expansion indicates that the population have reached carrying capacity within the woods. In fact, it is likely that the population met the carrying capacity of the woods within a decade of their introduction, as multiple sightings were reported south of Ballina prior to 2018. Expansion to the west and southeast of the woods was reported in 2020, and squirrels were observed to the north of the woods in 2022. Their ongoing expansion and establishment outside of the woods indicates that the population beyond Belleek is increasing, representing a significant step in the reestablishment of red squirrels in the west of Ireland.

The average weight of Belleek squirrels aligns with that of other healthy red squirrel populations (Flaherty, 2016; Tittensor, 1977; Tonkin, 1983), indicating a robust physical condition. The overall high fitness level of the population is apparent in the high proportion of reproducing females and the longer residence in the woods compared to Derryclare, indicating enhanced survival. While no urban syndrome was evident in the Belleek

population, they did show an increased habituation to humans, exhibiting a diminished flight response in their first trapping events compared to Derryclare. Additionally, males were noted to become more aggressive with increased trapping experience, potentially reflecting an adaptive change in escape tactics. A life history strategy trade-off between reproduction and survival was observed in females in Belleek and was suggested for males. These distinct life history strategies may be influenced by the individual's morphology (McAdam et al., 2007), contributing to the preservation of behavioural diversity in the population (Wolf et al., 2007). Home ranges in Belleek were significantly smaller than those estimated for Derryclare squirrels, indicating the high quality of the woodland (Lurz et al., 1997). Supplementary feeding bolsters the food availability of this wood, supporting an increased density (Magris & Gurnell, 2002; Shuttleworth, 1996; Verbeylen et al., 2003) and larger individuals (Takahata et al., 2023). Feeders were observed to be incorporated into the home ranges of seven of the eight radiotracked squirrels and the core ranges of three of those seven individuals, highlighting their importance to the population. The abundance of food facilitated by supplementary feeding, coupled with the stability of the habitat, and the population's habituation to human presence, is likely instrumental in the success of the Belleek translocation.

Genetic monitoring undertaken by Synnott (2024) has revealed high levels of inbreeding in both populations. Inbreeding effects are commonly found in translocated populations because the small number of founders creates a genetic bottleneck, reducing genetic diversity (Cardoso et al., 2009; Jamieson, 2011; Szűcs et al., 2017). This lack of diversity can lead to inbreeding depression, reducing the fitness of the population (Kirkpatrick & Jarne, 2000). If left unaddressed, the population may suffer a collapse (Kyriazis et al., 2021). The effect of low genetic diversity in Derryclare was modelled in a population viability analysis by Poole and Lawton (2009). This model predicted an extinction probability of 0.25 after 100 years based on a scenario involving inbreeding. They recommend that an unrelated pair of squirrels are introduced to the population every eight years, to maintain an extinction probability of 0.1. While the inbreeding effects identified by Synnott (2024) do not currently pose a significant threat to the immediate future of either population, further monitoring of these populations should aim to address this issue by introducing new unrelated individuals.

6.2 Considerations for future translocation projects

The translocations conducted at Derryclare and Belleek have provided various valuable insights into the planning and implementation of translocation projects. In particular, this project has highlighted the role that the quality of translocation site plays in determining

the outcome of the project. Additionally, this project has shown the importance of post-release monitoring beyond the initial few years after the translocation, highlighting how initial success may not reflect the true outcome of the project. We suggest a framework for evaluating the success of translocation projects. This framework helps to define the frequency and duration of post-release monitoring efforts, ensuring the accurate assessment of the project's true outcomes. Finally, we suggest that greater considerations of the behavioural variation within the target population are needed, considering the significant impact of individual behaviour on translocation success. These findings collectively contribute to the refinement of translocation strategies, aiming for more informed and successful conservation initiatives in the future.

6.2.1 Post-release monitoring

This study has highlighted the importance of post-release monitoring of translocation projects in the long-term. Post-release monitoring is considered an essential part of a responsible translocation project, according to IUCN guidelines (IUCN/SSC, 2013). It follows therefore that almost all translocation studies considered in a review by Bubac et al. (2019) conducted some form of post-release monitoring. However, some projects forgo any kind of post-release monitoring. For example, in the case of the release of captive bred red squirrels from Belfast zoo (Bell et al., 2022), no follow up monitoring was ever published, leaving the fate of the individuals and the potential conservation benefit of releasing individuals from a breeding programme unknown. Of those projects that did conduct post-release monitoring, the majority only conducted monitoring within four years of the original introduction, providing little information on the long-term success and persistence of the population (Bubac et al., 2019). Projects that are deemed to be successful within this time frame may experience subsequent collapses that go unnoticed or unrecorded. For example, the translocation of red squirrels to Thetford, East Anglia, England (Venning, 1997) was initially deemed successful, but later failed owing to several squirrel pox virus outbreaks (Carroll et al., 2009). Observations of the Derryclare population have further emphasised the fragility of a translocated population, despite initial success.

The lack of investigation into the long-term trajectory of translocated populations beyond the initial years leaves a critical blind spot in our understanding of the factors that determine translocation success or failure, resulting in less informed projects in the future. Additionally, this lack of monitoring hinders individual projects by failing to identify potential threats to the population that could jeopardize the overall success of the

translocation effort. For example, the threat posed by a lack of genetic diversity will not be apparent in the first few years following release. Mitigation measures such as the introduction of additional animals in the case of a genetic bottleneck, can only be implemented if the problem is identified, emphasising the need to monitor the population in the long-term. Other mitigation measures include the provision of supplementary feeding in poor quality habitats (Cabezas & Moreno, 2007), the control of predators (Rouco et al., 2008) and management of competitors (Shuttleworth et al., 2009). In the event of unexpected failure or failure despite intervention in a translocation project, the insights obtained from the investigation into the cause of failure provide invaluable feedback. Sharing this information can foster more informed decision-making and enhance the overall effectiveness of translocation efforts.

One issue preventing the implementation of an effective post-release monitoring strategy is a lack of consensus on the duration and frequency of such efforts. It is this lack of structure that also leads to the erroneous categorisation of a project as being successful when the true outcome has yet to come to light (Fischer & Lindenmayer, 2000). Seddon (1999) recommended goals by which translocation projects may measure their success, although we believe that further detail of the metrics of success are needed. For this purpose, we draw from the outline of translocation phases as described by the IUCN (2013) and suggest specific measures of success for each stage, adding to the work of Seddon (1999). We recommend that projects are investigated during the three phases of a translocation: establishment, growth and regulation as outlined by the IUCN (2013), and furthermore, that the success of the project is measured by the population's successful transition through these various stages. The establishment phase is the first stage of the translocation which starts immediately following release (IUCN/SSC, 2013). The success of this stage is measured by the survival of the founders and their continued presence in the release site. For red squirrels, it is recommended that at least 75% of the translocated animals are successfully released from the enclosure into the new habitat, and that 50% survive to the following year's breeding season (Venning, 1997). The following stage of the translocation is the growth phase (IUCN/SSC, 2013), which is measured by the successful reproduction of the founding population and their offspring, and expansion of their range. The final stage of the translocation is the regulation phase (IUCN/SSC, 2013). This phase is characterised by the continued presence of the population and a stabilised density.

This approach of measuring the success of the translocation based on these metrics has various benefits. Firstly, each stage has clearly defined goals, making the assessment of success a simple process, minimising ambiguity, or subjective interpretation. The

evaluation of a translocation's success frequently relies on the researcher's perception of success (Morris et al., 2021), which leads to premature assessments of the outcome and hinders the comparability of different projects. Standardisation is another benefit of using this approach. Standardised metrics of success facilitate effective communication among researchers, allowing for the comparison of projects using common language, and the dissemination of valuable insights across the scientific community. Thirdly, this approach is useful as it may be applied to any species. While the intervals between phases and the duration of each phase may differ depending on the life history of the target species, the metrics of growth, density and presence are applicable to all species. This consistency allows for the effective comparison of projects not only within a specific species but also across various taxa. Consequently, it facilitates the identification of patterns and trends that can inform best practices. Finally, by setting clear goals that are considered fully achieved only upon the successful transition of the population into the regulation phase, the researcher is motivated to continue post-release monitoring efforts beyond the initial period following release. Continued monitoring is required until all established goals are achieved or until the translocation is deemed unsuccessful. Not only does this allow for issues with the project to be identified and rectified, but it also ensures that the true outcome of the project is revealed. Management issues, such as a lack of funding, continued support from management bodies, and monitoring efforts, are one of the most commonly cited reasons for a translocation failure (Bubac et al., 2019). This approach facilitates efficient planning for the translocation, providing managers with a clearer understanding of the necessary personnel, financial costs, and project duration.

Determining the extent to which monitoring should be continued after a successful transition into the regulation phase is a nuanced decision and depends on the specific circumstances of the translocation. This decision should be based on the stability of the population, which is dependent on multiple factors including the stability of the habitat, the abundance of the population and the genetic diversity of the population. Unexpected events such as forest fires may prompt further monitoring of the population even after the project has been deemed successful. In the case of Belleek, the likelihood of the population persisting in the woodland is strong. The consistent and stable food availability, bolstered by the reliable supplementary feeding provided by the Belleek Forest Enhancement Committee, ensures a stable habitat. Disturbance threats to the habitat are low given the passion of the community for both the amenity of the park and the red squirrel population. The management plan for the woods involves increasing the broadleaf component of the woods (Tiernan et al., 2009), thus enhancing the natural food resources. The spread of the population out of the woods and its continued expansion

indicate the population's abundance, making it less vulnerable during population fluctuations. The genetic diversity of the population is currently under investigation and preliminary results show no significant inbreeding effects. Therefore, no intervention is determined to be necessary at this point in time. Continued monitoring is encouraged in order to ensure a more thorough understanding of the translocated population's long-term sustainability and to track the spread of the population. It is recommended this sustained monitoring incorporates the use of citizen science, given the cost-effectiveness of this technique and high value of the data generated by the public. Public surveys are capable of generating presence data that is more comprehensive than other non-invasive techniques (Goldstein et al., 2014), and local volunteers may be trained in non-invasive monitoring techniques, given the appropriate training (Granroth-Wilding et al., 2017). Specifically, the Belleek Forest Enhancement Committee, which is dedicated to the wellbeing of the red squirrel population within the woods, could play a crucial role in the ongoing monitoring of this population.

In the case of Derryclare, it is unfortunate to note that the red squirrel population has seemingly collapsed to a level below the minimum viable population, a threshold critical for long-term species survival. Addressing this challenge through continued monitoring and remedial measures presents a difficult task, with the effort required appearing to outweigh the potential for success. The continuing habitat loss caused by felling operations, and degradation of the quality of the habitat caused by the replacement of lodgepole pine with Sitka spruce, further exacerbate the issue, creating an environment increasingly unsuitable for red squirrels. However, it is possible that this anticipated replacement will not occur, as additional felling plans have been made to clear fell the majority of coniferous stands in Derryclare. The Wild Western Peatlands project, operated by Coillte Nature, a branch of Coillte, has the objective of restoring Derryclare to a bog landscape. Felling works began in September 2022 and will continue for several years, although the endpoint is unknown. If this project proceeds as planned, only the nature reserve will remain habitable for the red squirrels. The nature reserve has been estimated to be capable of supporting a total of 8 individuals (Poole & Lawton, 2009), which falls below the minimum viable population estimate for red squirrels (Wood et al., 2007). It is also likely that the disturbances caused by these felling operations will negatively affect the population, further reducing their likelihood of survival. It is therefore regrettable to say that the issues facing the Derryclare translocation, namely a deterioration in habitat quality and habitat loss, are insurmountable and will likely result in the extinction of this population. This shift in the woodland's future underscores the importance of stakeholder support in ensuring the success of a translocation. Coillte Nature have balanced the

benefits of continuing their long-term commitment to the red squirrel population against the broader conservation benefits of the bog restoration to Irish wildlife, and have decided to proceed with the latter. While we acknowledge the benefits and practicality of this decision, it is unfortunate for the red squirrel population that these plans are incompatible with their continued presence in the woods.

6.2.2 Habitat quality

The quality of a translocation site plays a pivotal role in the population's ability to survive and thrive. An assessment of the habitat's quality is based on its suitability for the target species. Beyond being of suitable size to maintain a self-sustaining population, the habitat must provide adequate and appropriate food resources, shelter, and breeding sites. The ecological community and inter-species interactions, including competitive and predator-prey relationships should not pose a threat to the survival of the introduced population. The connectivity of the site, with respect to the movement patterns and capability of the target species must be considered. Furthermore, the level of disturbance that the site is subject to, whether human-induced or of natural origin, affects its quality and therefore its suitability. The outcomes of the two translocation projects in this study were largely determined by the quality of their habitats. In Belleek, the population benefitted from a stable 60ha woodland with abundant food resources and continuous canopy cover, resulting in a successful transition into the regulation phase. In Derryclare however, frequent disturbances in the 202ha woodland accompanied by a deterioration of food resource quality created an unstable, fragmented habitat consisting of a substantial proportion of an unfavourable tree species. The population in this site failed to enter the regulation phase and are likely witnessing a population collapse.

Poor habitat quality is a common issue faced by translocations and has been reported to be a leading cause of translocation failures in other species (Bellis et al., 2019; Griffith et al., 1989; Wolf et al., 1996). Poor habitat quality may impact the success of all phases of a translocation. In the establishment phase, a low quality habitat may result in the death or dispersal of the population in the period immediately following their introduction. Death during this period is often caused by predation (Bubac et al., 2019). A lack of refugia and an increased foraging effort have been cited as characteristics of a low quality habitat that are responsible for increased predation (Bennett et al., 2013). The predation of founding animals has been proposed to be preventable if populations were introduced to areas of higher quality (Powell et al., 2012). Additionally, hyperdispersal, defined as the long-distance movement of individuals resulting in their failure to contribute to population establishment (Bilby & Moseby, 2023), poses a serious threat to the success of a translocation by reducing the size of the founding population (Bilby & Moseby, 2023;

Guilbert et al., 2007; Jones et al., 2003; Short & Turner, 2000; Steen, 1994).

Hyperdispersal is often caused by an unsuitable release habitat (Bilby & Moseby, 2023). Hyperdispersal may have occurred in Derryclare, as one individual was never caught following release into the woods (Poole & Lawton, 2009). However, if hyperdispersal did occur, establishment in neighbouring woodlands was not observed. The soft release technique used in this translocation (mean of 46 days in an enclosure) may be responsible for this high site fidelity (Bright & Morris, 1994; Tetzlaff et al., 2019).

The effects of poor quality extend beyond the establishment phase. The success of the translocation during the growth phase may be impacted by a poor quality habitat, owing to its impact on the fitness of individuals (Harig & Fausch, 2002). Increased competition for resources may limit the reproductive capacity of the population and hinder their growth and survival. Additionally, a lack of connectivity in a habitat may prevent the expansion of the population's range, limiting their growth. A deterioration in the quality of the habitat may threaten the success of a translocation in the long-term, affecting the regulation phase as the carrying capacity of the habitat is reduced. Deterioration may occur as a result of human disturbance, natural occurrences or a combination of both factors, exerting pressure on the translocated population.

The deterioration and loss of habitat in Derryclare, combined with the high level of disturbance were major contributing factors to the failure of this translocation. It was revealed by Waters (2012a) that the population had successfully entered the growth phase, characterised by their successful reproduction and range expansion. However, changes in the habitat altered its quality, negatively impacting both the carrying capacity and the actual squirrel abundance. The deterioration of the Derryclare habitat was caused by the natural replacement of lodgepole pine with Sitka spruce, as well as the increased fragmentation created by felling and a fire. The shift in tree species composition has resulted in a substantial loss of the more stable (Broome et al., 2007) and more nutritious (Lurz et al., 2000) crop for the red squirrel population. The current composition of the woodland contains increasingly abundant proportions of a tree species that is known to be less preferable to red squirrels (Gurnell et al., 2004a), and can support lower densities (Lurz et al., 1998). The high level of disturbance at Derryclare, in the form of regular felling and a fire, has likely impacted the population beyond the obvious loss of habitat. The fragmentation caused by these losses has reduced connectivity in the woods, creating a poorer quality habitat. Another byproduct of fragmentation witnessed in Derryclare is the creation of several small patches of woodland, that are unsuitable for habitation due to their size. Red squirrels are rarely found in small patches (Koprowski, 2005), and are believed to require a minimum of 3.5ha to facilitate occupation (Verbeylen

et al., 2003). Therefore, the carrying capacity may be overestimated when based on the overall available area. Other impacts of disturbances include increased vulnerability and stress, impacting fitness (Ewacha et al., 2017), an interruption to the breeding processes, impacting reproductive output (Wilson & Wilson, 1975), displacement, and increased predation risk (Pausas & Parr, 2018). It is therefore likely that regular felling operations, combined with a forest fire impacted the population indirectly, creating an unstable habitat and disturbing an already vulnerable population. It is therefore our recommendation that translocation sites are monitored for changes in habitat quality, and that sites undergo as few alterations as possible.

The outcomes of the translocations at Derryclare and Belleek highlight how the area of the habitat, traditionally thought to be the biggest determinant of success, may in some cases be secondary to the quality of that habitat. The carrying capacity of Derryclare woods is estimated to stand at 65 squirrels, based on a population in a woodland of similar composition. However, it is clear that the woodland cannot actually sustain such a large population, due to its poor quality. Belleek woodland, which is just over a quarter the size of Derryclare, resulted in the more successful outcome, despite its much smaller size. Considering that the ultimate goal of a translocation project is to expand a population's distribution, preventing extinction and restoring ecosystems (Gaywood et al., 2022), and that the ultimate goal of these particular translocations was to restore the red squirrel historical distribution in the west of Ireland, Derryclare stands as a more conventionally favourable choice for the translocation. Its rural setting in Connemara provides ample opportunities for range expansion. Interestingly, it is the urban Belleek population that have demonstrated a substantial range expansion, proving their ability to move through urban fabric, even becoming established in towns. This expansion represents a significant step in the recolonisation of the west of Ireland by red squirrels, which is the overall objective of both these translocations. It is clear in this study that the quality of the habitat rather than the size or location of the woodland was the true determining factor in the success of the translocation and its larger objectives. Therefore, it is crucial that the quality of the habitat is taken into consideration when conducting the habitat assessment of potential translocation sites, as per IUCN guidelines (IUCN/SSC, 2013).

6.2.3 Behaviour

The behaviour of a species is an important consideration when conducting a translocation project (IUCN/SSC, 2013). In depth knowledge on the behavioural aspects of a species' ecology such as their foraging patterns, predator responses, territoriality, social organisation, breeding patterns etc. is crucial for planning a successful translocation. This

knowledge of the species' behaviour will influence the project manager's choice of translocation site (Nafus et al., 2017), the method and timing of release (Garnier et al., 2021; Tavecchia et al., 2009), and the monitoring techniques utilised (Thompson, 2013). Despite these considerations, the nuanced effects of behavioural variation within a population are often overlooked during the planning stages of translocations. Considering that natural selection operates on the level of individuals (Austin et al., 2004; Lomnicki, 1988), it is important to consider the role of personality on the outcome of the translocation. Personality has been recorded to impact key processes such as dispersal (Cooper et al., 2017), responses to novel environments (Perals et al., 2017), and reproductive output (Both et al., 2005), all of which contribute to shaping the overall success or failure of the translocation.

The incorporation of animal personality into conservation management is a relatively new field (Carere & Maestripieri, 2013), having recently been considered in relation to translocation projects (Blumstein & Fernández-Juricic, 2010; Shier, 2016; Sutherland, 1998). Studies have shown that the personality of the founding individuals can impact their survival during the establishment phase, possibly influencing the success of a translocation. For example, in a swift fox (*Vulpes velox*) translocation, foxes that died within 6 months of being released had previously been deemed to be bolder than the cohort that survived past this point (Bremner-Harrison et al., 2004). Similarly, kangaroo rats (*Dipodomys stephensi*) that were categorised as cautious showed greater survival after being translocated compared to those who were bolder (Baker, 2014). Desert tortoises (*Gopherus agassizii*) who exhibited more exploratory personalities experienced higher survival rates following release into the new habitat, due to their increased likelihood of encountering a burrow (Germano et al., 2017). The proportion of these personality types within the founding population has the ability to impact the success of the translocation, by improving initial survival.

Although it is clear that personality affects an individual's survival chances following a translocation, it is unclear whether one specific behavioural type is better suited for post-release survival across all taxa. The axis of personality that is found to have the most significant impact on the survival chances of an individual immediately following a translocation is the shyness/boldness continuum (de Azevedo & Young, 2021; Martínez-Abraín et al., 2022). Generally, individuals who display a shy personality are found to survive for longer following introduction (Bamber et al., 2020; de Azevedo & Young, 2021; Lopes et al., 2017; May et al., 2016), although there are exceptions (Haage et al., 2017; Sinn et al., 2014). Shy animals are more likely to avoid risk, thereby reducing their chances of conflict, injury, and death (Boon et al., 2007). Additionally, shy animals have

been found to exhibit reduced dispersal tendencies (Cote et al., 2010), lowering the likelihood of hyperdispersal from the introduction site and improving establishment success. Bold animals tend to have larger home ranges (Bombieri et al., 2021), and exhibit greater risk taking behaviour, thus lowering their survival chances (Bremner-Harrison et al., 2004; Smith & Blumstein, 2008). However, bold animals have also been shown to have greater reproductive success compared to shy animals (Réale et al., 2000; Schuett et al., 2010), as noted in the Belleek female population. The trade-off between longevity and reproduction is well documented in the literature (Badyaev & Ghalambor, 2001; Biro et al., 2006; Biro & Stamps, 2008; Descamps et al., 2006; McAdam et al., 2007; Smith & Blumstein, 2008). The higher dispersal rates of bold animals also leads to a greater range expansion of translocated populations (Martínez-Abraín et al., 2022), which is advantageous during the growth phase of the translocation. Therefore, it has been suggested that a best practice approach involves a two stage release program, beginning with the initial release of shy animals, before later introducing bold animals to the population (Bamber et al., 2020; de Azevedo & Young, 2021). The initial introduction of shy animals enhances the likelihood of their continued presence and survival, thereby promoting successful establishment. Subsequently releasing bold animals during the following breeding season then contributes to the growth and expansion of the population during the growth phase. The authors conclude that a two-stage release program may result in the longer survival of the population, and a more successful reintroduction.

When choosing animals for release during a translocation it is particularly important that the resulting, final population consists of a mixture of personalities, rather than containing only shy or only bold individuals. Diversity within the personalities of the population has been demonstrated to be as important as genetic diversity for the survival of the translocated population (Cordero-Rivera, 2017; van Oers & Mueller, 2010). Behavioural syndromes that provide the greatest fitness advantage have been shown to alter over time depending on the environmental conditions (Dingemanse et al., 2004; Dingemanse & Réale, 2005; Sinn et al., 2010). For this reason, as many individuals should be released into a population as possible (Merrick & Koprowski, 2017b), to allow for greater adaptations to shifting environmental and population conditions (Wolf et al., 2007). Even in the stable habitat of Belleek, a mixture of personalities and life history strategies were observed within the population. The overall health of this population highlights the natural advantages of such behavioural diversity, which translocation managers should aim to replicate in their resulting populations.

Ideally, animals should be translocated from wild populations, rather than ones that were captive bred. Captive breeding programmes aim to preserve as much behavioural

diversity as possible (Princee, 2016). However, this result is not always achieved. The environmental conditions of captivity have been observed to confer advantages for certain personality types, leading to differing success (Mellen, 1991; Watters & Powell, 2012), and a selection for more docile and bold animals (McDougall et al., 2006). As discussed above, the trait of boldness is often disadvantageous for the survival of the founding population. Additionally, the inexperienced nature of captive-bred animals makes them particularly susceptible to predation, starvation and being outcompeted in the wild (Jule et al., 2008). Consequentially, captive-bred animals may be less favourable as translocation candidates, unless behavioural heterogeneity is maintained. Indeed, in a study on the translocation of both wild and captive-bred falcons (*Falco femoralis septentrionalis*), the wild falcon cohort had significantly higher survival and recruitment rates compared to their captive-bred counterparts (Brown et al., 2006). The disadvantageous effects of captive breeding may be offset by the provision of enrichment and diverse rearing habitats (Watters & Meehan, 2007). Animals may be trained on survival skills through enrichment practices, for example, by providing realistic foraging opportunities rather than making food readily available (Shepherdson, 1994). Additionally, antipredator training, which conditions animals to exhibit aversive behaviour towards predators, has been found to generally improve post-release survival (Tetzlaff et al., 2019).

Behavioural screening of founding individuals did not occur for either the Derryclare or Belleek population, and yet neither population collapsed during the establishment phase. However, the high failure rate of translocations is well-documented (Berger-Tal et al., 2020; Bubac et al., 2019; Griffith et al., 1989; Wolf et al., 1996, also, see case studies in Soorae, 2018 and for red squirrel translocations see Kenward & Hodder, 1998 and Lawton et al., 2015b), particularly in the immediate period following release (Novak et al., 2021). Notably, behaviour issues have been identified as one of the leading reasons for translocation failures in a review by Berger-Tal et al. (2020). The success of the establishment phase is largely controlled by the behaviour of individuals (Berger-Tal & Saltz, 2016), underscoring the importance of a comprehensive understanding of the effects of behavioural variation on the survival of released individuals. Behavioural monitoring of potential founders prior to release is recommended for several reasons. While this process may prove time-consuming and challenging in wild populations, it may improve the success of the translocation throughout all three phases, and will provide valuable insights into the impact of individual personalities on post-release survival, which may inform future projects. Understanding the personalities of potential founders allows for the selection of the most appropriate candidates, such as shy animals in the initial stages to enhance establishment, followed by the introduction of bold animals to increase

reproductive output and behavioural diversity. By assessing animals individually, it becomes possible to ensure behavioural diversity within the translocated population, thereby enhancing their ability to adapt to changing conditions and promoting the longevity of the population.

6.3 The future of red squirrels in Ireland

The resurgence of the pine marten in Ireland has allowed for the recovery of the red squirrel (Sheehy & Lawton, 2014). The increased predation on the grey squirrel by the pine marten, facilitated by a predator naivety in the grey squirrel (Sheehy et al., 2018; Twining et al., 2020a) has led to the decline and disappearance of the grey squirrel in areas where it was previously established (Lawton et al., 2019). The recovery of the red squirrel within the range of the pine marten has been facilitated by the inherent antipredator response of the red squirrel, hypothesised to originate from their shared evolutionary history (Twining et al., 2020, also see chapter 5). However, the red squirrel's distribution in the west remains relatively patchy due to fragmentation and a lack of suitable corridors (Flaherty & Lawton, 2019; Waters, 2012b) (Figure 6.1). For this reason, we recommend that the expansion of the Belleek population is monitored to give insights into the use of corridors in this region. The grey squirrel is now primarily found in urban regions such as Dublin and Belfast, due to the absence of the pine marten in these areas (Lawton et al., 2019). Despite the apparent positive outcome of the decline of the grey squirrel, it's essential to recognise that the threat posed by the grey squirrels may not be permanently alleviated.

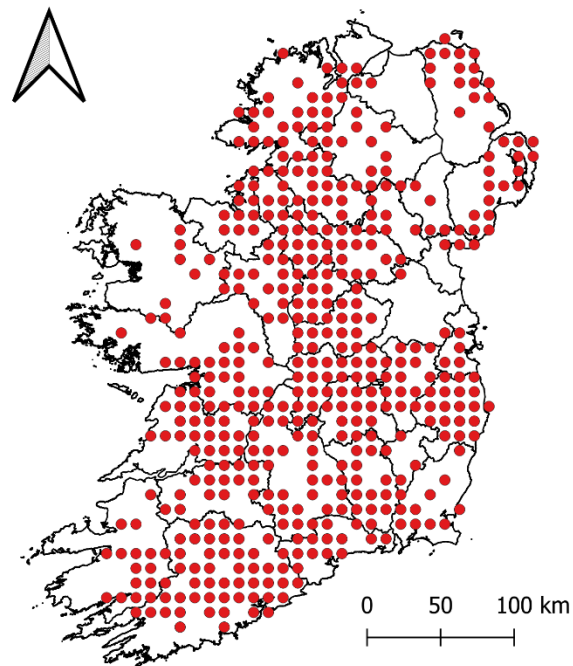


Figure 6.1 The distribution of red squirrels in Ireland according to the All-Ireland Squirrel and Pine Marten Survey of 2019 (Lawton et al., 2019). The distribution of red squirrels in the west remains relatively patchy.

A learned recognition of predators in previously naïve prey has been demonstrated to be inducible through experience with the predator (Banks & Dickman, 2007; Kelley & Magurran, 2003; Steindler et al., 2020). For example, the bush rat (*Rattus fuscipes*) has developed an antipredator response to dogs (*Canis lupus familiaris*), despite their relatively recent introduction to Australia ~150 years ago (Carthey & Banks, 2016). However, this rapid response is hypothesised to have been facilitated by prior experience with the close relative of the dog, the dingo (*Canis lupus dingo*). It is possible that the dissimilarity of the cues associated with the pine marten and those associated with the grey squirrels natural predators, primarily raptors, will inhibit the ability of the grey squirrel to recognise the threat (Carthey & Blumstein, 2018a; Carthey et al., 2017; Steindler et al., 2020). The escape strategy that is most effective for aerial predation events, such as hiding under the cover of vegetation (Wywiałowski, 1987), may not be effective when faced with the terrestrial pine marten. Additionally, grey squirrels and pine marten occupy the same habitat for only a relatively brief period before the grey squirrel population disappears, limiting their opportunity for adaptation. Therefore, it is uncertain how quickly grey squirrels might learn to recognise the danger posed by pine martens, although such an adaptation is not impossible. If the grey squirrel was to lose its predator naivety, the

current barrier inhibiting their expansion would disappear. This could lead to their recolonization of the rest of Ireland, posing a renewed threat to red squirrels. However, it is likely that the barrier of the River Shannon and surrounding unsuitable habitat, which has historically prevented the establishment of the grey squirrel in the west of Ireland (Carey et al., 2007; Lawton et al., 2015a; O'Teangana et al., 2000), would continue to prevent expansion to this region. The Belleek population, situated in the west of Ireland would therefore act as a stronghold for red squirrels in Ireland, highlighting the importance of the success of this translocation.

While the overall effect of the resurgence of the pine marten in Ireland has clearly been beneficial for the red squirrel, it may have adverse effects on individuals or specific populations. As the native predator of the red squirrel, the pine marten's increased presence may negatively affect individuals both directly and indirectly. Increased likelihood of mortality of the red squirrel by the pine marten is an obvious drawback of this resurgence (Sheehy et al., 2014; Twining et al., 2020b). While not detrimental to the red squirrel in the same manner as the grey squirrel, as evidenced by their expanded range (Lawton et al., 2019), the increasing presence of a predator is likely to induce a greater stress response in individuals (Gaynor et al., 2019), creating a landscape of fear (Altendorf et al., 2001). Fear may be expressed physiologically (Clinchy et al., 2013), or behaviourally in the form of increased vigilance (Welp et al., 2004), a decrease in foraging effort (Brown, 1988) and altered space use patterns (Gaynor et al., 2019), among other responses. Increased vigilance has been recorded in red squirrels in response to recent pine marten presence (chapter 5). Additionally, Twining et al. (2020a) found that red squirrels decreased their feeding activity, avoided feeders and displayed increased vigilance following a simulation of pine marten presence. This adverse effect on the foraging opportunities of red squirrels, combined with the physiological stress effects of increased predation risk may negatively impact their fitness (Clinchy et al., 2013).

The altered behaviour of the red squirrel in a habitat containing the pine marten may affect the effectiveness of monitoring efforts. Baiting is a common practice in both non-invasive and invasive monitoring techniques to attract target species to monitoring devices, such as traps or hairtubes. However, bait is frequently discovered and consumed by individuals of other species, including predators, when there is an overlap in their diets. The presence of a predator's cue on a baited device has been demonstrated to modify the prey species' utilisation of that device (Shrader et al., 2008; Twining et al., 2020a; Willems & Hill, 2009), resulting in a reduced detectability. In this study, the use of both baited hairtubes and traps by pine martens was documented using trail cameras (Chapter 5), live trapping (Chapter 3), and scat presence (personal observation). This use was

particularly pronounced in Derryclare. When access to bait was limited for the pine marten in Derryclare, there was an increase in red squirrel trapping efficiency. While additional research is necessary to validate these findings, they do suggest that the use of baited equipment by pine martens may have hindered monitoring efficiency. This observation highlights the complexity of ecological interactions and the importance of incorporating this understanding into the design and implementation of monitoring programmes.

While the presence of the pine marten has been shown to allow for the recovery of the red squirrel on a landscape scale, it has also been observed to have a negative effect on the occurrence of the red squirrel in non-native commercial conifer plantations (Twining et al., 2022b). The authors hypothesise that a lack of biodiversity in these plantations limits the prey availability for pine marten, necessitating the predation of red squirrels. Pine martens have been observed to exhibit a higher predation rate on murine rodents when the rodent population levels are elevated, opting not to prey on red squirrels during such periods (Zheltukhin et al., 2017), supporting this hypothesis. Derryclare is a non-native commercial conifer plantation, with a substantial pine marten population (chapter 5), however, predation was not observed to inhibit the establishment or initial growth of the red squirrel population, meaning that pine marten presence is unlikely to be a leading cause of their decline. Nonetheless, considering the negative impact of pine marten presence on red squirrel abundance in non-native commercial conifer plantations (Twining et al., 2022b), along with other drawbacks associated with this type of habitat, such as a lack of tree species diversity and the potential for disturbances and habitat loss, we recommend opting for alternative habitats in future red squirrel translocations.

Despite these fitness implications, monitoring challenges and negative impact on red squirrel occurrence in non-native commercial conifer habitats, the resurgence of the pine marten in Ireland has proven to clearly be beneficial for the red squirrel population. Indeed, it is possible that the red squirrel's recovery has negated the need for further translocations of this species in Ireland in the future. The recovery of the pine marten in Ireland has demonstrated the utility of lawmaking in conservation efforts, as well as the benefits of conserving nature species. The pine marten became protected in Ireland under the terms of the Wildlife Act in 1976, and in Northern Ireland under the Wildlife Order of 1985. This protection has created a cascading effect that has led to the red squirrel recovery. An increased pine marten abundance has been observed in countries such as Italy (Balestrieri et al., 2016), where red squirrel populations are endangered, and grey squirrel populations are abundant. However, their distributions remain sparse, as does the distribution of the red squirrel (Wauters et al., 2023). In Scotland, pine marten abundance has increased, (Sainsbury et al., 2019), positively affecting the red squirrel

population (Sheehy et al., 2018). Recently, pine marten translocations have been undertaken in Britain (Macpherson & Wright, 2021; McNicol et al., 2020), in an attempt to bolster population numbers, and reduce grey squirrel abundance. However, despite these reintroductions and concerted grey squirrel culling efforts, the red squirrel remains endangered in these areas (Wauters et al., 2023). This highlights the importance of the red squirrel stronghold in Ireland and its significance in contributing to the conservation and protection of this endangered species.

6.4 Conclusion

This project offers various insights into the factors affecting the success or failure of a translocation effort. By investigating the outcomes of two red squirrel translocations in the west of Ireland, it was possible to analyse the factors that contributed to the success of the Belleek translocation, in contrast to the failure of the Derryclare translocation. In Derryclare, the frequent disturbances, habitat loss and poor quality habitat were the primary reasons for their decline. In Belleek, the high food availability and stable environment contributed to their success. Through these investigations we have identified several important aspects of this type of conservation effort that merit emphasis. Firstly, we have shown the importance of post-release monitoring in assessing the true outcome of the project in order to determine and implement appropriate mitigation measures. We have suggested a framework for future translocation projects by which the success of the project can be measured, standardising assessments of translocation outcomes and encouraging long-term monitoring. Secondly, we have highlighted the importance of the role of habitat quality in the outcome of the translocation. In particular, we emphasise how the area of the translocation site is sometimes secondary to the quality of the translocation site. Finally, we show the importance of considering the behaviour of individuals within the translocated population, particularly in the choice of founding individuals. We recommend that future translocations conduct behavioural screening in order to contribute to our understanding of the impact of behaviour on translocation outcomes.

We recommend that future Irish red squirrel conservation efforts focus on the expansion of the red squirrel's range, particularly in the west of Ireland where it is patchiest. This approach includes but is not limited to: the establishment of corridors to facilitate dispersal to suitable habitats, the creation of appropriate green spaces in urban areas, and a continued monitoring of the distribution of both squirrel species. Red squirrel dispersal in the west is hindered by factors such as fragmentation, a lack of dispersal routes, and uninhabitable land. Less than 13% of Connacht is forested, and current forestry is highly fragmented (Carey et al., 2007). Additionally, hedgerows, which act as corridors between

woodlands (Wauters et al., 1994a) are scarce in both Mayo (Foulkes, 2007) and west Galway (Foulkes, 2006). Blanket bog, which is uninhabitable for red squirrels, is a prominent feature in the landscape of the west of Ireland. We recommend identifying dispersal woodlands based on suitability and proximity to existing populations and establishing corridors to connect these sites and facilitate dispersal. Exploring the expansion of red squirrel populations, with a specific focus on understanding their movement patterns and identifying barriers, can unveil valuable insights into potential corridors. We also recommend that more green spaces are created within built up areas, considering the adaptability of red squirrels to the presence of humans and human activity (Fingland et al., 2022; Jokimäki et al., 2017; Krauze-Gryz et al., 2021), as witnessed in the Belleek population. Additionally, it is crucial to monitor the distribution of the grey squirrel for signs of recolonization and observe its response to the pine marten to identify early indications of learned antipredator behaviour. By embracing these strategies, we aspire to safeguard the future of the red squirrel in Ireland and contribute to the broader conservation effort for this species.

7 References

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