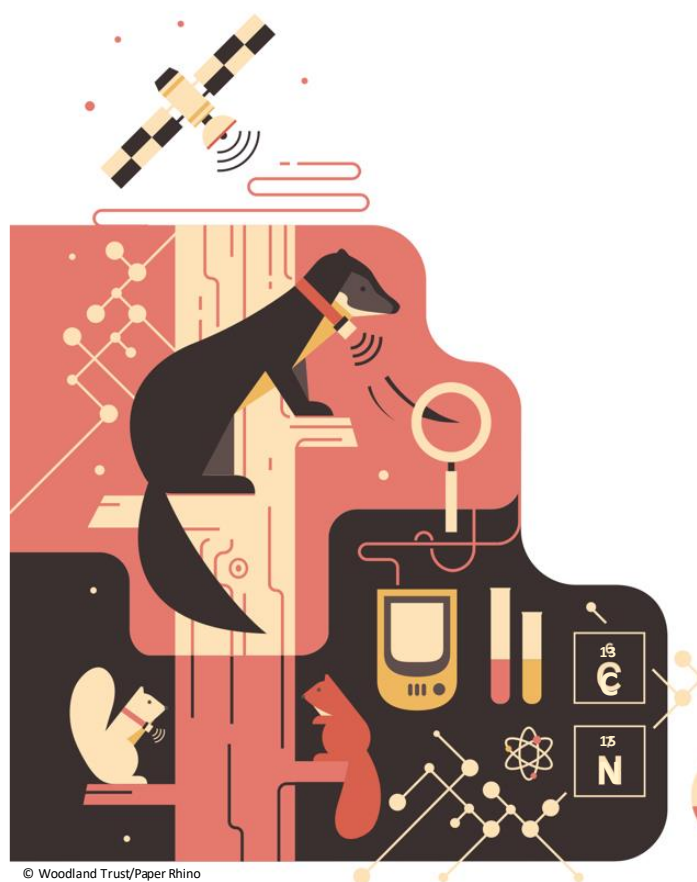


# Ecology of translocated pine martens *Martes martes* and their impacts on grey squirrels *Sciurus carolinensis*

Submitted by Catherine M McNicol to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, May 2019.



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(Signature).....



**“And into the forest I go, to  
lose my mind and find my  
soul”**

*John Muir*



## Abstract

The rate of biodiversity loss has been increasing since the beginning of the Anthropocene, driven by climate change, human population expansion and environmental degradation. Consequently, ecosystems have become simplified through the loss of important processes and species. Ecological restoration aims to reverse such changes through reinstating habitats, native species and their associated relationships, as well as removing invasive, non-native species. One strategy to restore ecological function is through the re-establishment of top-down processes driven by predators. The cascading effects of these predators, through direct predation and the fear they induce in prey can restore predator-prey dynamics in a disrupted food web.

In this thesis, I investigate the restoration of a native and recovering predator, the pine marten *Martes martes*, with particular focus on its ecology and behaviour after a translocation event from Scotland to Wales. Subsequently, I assess its impact on the behaviour of one of its prey species, the invasive, non-native grey squirrel *Sciurus carolinensis* to better understand the relationship between these two species.

I first introduce predator restoration using translocation in a project that aims to reintroduce and restore the native pine marten. I demonstrate that the phases of post-translocation movement comprise a period of 'exploration' followed by 'settlement' in all individuals, however the extent and duration of these movements differ between release groups. I show that conspecific presence is important in site fidelity and the resulting habitat in which martens establish themselves. I then investigate the diet of translocated martens at a population and individual level, before and after translocation. I reveal that pine martens consume a more diverse diet post-translocation, which incorporates grey squirrels, a prey item not found in their source sites in Scotland. Furthermore I document a degree of dietary specialisation within individuals, which is maintained relative to others after translocation. This suggests pine martens are facultative specialists with dietary preferences that they are able to supplement with readily available prey groups, enhancing their probability of survival after translocation.

Next, I address the impact of translocated pine martens on grey squirrel space use and survival. Grey squirrel range size and daily distance travelled was found to increase with increasing marten exposure. However, an impact on grey squirrel survival and range location was not found within the timeframe of this study. I then investigated the role that fear plays in the relationship between pine martens and grey squirrels. Using feeding experiments, I document a reduced volume of food consumed by squirrels in woodlands containing pine martens, suggesting that squirrels 'give-up' foraging earlier under such conditions. This suggests that squirrels display a fear-mediated response to pine marten risk, which in time may be detrimental to grey squirrel fitness. I consider the role of predation and fear in predator-prey dynamics and its importance in species management.

Finally I conclude the key findings of this thesis with regards to pine marten and grey squirrel management in the UK, as well as their contribution to carnivore restoration and species management strategies. This work identifies that social structure and dietary flexibility are key considerations for predator restoration projects. Furthermore, the cascading effects of predators can play a potential role in the management of invasive non-native species, which may be more economically and socially acceptable than current strategies. This work highlights the importance of studying ecological processes underlying landscape-scale patterns to better inform the management of native and non-native species alike.

## Acknowledgements

The road has not been a straight or an easy one but I would like to thank my supervisors Robbie McDonald and Stuart Bearhop for setting me on the right path when times were tough and I couldn't find my way. Together you have tested my resilience and helped me to remember the bigger picture when I have felt bogged down in details. I hope I leave you now with a better sense of direction than when I began. I am also grateful to my co-supervisors Jenny Macpherson (Vincent Wildlife Trust) and Robin Gill (Forest Research) who have been brilliant sources of knowledge and advice. I look forward to continuing working with you all.

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### *Authors declaration for co-authored manuscripts*

Chapters 2,3,4 and 5 have been submitted or written for publication as co-authored papers. I developed the direction and research design for Chapters 2,3,4 and 5 in conjunction with Robbie McDonald, Stuart Bearhop, Jenny Macpherson and Robin Gill.

For Chapters 2 and 4, pine marten telemetry data were collected by David Bavin, Josie Bridges, Alastair Willcox and Jenny Macpherson from the Vincent Wildlife Trust with assistance from volunteers.

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For Chapter 4, I carried out squirrel trapping and collaring with assistance from Mark Ferryman from Forest Research.

For Chapter 5, I collected all field data with assistance from MSc students Emily Strong and Nick Burnham.

I conducted all of the analyses, with advice from Cecily Goodwin, Daniel Padfield and Matthew Silk. I wrote all manuscripts, then amended and revised them in response to comments, suggestions and advice from Robbie McDonald and Stuart Bearhop and other co-authors.

Cover image of this thesis was provided by the Woodland Trust and © Paper Rhino. Other illustrations in this thesis are by Catherine M McNicol & Tanya Venture.



## Chapter 1

# **Introduction**

## Chapter 1: Introduction

### ***Ecosystem restoration***

Since the beginning of the Anthropocene, rates of global biodiversity loss have been increasing (Barnosky et al. 2004; Christopher et al. 2014; Rounsevell et al. 2018). As a result, important ecological processes have been lost and ecosystems have become simplified or dramatically altered, requiring increased management and monitoring (Estes et al. 2011; Svenning et al. 2016). In recent decades, a solution to reduce the need for ongoing human intervention has been to reinstate natural processes and re-establish self-sustaining ecosystems. This is broadly known as ecological restoration (Jackson & Hobbs 2009).

Ecological restoration is defined as ‘the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed’ (SER 2004). The primary aim of restoration is to return environments to a ‘pre-disturbance’ state, often through reinstating biotic conditions, which particular target species require to thrive (Miller & Hobbs 2007; Sandom et al. 2013). However, with an ever-shifting baseline and a history of environmental manipulation by humans, the ‘natural’ state of an ecosystem can vary depending on what point in history is perceived to be pre-disturbance (Jackson & Hobbs 2009). The time period to which ecosystems should be restored, and what is truly ‘natural’ remains a contentious issue (Jackson & Hobbs 2009; Jørgensen 2015). However, there is agreement that restoration should consider entire ecosystems and the processes that help to sustain them (Atkinson 2001). Ecological restoration therefore exists as a spectrum (Jørgensen 2015), from passive restoration, where there is minimal human interference (Höchtel et al. 2005; Jørgensen 2015; Navarro & Pereira 2015), to the managed introduction of non-native taxa to fill the ecological niches of extinct species (ecological replacement; Hansen 2008). Since the late 1980s, ecological restoration has increasingly been referred to as ‘rewilding’ (Soulé & Noss 1998). A term, which, in its most literal sense, means ‘to make wild again’ (Jørgensen 2015). However, this word has been interpreted in a multitude of ways over time, varying in scale, scope and predicted timelines (Jørgensen 2015; Prior & Ward 2016).



### *Rewilding*

The model for rewilding was initially centred on the three main concepts; cores, corridors and carnivores (Soulé & Noss 1998) and primarily focussed on 'restoring the big wilderness based on the regulatory roles of predators' (Soulé & Noss 1998). Rewilding in its current state is primarily focussed on keystone species (Sandom et al. 2013) and their function as ecosystem engineers (Paine 1969; Hastings et al. 2007), with less emphasis on cores and corridors (Jørgensen 2015). Although occurring in disproportionately small numbers in relation to other species within a food web, keystone species, particularly large predators, can have significant impacts on entire ecosystems and their function (Donlan et al. 2006; Sandom et al. 2013). These impacts are often manifest as cascading effects (Terborgh et al. 1999; Estes et al. 2011), from the alteration of species interactions and population numbers, to changes in vegetation structure and soil nutrient levels (Estes et al. 2011). In degraded systems, restoring processes that are driven from the top-down can enable the re-establishment of complete food webs and predator-prey cycles that aid population control and enhance biodiversity (Estes et al. 2011; Svenning et al. 2016). If a natural state of predation and population regulation is attained, the need for human involvement and the resulting economic costs could be much reduced. However, for rewilding to be successful, a thorough understanding of ecological processes and species interactions is required (Sandom et al. 2013). These processes can manifest differently across spatial and temporal scales, resulting in a complex array of relationships (Sandom et al. 2013).

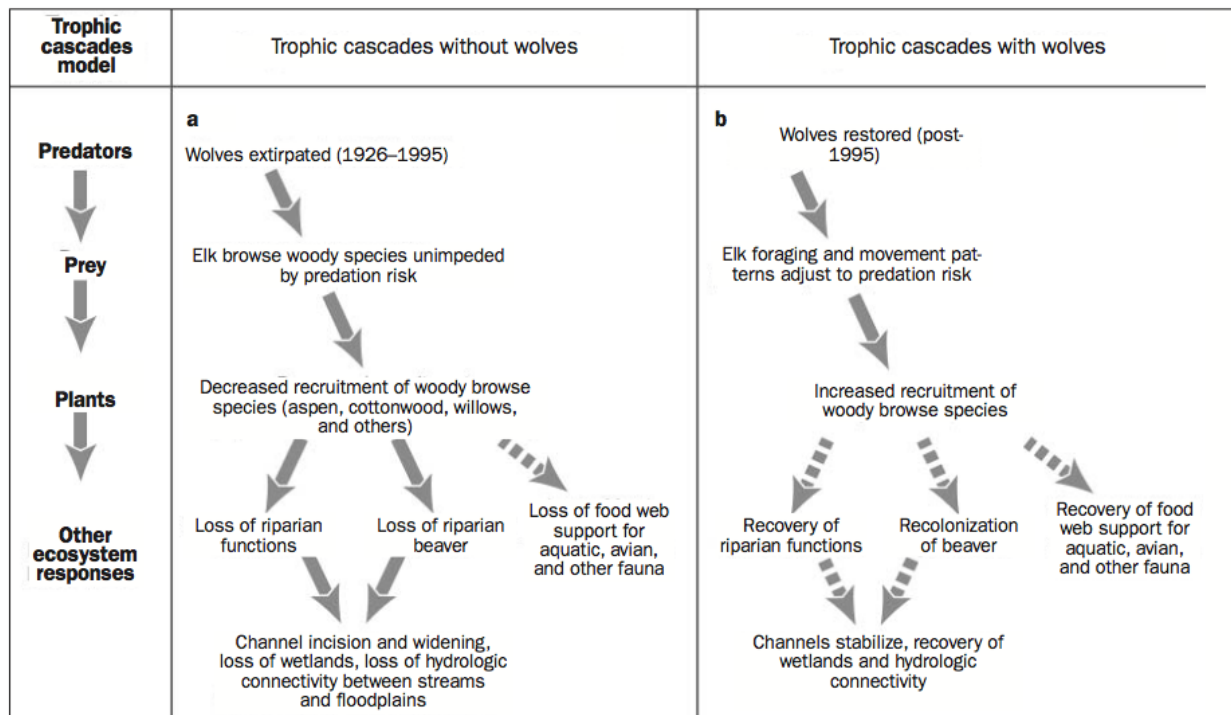
### *Predator restoration & cascading effects*

The restoration of predator populations is often the primary approach for rewilding projects (Seddon 2010). This can be achieved through augmentation of depleted populations (re-stocking or reinforcement; IUCN/SSC 2013) or through the release of wild-caught or captive-bred animals into regions of their historic range (reintroduction; IUCN/SSC 2013). Both approaches aim to create viable, self-sustaining populations (Seddon 2010). The top-down effects of restoring these predator populations often result in regulating the density and behaviour of species at lower trophic levels, whether these are herbivores and/or mesopredators (Svenning et al. 2016), through mechanisms including predation, fear and competition. The most well-known,

although contentious, example of rewilding and the associated trophic cascades is that of the restoration of grey wolves *Canis lupus* to Yellowstone National Park (Fig.1.1). The absence of these native carnivores for 70 years had resulted in largely unregulated numbers and movement of elk *Cervus elaphus* populations, whose browsing had negatively affected aspen and cottonwood *Populus* spp. recruitment. After their reintroduction in 1995, the landscape scale impacts of wolves on elk were first documented 5 years later, indicating the potential role they may have in ecosystem restoration (Fig. 1.1; Ripple et al. 2001). Elk distribution and behaviour was altered such that they remained in open areas, away from aspen saplings, to be able better to detect approaching predators (Ripple et al. 2001). Such restoration effects became evident in following years as saplings were allowed to escape browser suppression and develop into trees (Ripple & Beschta 2003, 2004). The processes underlying such changes were then investigated, revealing that a combination of lethal and non-lethal effects were at play, establishing the existence of a 'landscape of fear' (Halofsky & Ripple 2008; Laundré et al. 2010). The cascading effects of wolves on the overall ecosystem are still being studied, revealing indirect effects of wolves on other species such as beavers *Castor canadensis* through an increase in willow *Salix* spp. communities (Ripple & Beschta 2012), grizzly bears *Ursus arctos horribilis* through an increase in serviceberry *Amelanchier alnifolia* shrubs (Ripple et al. 2014) and red foxes *Vulpes vulpes* through interactions with coyotes *Canis latrans* (Newsome & Ripple 2015).

Predator restoration and the resultant top-down effects have also been demonstrated in other ecosystems. Re-introduction of Eurasian lynx *Lynx lynx* has shown such an effect in Fennoscandia, resulting in large mesopredator suppression and enabling the recovery of smaller mesopredators and black grouse *Lyrurus tetrix* (Ludwig 2007; Ritchie et al. 2012). In arid Australia, the loss of the dingo *Canis lupus dingo*, a top predator, has been associated with the increase of invasive mesopredators and the resulting decline of native mammals (Letnic et al. 2012). Restoration of dingo populations has thus been suggested as a strategy to control invasive red fox and feral cat *Felis catus* populations, which in turn could aid native mammal and vegetation recovery (Letnic et al. 2012). Such predator reintroduction and recovery is not limited to terrestrial mammals and has been undertaken with numerous birds of prey. Through conservation efforts, white-tailed eagle *Haliaeetus albicilla* populations have been able

to recover in the archipelagos of Finland. Fear of predation by eagles has had knock-on effects on invasive American mink *Neovison vison* found there, leading to reduced movement and associated reduction in predation pressure on native species at lower trophic levels (Salo et al. 2008; Ritchie et al. 2012).



**Figure 1.1. Trophic interactions with and without predators in northern ecosystems of Yellowstone National Park** where a) shows the system when wolves had been extirpated (1926-1995) and b) shows the system after wolf recovery (1995 onwards). Solid arrows indicate documented responses, dashed arrows indicate predicted or inferred responses. Figure from Ripple & Beschta (2004).

Although apex predators are often the primary focus of reintroductions, particularly with regards to reinstating trophic cascades and controlling smaller predators and herbivores, the recovery of smaller mesopredators (predators weighing <15kg) has also been advantageous to ecological processes. The restoration of sea otter *Enhydra lutris* populations in North America has enabled the recovery of kelp beds and their associated fauna through the depredation of grazing sea urchins *Mesocentrotus franciscanus* (Estes & Palmisano 1974). Mesopredators are often found in a higher abundance than apex predators, but due to their small size and diverse ecology their role in ecological processes is frequently overlooked (Roemer et al. 2009). In the absence of apex predators, mesopredators ascend to an apex position, however their

ecology and impact can be substantially different to that of their predecessors (Roemer et al. 2009). These species often demonstrate greater dietary flexibility than apex predators, resulting in more complex ecological interactions and cascading effects than experienced in communities structured by apex-predators.

### *The landscape of fear*

It is clear that the impacts of predators extend beyond the straightforward effects of predation, and the restoration of top predators or keystone species can alter the roles and importance of other predators and prey animals in a system (Ritchie et al. 2012). Alongside the lethal effects of predators on their prey, non-lethal impacts, such as the creation of a 'landscape of fear' can have a multitude of consequences for the surrounding ecosystem. The landscape of fear is a conceptual landscape perceived by prey, comprising areas of high and low predation risk. The way in which prey animals perceive and respond to this risk within the landscape can alter the physical environment in a multitude of ways. With this in mind, the restoration of predation risk might be used as a tool in conservation to manage populations of species that are over-abundant or deemed to be pests (Estes & Palmisano 1974; Salo et al. 2010; Letnic et al. 2012; Suraci et al. 2016). This 'biological control' is, in essence, part of a trophic cascade and if these top-down effects of fear and predation are reinstated, they might help re-shape and restore ecosystems. Therefore, not only the species, but the density, social structure and context of predator reintroductions must be thoroughly considered prior to their implementation (Ritchie et al. 2012). These factors may influence the strength of the reintroduced predators' impact and the success of their reintroduction.

### *Reintroduction failures*

For every successful reintroduction, there are numerous failed attempts, which often go unreported in scientific literature (Fischer & Lindenmayer 2000; Armstrong & Seddon 2008). Failure has been attributed to inadequate translocation methods (Oro et al. 2011), insufficient numbers of individuals being translocated (Fischer & Lindenmayer 2000; Armstrong & Seddon 2008), failure to remove the cause of the initial species decline (Bright 2000), predation (Moseby et al. 2011), unsuitable habitat, and long-distance dispersal from release sites (Armstrong & Seddon 2008). The role

of social context, with regards to humans, in reintroduction projects is also being acknowledged as more central to restoration success than ever before (Armstrong & Seddon 2008; Sandom et al. 2013). Without stakeholder engagement, social feasibility assessment and effective communication, the introduction of predators can lead to social conflicts (O'Rourke 2014). This can also lead to reintroduction failure through hunting or persecution of reintroduced species (Davies & Du Toit 2004) and overall lack of support for the reintroduction project (Graham et al. 2005). There is therefore a degree of risk accompanying the introduction of a species. However, the return of a native predator that had declined as a result of human influence is typically considered to be a relatively low threat due to evidence that it had previously co-existed with humans in the region (Wolf et al. 1996). The historic presence of the species would also suggest the habitat and prey base is appropriate for species persistence and establishment. Therefore, with an aim to reinstating self-sustaining ecosystems, native species restoration is an attractive and potentially viable option.

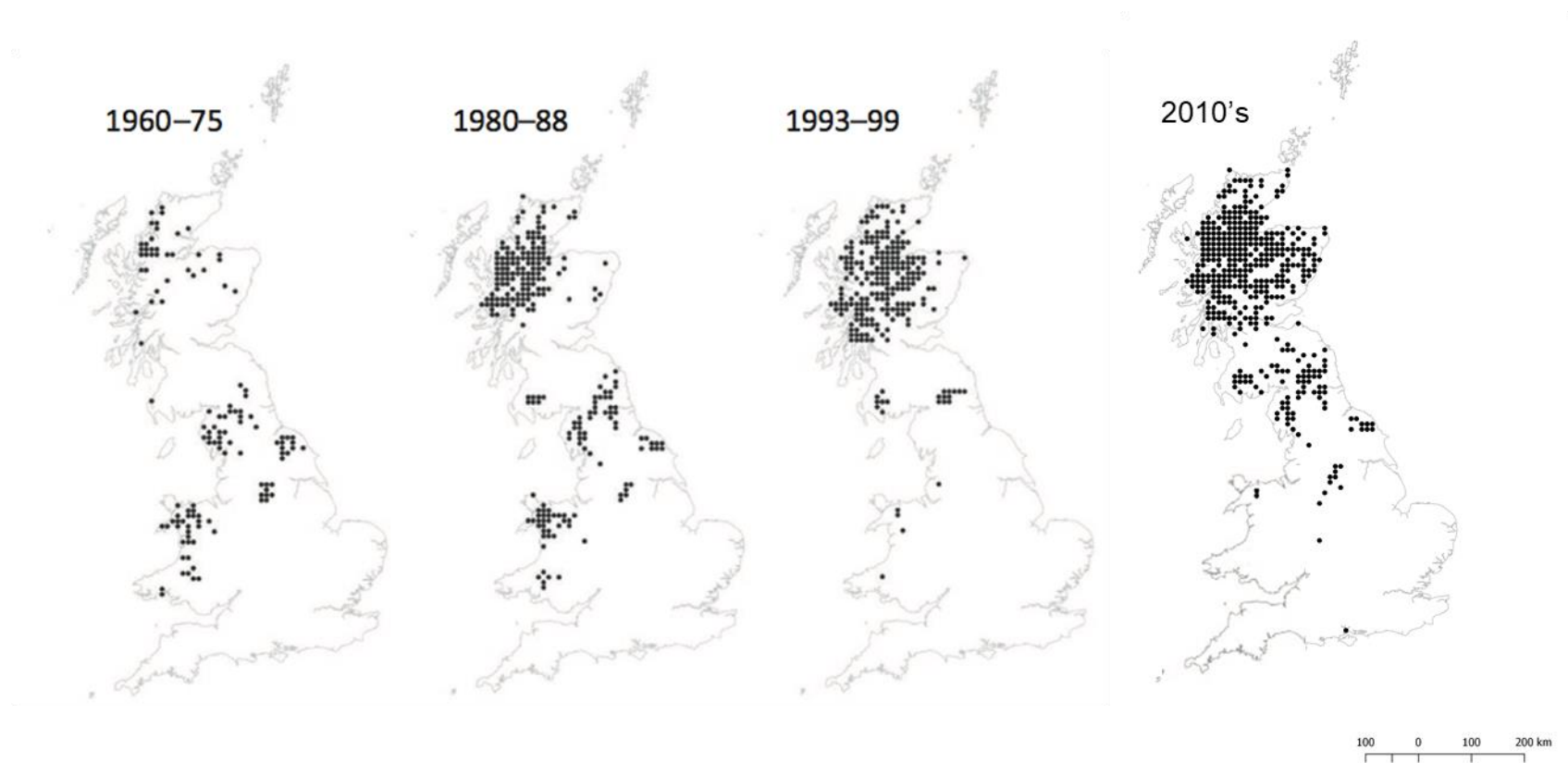
### ***UK species restoration & recovery***

In recent years, species restoration in the UK has been undertaken through official means, however there is a history of restoration actions, particularly with regard to carnivores and other medium-sized mammals, that has occurred on an ad-hoc basis, sometimes undertaken by enthusiasts. This has resulted in the sporadic appearance of small numbers of pine martens *Martes martes*, polecats *Mustela putorius* (Birks 2008; Sainsbury et al. 2019) and beavers *Castor fiber* (Crowley et al. 2017) outside of their current ranges. Although some of these releases have resulted in the local establishment of animals, such as polecats in Cumbria and Argyll (Birks 2015) and, more recently, beavers in Devon (Crowley et al. 2017) and Tayside (Campbell et al. 2012), the long-term success of these reintroductions has generally been poor. Notwithstanding these interventions, the recovery of many UK carnivore populations has been occurring naturally. Native carnivores experienced dramatic declines throughout the 18<sup>th</sup> and 19<sup>th</sup> century as a result of predator control, hunting and habitat loss (Langley & Yalden 1977; Sainsbury et al. 2019). Since the late 1900s, following increased legal protection, changes in management practices, reduction in environmental pollutants, species conservation and public support, many species

have shown signs of recovery (Sainsbury et al. 2019). Since the 1970s, native mesocarnivores, particularly the polecat, badger *Meles meles*, otter *Lutra lutra* and pine marten, have shown rapid signs of population recovery (Sainsbury et al. 2019).

### *The pine marten*

Of these mustelid carnivores, the pine marten has the most limited distribution and, although expanding from its strongholds in the Scottish Highlands, in 2015 this species was still restricted in its distribution in England and Wales with very few, low density populations only existing in Northumberland (Fig. 1.2.; Croose et al. 2013). The latter population is likely a result of a combination of spread from reintroductions in Galloway in the 1980s (Shaw & Livingstone 1992), releases of rehabilitated animals in the Borders and potential relict populations in Northumberland and the Borders. However, despite recurring surveys (reviewed by Sainsbury et al. 2019), there has been little evidence of substantial marten numbers in England or Wales. The further expansion of the species' native range in Scotland is thought to be constrained by the relatively slow life history of martens, combined with urban development of Scotland's central belt, reducing connectivity of the population with southern parts of the UK (Croose et al. 2013). The arboreal nature of marten species, and their preference for forested areas over open ground (Balharry 1993; Balestrieri et al. 2010; Manzo et al. 2012) likely makes this type of fragmented and urban environment a constraint on dispersal and expansion. As a result, additional locations for marten reintroduction have been sought. After extensive UK-wide feasibility studies (Bright & Harris 1994; Macpherson 2014), woodland blocks in mid-Wales were selected as optimum sites for a pine marten reintroduction (Macpherson 2014). This region not only had high availability of forested habitats but a low-density road network, reducing this risk of mortality for introduced martens. Scat surveys carried out between 2011 and 2015 found no evidence of pine marten occupation in this part of the species' historic range, suggesting any population of remaining individuals in the region was, at best, functionally extinct. The Vincent Wildlife Trust's 'Pine Marten Recovery Project' therefore aimed to create a viable population of martens in Wales, which, with time would facilitate the species' spread throughout Wales and into western England.



**Figure 1.2. European pine marten *Martes martes* distribution in Great Britain from 1960 to 2018.** Black circles indicate presence. All presence points were scaled to hectads. Only verified records are included. No surveys were carried out in Scotland in the 2000s, and the 2010s Scotland surveys covered only central and southern Scotland. Figure and legend adapted from Sainsbury et al. (2019).

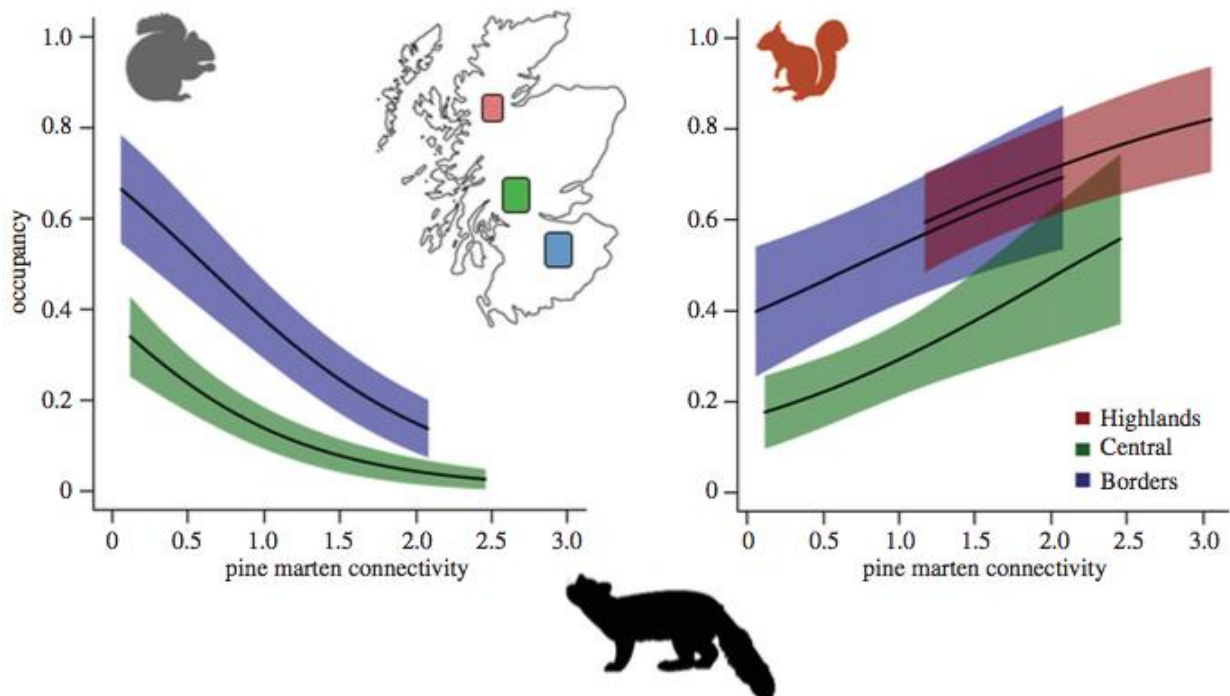
## ***Pine marten & grey squirrel***

The return of the pine marten has received wide attention from conservationists and practitioners alike, following findings from a study by Sheehy and colleagues in Ireland (2014). Their research suggested that the resurgence of the pine marten in the Irish Midlands had resulted in a population crash and range shift of the invasive, non-native grey squirrel *Sciurus carolinensis* (Sheehy & Lawton 2014). Their findings suggested that martens could play a role in the biological control of this pest species and in turn enable vegetation recovery (in the form of reduced tree damage), much like the positive, cascading impacts of predator recovery elsewhere (Estes & Palmisano 1974; Ripple et al. 2001; Letnic et al. 2012). Distributional evidence from this study in Ireland was the first attempt to substantiate the potentially negative impacts that pine martens could have on grey squirrel populations (Sheehy & Lawton 2014). Non-invasive survey techniques, including collation of sightings data and hair-tube surveys, were employed to determine the location, density and distribution of pine martens, grey squirrels and the native red squirrel *Sciurus vulgaris*. In the last century, the red squirrel has declined considerably in the UK, predominantly due to competitive exclusion by, and disease transmission from, grey squirrels (Tompkins et al. 2002; Gurnell et al. 2004; Bertolino et al. 2014). As a result, the suppression of grey squirrel populations was considered to have positive ramifications for red squirrel recovery (Rushton et al. 2006). Results from the study in Ireland showed that where pine martens were found in high densities, grey squirrels numbers had declined, whereas red squirrels populations had increased and were co-existing with the low number of remaining greys (Sheehy & Lawton 2014). These findings have led to the proposition that pine marten presence is somehow inhibiting the persistence of, and causing range contraction in, grey squirrel populations in the region. Furthermore, it was concluded that red squirrels may have experienced competitive release and their populations may have benefited in the presence of pine martens.

The results of this study were further substantiated in 2018 when a similar survey was undertaken in Scotland (Sheehy et al. 2018). The study assessed the density and distribution of pine martens, grey squirrels and red squirrels across the country, ranging from where the marten population had been long-established and was at a



relatively high density in the Highlands, to the Scottish Borders, an area that martens had only recently populated. This study found similar distributional patterns to Ireland; where marten connectivity (a function of marten density and the extent to which they used their landscape) was highest, the occupancy of grey squirrels was lowest. Red squirrels showed the opposite trend and their occupancy was positively correlated with marten connectivity (Sheehy et al., 2018; Fig 1.3.). Where recovering marten populations were more established, such as in the Highlands, the strength of the relationship between the three species was strongest, suggesting a predator-mediated change in competition between the two squirrel species (Sheehy et al. 2018).



**Figure 1.3. The relationship between pine marten connectivity and squirrel occupancy in three regions of Scotland.** Plots depict model-averaged predictions of relationships between squirrel occupancy (the probability of squirrels being found in the habitat and being detected), and pine marten density weighted connectivity (a measure representing marten density and their space use). Invasive grey squirrels are negatively affected by pine marten connectivity (left panel), whereas native red squirrels are positively affected (right panel). Figure from Sheehy et al. 2018.

### *The grey squirrel*

The grey squirrel is native to North America and is considered an invasive non-native species in Europe. It has not only driven the decline of red squirrels through competition and transmission of the squirrel-pox virus (Rushton et al. 2006), but continues to have significant impacts on native flora and plantations. Bark stripping, the removal of outer bark and consumption of unlignified tissue beneath (Mayle et al. 2007), is intermittently undertaken by grey squirrels and can permanently damage trees, making them more vulnerable to insects and fungi (Kenward & Parish 1986; Lurz et al. 2001; Mayle et al. 2009), as well as altering main stem growth (i.e. apical dominance). The reasons for this behaviour are unknown, although aggression, calcium deficiency (Nichols et al. 2016) and squirrel density have been proposed as influential (Kenward & Parish 1986; Mayle et al. 2007). Bark stripping degrades the quality of timber and it is estimated that, when combined with the cost of control programmes, the grey squirrel incurs costs in the UK of approximately £6 million per annum (Bertolino & Genovesi 2002; Forestry Commission 2002; Williams et al. 2010). The species has been resident in the UK for over a century, with the first individuals documented in Great Britain in the 1830s (Middleton 1931), reaching Ireland in 1911 (Lawton & Rochford 2007), and introductions continuing into the 1920s. The intentional introduction and dispersal of the species as gifts, began in Bedfordshire (Signorile et al. 2016) however their rapid success and population establishment could not have been predicted. By the mid-20<sup>th</sup> century the grey squirrel was found across most of the UK and its population continues to expand. The species' ability to reproduce rapidly and colonise new areas has been the key to its success. This species has yet to colonise mainland Europe, however a population has been established in north-west Italy since 1948 (Bertolino & Genovesi 2002). Since the 1970s, the range of these individuals in Italy has been increasing and, aided by the presence of contiguous woodland patches, the spread of grey squirrels in Europe continues (Bertolino & Genovesi 2002). In order to conserve the native red squirrel and limit damage caused by bark-stripping, programmes for grey squirrel control have included shooting, poisoning and trapping (Lawton & Rochford 2007). Success has been demonstrated on the Isle of Anglesey, where, after an extensive culling operation spanning many years, the grey squirrel has now been eliminated allowing the recolonization of a red squirrel population (Schuchert et al. 2014). However these approaches are highly labour intensive, fragmented and, unless performed in a co-ordinated manner during

the correct seasons for an extended period of time, are ineffective (Forestry Commission 2002; Tattoni et al. 2006). Grey squirrels are able to re-colonise managed areas soon after culling operations and often the removal of a proportion of individuals from a densely populated woodland reduces pressure on remaining squirrels, allowing them to thrive and facilitating immigration of others (Lawton & Rochford 2007). It would appear, as is often the case with well-established invasive species, that complete eradication of the grey squirrel in the UK is currently unfeasible (Bertolino & Genovesi 2002).

### *Context for this study*

The proposed impact of pine martens on grey squirrels, as demonstrated by Sheehy *et al.* (2014, 2018), provides a promising solution for the reduction or control of this invasive pest. If a similar situation is replicated in other regions where martens and both squirrel species co-occur, the potential ramifications for the control of grey squirrels and recovery of red squirrels are profound. However, the conclusions of Sheehy *et al.* (2014, 2018) are somewhat tentative and their findings are based on non-invasive monitoring techniques, lacking study system manipulation. The predator-mediated change in competition and the resulting differences in squirrel occupancy are therefore correlative, rather than causative. To truly understand this relationship, interactions between pine martens and grey squirrels should ideally be tested more experimentally. The processes underlying the landscape-scale patterns observed in Scotland and Ireland may be driven by lethal or non-lethal effects, or a combination of both. A more thorough understanding of grey squirrel-pine marten interactions will help to inform current grey squirrel management strategies. With further pine marten reintroductions proposed elsewhere in the UK (for example, in 2019 in the Forest of Dean by Gloucestershire Wildlife Trust), understanding the impacts of the recovery of this native carnivore are vital for managing the expectations of stakeholders and funders. This thesis therefore aims to provide further insight into the viability of marten reintroductions and their impact on invasive squirrel populations. The Vincent Wildlife Trust 'Pine Marten Recovery Project' in mid-Wales, which commenced in 2015, provided a unique opportunity to study the behaviour of newly translocated pine martens in an unoccupied part of their historic range. Furthermore, in the presence of

an established grey squirrel population, it is possible to assess the immediate impacts of pine martens, and their interactions with grey squirrels.

### ***Thesis aims and outline***

In this thesis, I investigate the spatial and behavioural ecology of pine martens and grey squirrels using a combination of biotelemetry, experimental and observational techniques. The initial focus of the thesis is to investigate the behaviour of pine martens in Wales within the first two years of their release, and understand how this might have impacted resident invasive grey squirrel behaviour and populations. In so doing, I aim to contribute to the developing field of predator restoration, as well as addressing the ongoing need for grey squirrel management strategies. Specifically, I aim to i) investigate the post-release movement of translocated pine martens in mid-Wales, to understand how these animals move and settle, providing new information on marten colonisation in novel environments ii) document the dietary habits of pine martens before and after translocation to observe marten response to a sudden change in habitat and differing prey base. These are both hoped to enable review of feasibility work and inform future translocation studies, iii) explore the response of grey squirrels to pine marten introduction with regards to space use, movement and survival, and iv) understand the behavioural responses of grey squirrels to the risk of predation by pine martens to try to better understand the relationship between the two species on a fine scale. This thesis is comprised of four chapters addressing these objectives, concluding with a general discussion. In each chapter, I have addressed gaps in the current knowledge with regards to mesocarnivore restoration and the impacts pine martens might have on grey squirrels.

In **Chapter 2** I have described the post-release movement of two cohorts of pine martens translocated from Scotland to mid-Wales in 2015 and 2016. In this chapter, I reveal distinct phases of movement comprising dispersal and settlement and the effect of resident conspecifics on marten movement strategies.

In **Chapter 3**, I investigated the diet of pine martens before and after translocation, at their source sites in Scotland and release sites in Wales, through hard-part analysis

of scats, and stable isotope analysis of tissues from martens and their putative prey. This chapter explores dietary variability within and between martens at population and individual levels as well as the role of grey squirrels in marten diets.

In **Chapter 4**, I have documented space-use by grey squirrels in response to pine marten presence using GPS and radio tracking data. This chapter investigates the impact of variation in exposure to martens on the survival, range sizes, daily movements and range locations of grey squirrels.

In **Chapter 5**, I assayed squirrel foraging environments to understand if pine martens create a 'landscape of fear' for grey squirrels. This chapter combines a 'giving-up density' framework with behavioural observations to investigate grey squirrel responses to pine marten predation risk.

Finally, in **Chapter 6** I have provided a synthesis and general discussion of my findings. I have addressed the contribution of my work to understanding of pine marten and squirrel interactions, as well as the broader implications for native species recovery, invasive species management and trophic cascades.



## Chapter 2

### **Post-release movement and habitat selection of translocated pine martens *Martes martes***



## Chapter 2: Post-release movement and habitat selection of translocated pine martens *Martes martes*

This chapter has been submitted for publication as:

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### **Abstract**

Translocation is now common practice in population restoration and vertebrate conservation. Monitoring of post-release movement patterns made by animals is important in evaluating translocation protocols and outcomes, though the processes of establishment are often poorly understood. We translocated 39 wild pine martens *Martes martes* (19 females and 20 males) from Scotland to mid-Wales. We released them into forested areas with no conspecifics in 2015, followed by a second release in 2016, alongside the animals released the previous year. We used VHF radio tracking to describe their post-release movement and habitat selection. 15% of individuals ( $n=6$ ) were not re-encountered during the tracking period and four of these were thought to have undertaken long-distance dispersal. For the remaining individuals we characterised two main phases of movement, 'exploration' followed by 'settlement'. The rate and duration of exploration differed between the two releases. In the first year, martens remained in the exploration phase for a mean of 14.5 days (SE = 3.9 days,  $n = 23$ ) and settled at a mean distance of 8.7 km (SE = 1.8 km,  $n = 23$ ) from the release sites, whereas animals released in the second year, when conspecifics were present, travelled away from release pens at a faster rate, settling after a lower mean of 6.6 days (SE = 1.8 days,  $n = 23$ ) but at a greater mean distance of 14.0 km (SE = 1.7 km,  $n = 23$ ) from release sites. Animals released in year one did not exhibit strong habitat preferences overall but within forests they favoured recently-felled areas. In contrast, animals released in year two showed strong selection for forested habitat but did not discriminate between forest types. Our results show that the presence of conspecifics appeared influential for settlement and site fidelity of translocated pine martens but was also associated with more distant but more rapid



dispersal of the second release cohort. Intense tracking of released animals in the first few weeks post-release ensured contact was maintained and reintroduction success criteria can be assessed. The release of cohorts of animals in close spatial proximity appeared to maintain site fidelity and promoted the rapid establishment of ranges in the new environment.

## ***Introduction***

Translocation, the deliberate movement of organisms from one site for release in another (IUCN/SSC 2013), is a long-established and frequently used tool in species conservation. In recent years, conservation translocations have increasingly been associated with restoration ecology (Seddon 2010) as well as being effectively implemented in threatened species recovery projects (Hayward et al. 2007). The return of species to their historic ranges can benefit not only the species in question, but improve functionality and biodiversity within the recipient ecosystem (Seddon 2010). Successful reintroductions require a sound knowledge of the species' ecology within its native range as well as some insight into its likely post-release behaviour and habitat requirements. Understanding post-release movement, habitat selection and the drivers of these is therefore necessary for appraising and improving current and future translocation projects.

Two key components of the success of translocation and reintroduction projects are release site fidelity and the survival rate of the translocated individuals (Armstrong & Seddon 2008). The selection of appropriate habitat for release sites and, thereby, access to adequate resources for individual animals, is paramount for their retention on, or near, the release site (Armstrong & Seddon 2008). Alongside site characteristics, sex ratio, release schedule and numerous other factors can influence the likelihood of a new population establishing successfully (Letty et al. 2007; Armstrong & Seddon 2008). Lack of site fidelity is clearly unfavourable and often implies poor selection of release sites, inappropriate release protocols and/or unforeseen conspecific interactions (Letty et al. 2007). Thus, understanding the

patterns of movement of translocated individuals after their release, and the characteristics of their selected habitats during the initial release period, are vital in evaluating and improving conservation translocations (Armstrong et al. 2013).

The first individuals to be released into a new area may be more likely to leave the vicinity of release sites, due to the inherent absence of resident conspecifics and/or lack of mating opportunities (Mihoub et al. 2011). Exploration by the introduced animals of the novel environment in search of ideal habitat is a central but unpredictable part of a reintroduction project (Armstrong et al. 2013). Such exploratory movements by translocated individuals can be detrimental to survival, since extended periods of exploration and habitat searching are often erratic and extend over long distances, making them energetically costly (Robertson & Harris 1995; Yott et al. 2011; Spinola et al. 2018) and exposing animals to diverse hazards. Three major post-release movement patterns have been identified: i) immediate settlement, ii) dispersal followed by settlement and iii) long-distance dispersal or failure to settle (Davis 1983; Slough 1989; Broquet et al. 2006; Woodford et al. 2013; Tolhurst et al. 2015). Among translocated carnivores, these patterns have been described in American marten *Martes americana* (Davis 1983; Slough 1989; Woodford et al. 2013), otters *Lontra canadensis* (Sjoasen 1997; Spinola et al. 2018), red foxes *Vulpes vulpes* (Tolhurst et al. 2015) and swift foxes *Vulpes velox* (Moehrensclager & Macdonald 2003). However, explanations for the ecological mechanisms driving among-animal variation in the observed patterns remain ambiguous, with conspecific attraction, habitat suitability and predation risk all thought to play a role (Davis 1983; Sjoasen 1997; Letty et al. 2007). Reduction of problems arising from exploration, long-distance dispersal or attempted 'homing' has most commonly been achieved through adopting a soft-release protocol, allowing acclimatisation of individuals to the release site in an enclosure provisioned with food for a short period of time prior to release (Moehrensclager & Macdonald 2003; Tolhurst et al. 2015).

The presence of conspecifics may be beneficial at low densities, and founding individuals might discriminate less between habitat types and instead favour proximity to other founder members and the establishment of a 'neighbourhood' (Ydenberg et al. 1988; Stamps 2001; Shier & Swaisgood 2011). Alternatively, founding individuals might intuitively be expected to select the highest quality locations in an uninhabited

landscape, in line with an ideal free distribution (Fretwell & Lucas 1962; Stamps 2001). With a continual influx of translocated animals, however, competition would be expected gradually to increase (Stamps 2001; Stamps & Krishnan 2005), perhaps leading later arrivals to disperse away from otherwise ideal release sites (Selonen & Hanski 2007; Stamps & Swaisgood 2007). Therefore, the social structure of the species as well as the habitat, site and landscape characteristics must be key considerations in translocation project design and implementation.

Reintroductions have been proposed and implemented as measures to combat the decline of carnivores worldwide. In Great Britain, several native mammalian carnivores have experienced historic declines as a result of predator control, environmental contaminants, deforestation and demand for fur (Sainsbury et al. 2019). Current efforts are being made to reverse these declines. Since the mid-20<sup>th</sup> century, considerable recoveries in the ranges and populations of otter *Lutra lutra*, polecat *Mustela putorius*, badger *Meles meles* and pine martens *Martes martes* have arisen largely through combinations of increased legal protection, changed control practices, reduction in pollution and habitat enhancement (Sainsbury et al. 2019). Translocations have also played a role in these species' recoveries with releases of captive bred, wild-caught or escaped individuals (Sainsbury et al. 2019). The recovery of British otter populations was accelerated by captive breeding and release of otters (Jefferies et al. 1986). Polecats have also benefited from reintroduction, primarily through illicit releases such as those in Cumbria & Argyll (Birks & Kitchener 1999). The pine marten is currently showing natural range extension in Scotland (Sainsbury et al. 2019), though its expansion has also been aided by translocation to southern Scotland (Shaw & Livingstone 1992) and there have likely been sporadic illicit releases in England (Birks & Messenger 2010; Jordan et al. 2012).

Recovery of the pine marten throughout the UK has been an area of focus for statutory (Bright & Smithson 1997) and non-governmental organisations (Macpherson 2014), with an aim to expand the range extent of what was a sparse and fragmented population through translocations and population reinforcements. Previous translocation studies on *Martes* species have indicated strong site affinity by released individuals (Davis 1983; Slough 1989; Shaw & Livingstone 1992; Woodford et al. 2013). This may partly have been related to the use of soft-releases (Davis 1983;

Woodford et al. 2013). Martens are, however, highly mobile animals and are capable of dispersing large distances (Broquet et al. 2006). Long-distance post-release movements have been attributed to territorial saturation or the absence of suitable habitat near to release sites (Woodford et al. 2013). In some instances, male martens have been found to disperse further than females (Slough 1989). This is likely related to sexual dimorphism with regards to body size, energetic demands of reproduction and ranging extent (Zalewski 2007; Caryl et al. 2012), as well as pronounced intra-sexual territoriality, allowing for the overlap of male and female ranges, but exclusivity of ranges within each sex (Powell 1979; Erlinge & Sandell 1986; Balharry 1993). These studies also found that although many translocated individuals settled in mature forest, their movement was not impeded by landscape features or the presence of different habitat types (Slough 1989).

Martens are predominantly viewed as forest-specialists (Slough 1989; Storch 1990; Balharry 1993; Balestrieri et al. 2010; Manzo et al. 2012; Weber et al. 2018) and often den in tree cavities found in ancient woodland. Nevertheless martens can traverse and utilise areas of scrub and low canopy cover (Pereboom et al. 2008; Balestrieri et al. 2010; Manzo et al. 2012; Lombardini et al. 2015; Moll et al. 2016). In many regions with fragmented forest, pine marten diet is dominated by grassland voles *Microtus* spp., found in edge and open habitats containing tussock grass (Hansson 1978; Caryl et al. 2012). This contrasts with studies in highly forested regions which have identified the greater importance of forest-dwelling voles *Myodes* spp.. Although mature forest provides the structural complexity required for marten denning and foraging (Caryl 2008), varied habitat use is linked not only to the level of forest fragmentation but also prey availability and conspecific density (Powell 1979; Caryl et al. 2012; Lombardini et al. 2015). This suggests that martens are capable of exploiting both forest interiors and the edge habitats abundant in mosaic habitat structure. However, few of these studies have looked at marten movement and habitat selection after a translocation event.

Mid-Wales was identified as the optimal location for a species recovery programme (Macpherson 2014) to facilitate the spread of martens throughout Wales and into England due to its high availability of forested habitats and low-density road network. Scat surveys undertaken between 2011 and 2015 found no evidence of pine marten

presence in this part of the species' historic range, suggesting the former resident population of pine martens was, at best, functionally extinct in the region. Our study examined the movements and habitat use of translocated pine martens immediately after their release. We tracked two cohorts of martens taken from the wild in their core range in Scotland and released in an unoccupied region of their historic distribution in mid-Wales. First we describe the initial post-release movements of martens, characterising phases of exploration and settlement in years with and without resident conspecifics in a novel environment. Second, we investigate habitat selection by individual martens across a large and diverse habitat matrix and within wooded areas, again in the absence (year 1) and presence (year 2) of conspecifics. The results of our study improve understanding of marten habitat requirements and post-translocation movement ecology in unoccupied areas of their historic range. This can be used to inform and maximise the success of future reintroduction programmes and to understand the movement ecology of a recovering and expanding population.

## **Methods**

### *Trapping, translocation and release*

Between September and November in both 2015 and 2016 pine martens were translocated from forests in the Scottish Highlands to mid-Wales (Fig. 2.5). Source sites in Scotland were surveyed for marten scats before live-capture traps (Tomahawk 205, Tomahawk Live Trap, Hazelhurst, USA) were installed and pre-baited for 2-3 weeks. Traps were monitored for marten activity by motion sensitive trail cameras (Bushnell NatureView HD, Bushnell Corp, Kansas, USA) before being set for one night per week until 2-4 individuals per woodland had been caught. This reduced the chance of translocating related individuals and unsustainably depleting resident populations. Trapped individuals were anaesthetised and given a full health screening by a wildlife veterinarian. Adult martens in good physical condition, at an equal ratio of males to females, were selected for translocation. Any juveniles, surplus individuals, those with any obvious injuries or deemed too old (on the basis of their dentition) were re-released at their site of capture. Individuals to be translocated were tagged with a sub-

cutaneous passive integrated transponder (PIT: Avid Identification Systems Inc., California, USA) and fitted with a collar equipped with a VHF transmitter (Biotrack Ltd., Wareham, UK).

Martens were translocated overnight from Scotland to four main sites in mid-Wales. The sites were dominated by commercial conifer plantations managed on a short rotation clear fell regime. The forest was dominated by Sitka spruce *Picea sitchensis* with varying proportions of Norway spruce *Picea abies*, Douglas fir *Pseudotsuga menziesii*, larch *Larix kaempferi*, *L. eurolepis* and lodgepole pine *Pinus contorta*. Deciduous and mixed woodland within and surrounding these sites is characterised by small proportions of these conifers alongside sessile oak *Quercus petraea*, beech *Fagus sylvatica*, rowan *Sorbus aucuparia*, birch *Betula* spp. and willow *Salix* spp.

The translocated martens were placed in individual soft-release pens furnished with vegetation and containing a den box and camera trap to enable behavioural observation. Animals were held in these pens for up to 5 days and supplied with food (day-old chicks, raw eggs, peanut butter and raisins) *ad lib*. Release was subject to confirmation, from serological testing of samples taken at the time of capture in Scotland, that individuals had not been exposed to canine distemper virus, following which, the pen door was then opened and animals were allowed to leave. Upon removal of soft release pens, a den-box was installed nearby and food was provided until the martens ceased to return. Trapping and release protocols in year 1 and year 2 were consistent.

Telemetry locations of pine martens were collected for up to 10 months post-release with each marten being relocated at least once per week. Tracking was undertaken at dusk and after sunset to ensure locations were representative of marten movement during their active hours (Zalewski 1997; McCann et al. 2017). Animals released in 2015 (year 1) were not monitored in 2016 (year 2) as VHF collars were removed 6-10 months after their release. Pine marten locations were triangulated from locations and bearings taken in the field (two bearings used to calculate each location) using Location of a Signal (LOAS) software (Version 4.0; n=1413, mean=37 locations per individual, range=1-110). Single bearings that were taken over one hour apart, or did not converge to give a triangulated location, were excluded from the final dataset. To

estimate the error of VHF triangulated locations in relation to true collar locations, two observers took simultaneous bearings on collars in unknown locations ( $n=14$ ). These points were triangulated and the distance (m) of the triangulated location from the true collar location was then measured. The median error of VHF locations was estimated as 70m ( $n=14$ , IQR=98m).

### *Post-release movements*

For each individual we calculated the straight-line distance (km) from the release pen to each triangulated location and modelled these with time since release from pen, measured in days, as a predictor. We fitted a piecewise ('broken-stick') linear regression model (Toms & Lesperance 2003) forced through the origin, representing a period of exploration, followed by settlement. The piecewise regression model was constrained to fit two segmented linear relationships with one intersection point (breakpoint), taken as the point at which settlement took place. The time to settlement ( $t$ ) in days (i.e. where the breakpoint lies on the x-axis), distance to settlement ( $d$ ) in km (i.e. where the breakpoint lies on the y-axis), and the rate of dispersal ( $r$ ), in km day<sup>-1</sup> (i.e. the slope of the initial exploration period from the origin to the breakpoint) were treated as parameters of post-release behaviour. As model convergence of piecewise regression can be sensitive to the start parameters and number of iterations, the model fitting was attempted up to 1000 times, with the first successful fit being extracted. The fit of the piecewise model was compared to that of a simpler linear least squares model of distance and time since release using Akaike's Information Criterion, adjusted for sample size (AICc; Burnham & Anderson 2004). In six cases, a piecewise model could not be fitted due to sparsity of data in the earliest stages following release (i.e. animals went missing for a number of days before being located for the first time), which caused problems with model fit. These individuals were excluded from further post-release movement analyses.

An individual was considered to be 'settled' if the distance moved from their release pen reached a plateau (i.e. the slope of the second line was not significantly different from zero). Before analyses of the post-release movement parameters, we confirmed there was no correlation between the distance ( $d$ ) and the number of days since release ( $t$ ) at which martens moved from the transition into the establishment phase

(Pearson's correlation;  $\rho=0.21$ ,  $t= 1.00$ ,  $df=21$ ,  $p=0.32$ ). Piecewise regressions were fitted using the *R* package 'segmented' (Muggeo 2017) and all analyses were undertaken in *R* version 3.3.3 (R Core Team 2017).

### *Analysis of movement*

Generalised linear models (GLMs; Marschner and Donoghoe, 2018) were used to examine the effect of sex and year of release on the three response variables; time to settlement ( $t$ ), distance to settlement ( $d$ ; rounded to whole numbers) and rate of dispersal ( $r$ ). We did not include an interaction term between sex and year in any of the models due to the small sample size of each sex within each group. Day of settlement ( $t$ ) was modelled using a negative binomial GLM with a (default) log-link, distance of settlement ( $d$ ) was modelled using a Gaussian GLM with a square-root link and rate of dispersal ( $r$ ) was log-transformed to normalise distribution of residuals. We used backwards stepwise elimination to determine the minimum adequate model. Variables were retained at each stage if removing them had a significant effect on model fit, as measured using an ANOVA ( $\alpha=0.05$ ). We back-transformed model estimates from the final model to the original scale to obtain response values using the *R* package 'emmeans' (Lenth et al. 2019).

Range size asymptotes were produced prior to generation of home range kernels to ensure ranging data were only generated using individuals with adequate relocation data and stable range sizes. Asymptotes with 95% confidence intervals (CIs) were calculated using an increasing number of resampled locations (Laver & Kelly 2008) taken after the breakpoint only, up to 100 days post-release (i.e. during the 'settlement' phase). All individuals were initially included in this analysis ( $n=29$ ), including those for which a segmented model (and thus breakpoint) could not be fitted ( $n=6$ ). For these 6 martens, linear model plots were visually inspected and a breakpoint of zero days was assigned, therefore including all of the locations recorded (Fig. 2.1). Individuals ( $n=3$ ) with an inadequate number of relocations were excluded from calculation of ranging metrics. Home ranges of remaining individuals (from the breakpoint until 100 days post-release;  $n=26$ ) were then characterised by 90% Kernel Density Estimates (KDEs), with 95% CIs calculated using 100 bootstrap samples with replacement. KDEs were calculated with the reference smoothing parameter  $h\text{-ref}$  which is suited to



small sample sizes and reduced over-smoothing of data (Fieberg & Kochanny 2005; Borger et al. 2006; Laver & Kelly 2008), in the *R* package '*adehabitatHR*' (Calenge 2012). We investigated the effect of sex, year of release, distance to settlement ( $d$ ), time to settlement ( $t$ ) and an interaction between year of release and sex on the mean home range size of martens using a Gaussian linear model. Range size was log-transformed to normalise the distribution of residuals. Model selection was undertaken using backward stepwise elimination as above.

### *Habitat preference*

Preferences for broad habitat types and then for forest types were investigated separately. Geo-referenced land-use data were obtained from the CORINE Land Cover (CLC) 2012 database (scale 1:100,000; created in 2011-2012, released in 2016). Land use classifications were grouped into three biologically relevant classes; Agricultural land, Forest and Grassland (Table 2.1). Forest-type data were acquired from the National Forest Inventory (NFI) 2016 database (created and released by Forestry Commission 2016). Forest-type classifications were condensed into five major groups; Broadleaf, Conifer, Felled, Open areas and Young or sparse woodland (Table 2.1).

The habitat preferences of all pine martens (for both broad land-use and forest type) during the post-release 'settlement' period, up to 100 days post-release, were assessed using a use-availability design, where preference is the ratio of used to available habitat (Aebischer et al. 1993; Warton & Aarts 2013). We compared the habitat types and characteristics of 'used' locations with 'available' habitat at randomly sampled locations. Available habitat was sampled randomly from a uniformly-sized area around the home-range centroid of each marten. The radius of this area (7.15km) was defined by calculating the mean maximum Euclidean distance that each marten with an adequate fix number ( $n=26$ ) was located from their home range centroid. To ensure thorough representation of 'available' habitat, each 'used' location had five corresponding 'available' locations. This unequal ratio was then accounted for by weighting locations within subsequent models so that five 'available' points were equivalent to one 'used' point. Both 'used' and 'available' points were overlaid on habitat spatial polygons and the underlying habitat-type data were extracted. For

analysis of forest type preference, available locations were only generated within NFI forest polygons to ensure complete representation of available forested habitat. For individuals situated close to the coast, areas were clipped to avoid selection of the marine environment and intertidal zones (< 500m of the low water mark). All habitat use data was processed using the *R* package ‘*sp*’ (Pebesma & Bivand 2012).

We fitted generalized estimating equations (GEEs) in a general linear model (GLM) framework to investigate the habitat preference of martens in different release years and between sexes. GEEs enhance GLMs by accounting for the spatial and temporal autocorrelation within locations recorded for individuals. The assumption of independence, made in a GLM, is replaced with a correlation structure that groups individuals, allowing for correlation within but not between individuals. GEE-GLMs use the empirical standard error in analysis, which is more robust to misspecification of correlation structure and non-independence of data points, an inherent feature of telemetry data (Zuur et al. 2009; Booth et al. 2013). Incorporating these correlation structures makes it possible to generate a population mean response rather than making inferences about single individuals (Zuur et al. 2009; Braaker et al. 2014). GEE-GLMs with a binomial error distribution and logit link function were used to model the habitat preference of pine martens. The response variable was binary: used vs. available. Habitat type, and its interaction with both release year and sex were factor variables. The weight of the point (used = 1, available = 0.2) was also specified. Release year, either 2015 or 2016, was included to test for variance arising from a) differences in release sites between years and b) the presence of conspecifics in the second year of releases. Animals released in 2015 (year 1) were not monitored in 2016, and therefore each year contains a different set of newly released individuals. Individual martens were defined as clusters and the correlation structure was assumed to be independent, i.e. correlation structure was expected among locations from the same individual but not between individuals (Fieberg & Kochanny 2005; Pirotta et al. 2011; Braaker et al. 2014).

Models contained fixed effects of sex, habitat type and year. We included all main effects and the two-way interactions between sex and habitat type, and year and habitat type. We used backward-step selection using GEE-GLM *p*-values to obtain the minimum adequate model. Models were assessed using Wald’s tests (GEE-GLM

anova function in *geepack*) to ensure that all retained variables had a  $p$ -value  $<0.05$  (Ventura et al. 2019). Based on the significance of an interaction term, data from each year or sex were then modelled separately to identify the differences in preference within each group. Parametric bootstrapping 1000 times using GEE-based uncertainty parameters was implemented to calculate 95% CIs around the population mean (Pirodda et al. 2011; Russell et al. 2015). All models were fitted using the '*geeglm*' function in the '*geepack*' package (Halekoh 2006) in *R* version 3.5.1.

#### *Ethical statement*

The study was approved by The University of Exeter Animal Welfare and Ethical Review Board and under licences from Scottish Natural Heritage and Natural Resources Wales and from The Home Office under the Animals (Scientific Procedures) Act.

**Table 2.1. Broad habitat and forest types and grouping for marten habitat preference analysis.** All 'Forest' habitat identified in 'Broad habitat type' was then subset and assigned 'Forest type'. These categories assigned within the National Forest Inventory (NFI) are grouped into types are based on structural and ecological similarities.

<b>Broad habitat type</b>	<b>CORINE Level 3 Description</b>	<b>CORINE Level 3 Code</b>
Agricultural	Non-irrigated arable land	211
	Land principally occupied by agriculture, with significant areas of natural vegetation	243
	Pastures	231
Forest	Broad-leaved forest	311
	Coniferous forest	312
	Mixed forest	313
Grassland	Natural grasslands	321
	Moors and heathland	322
	Transitional woodland-shrub	324
	Beaches, dunes, sands	331
	Bare rocks	332
	Sparsely vegetated areas	333
<b>Forest type</b>	<b>NFI description</b>	
Broadleaved	Broadleaved	
	Mixed mainly broadleaved	
Conifer	Conifer	
	Mixed mainly conifer	
Felled	Felled	
	Windblow	
	Ground Prep	
Open	Agricultural land	
	Bare area	
	Windfarm	
	Grassland	
	Open water	
Undefined	Young trees	

## Results

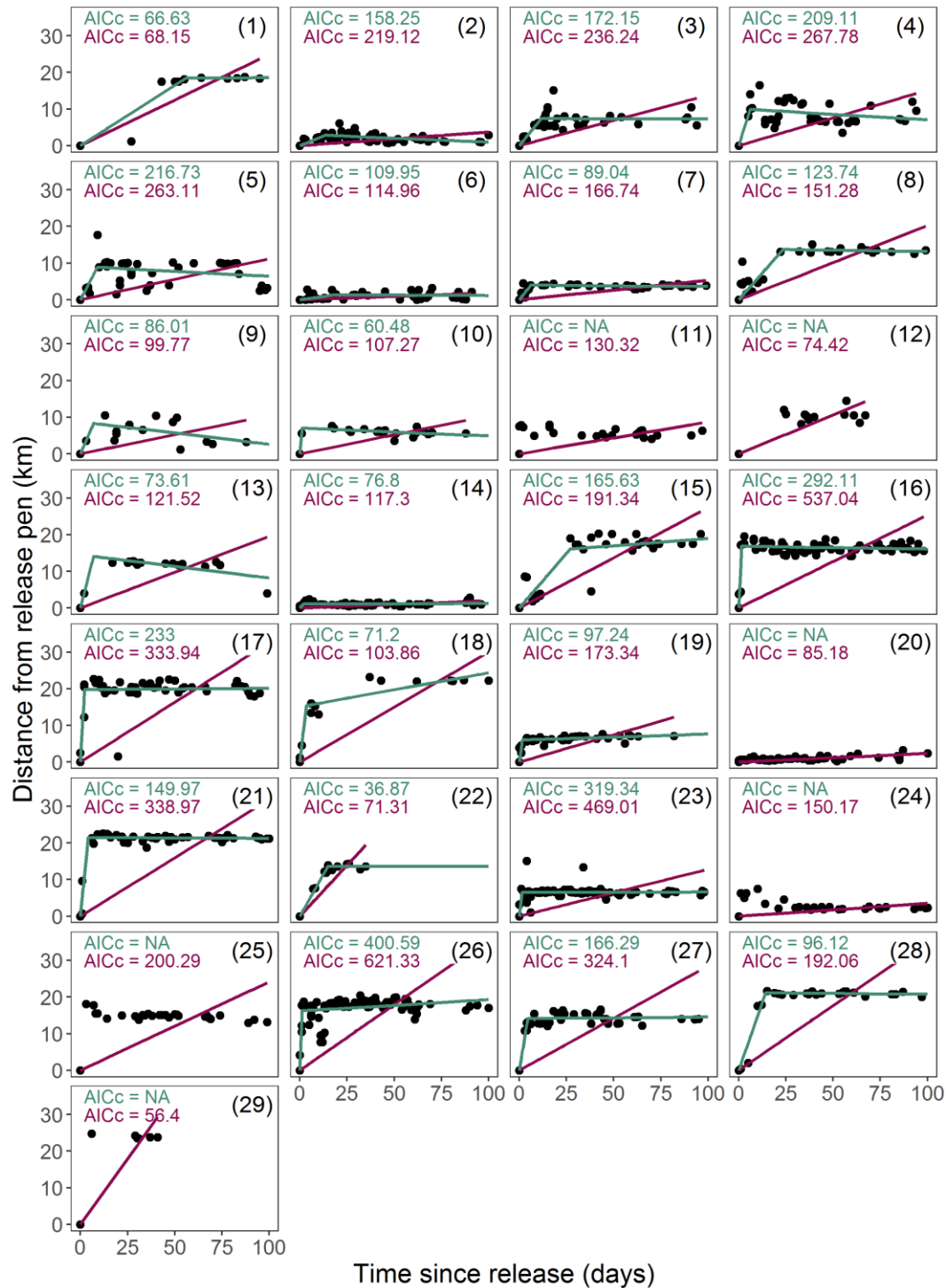
In 2015 and 2016, 39 pine martens (10M and 10F in 2015 and 10M and 9F in 2016) were translocated from Scotland and released into mid-Wales. Ten individuals were completely excluded from subsequent analyses due to an inadequate number of fixes ( $<6$ ) within 100 days. This was a result of either shedding the radio collar in the release pen ( $n=1$ ), mortality ( $n=3$ ; two individuals died after 13 days due to infection and one individual was thought to have been predated after 16 days), or inability to relocate animals for a long period of time immediately after release ( $n=6$ ; although 4 of these were subsequently relocated and identified 27-230 days post-release, they were not included in the analyses). Within the first 100 days post-release, the mean number of fixes recorded for the 29 (6M and 7F in 2015 and 9M and 7F in 2016) successfully tracked individuals was 35 (SD = 20 fixes; range = 7-84).

We identified two clear stages of post-release movement by translocated pine martens within the first 100 days post-release of 'exploration' followed by 'settlement'. For 23 of the 29 pine martens, a segmented linear model with two stages characterised marten movements post-release better (lower AICc score) than a simple linear regression (Fig. 2.1). The distance ( $d$ ) and time ( $t$ ) taken to settlement differed significantly between the two release years, while the rate of exploration ( $r$ ) varied both with year of release and pine marten sex. The minimum adequate model for settlement time identified an effect of year of release on settlement time ( $t$ ) ( $\chi^2_{2,1} = 3.83$ ,  $p = 0.05$ ). Pine martens released in the second year took significantly less time to settle than those released in the first. Settlement occurred at a mean of 14.5 days (SE = 3.9 days) in the first year, compared to 6.6 days (SE = 1.8 days) in the second year. The longest time taken to settle by an individual was 56 days. There was no difference between the sexes ( $\chi^2_{2,1} = 0.078$ ,  $p = 0.78$ ). The minimum adequate model for settlement distance ( $d$ ) showed that year of release significantly affected settlement distance ( $\chi^2_{2,1} = -161.48$ ,  $p = 0.03$ ). Pine martens released in the first year settled closer to their point of release than those in the first year. Animals in the first year settled a mean of 8.7 km (SE = 1.8 km) away from the release site, whereas animals in the second year travelled a mean of 14.0 km (SE = 1.7 km; Fig. 2.2a). The maximum distance at which the tracked martens settled within 100 days was 21.5 km and the minimum was 1.1

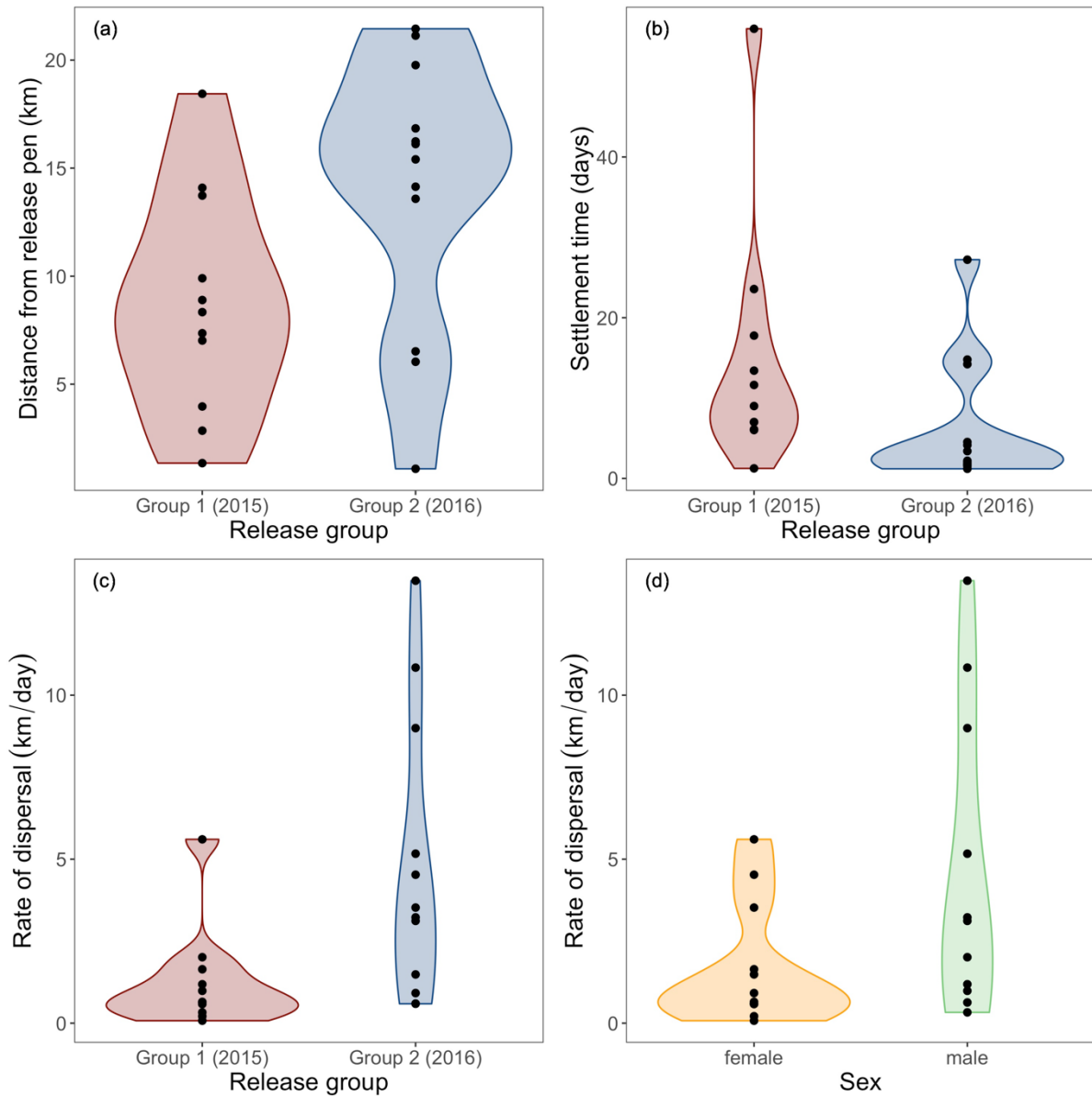
km. There was no difference in settlement distance between male and female martens ( $\chi^2_{2,1} = -115.01$ ,  $p = 0.074$ ). Of the 6 individuals that were not relocated immediately after release, 4 were later found 1.0 – 103.0 km from their release locations. The minimum adequate model for exploration rate ( $r$ ) included effects of year of release ( $\chi^2_{2,1} = -10.92$ ,  $p = 0.001$ ) and sex ( $\chi^2_{2,1} = -5.22$ ,  $p = 0.026$ ). When averaged over sex, animals released in the second year dispersed from their point of release at a greater rate than those released in the first year. Year one animals travelled at a rate of 0.8 km day<sup>-1</sup> (SE = 0.2 km day<sup>-1</sup>) compared to year two animals at a rate of 3.0 km day<sup>-1</sup> (SE = 0.9 km day<sup>-1</sup>). When averaged over years, males also showed a significantly greater rate of dispersal than females. Females travelled at a mean rate of 0.9 km day<sup>-1</sup> (SE = 2.8 km day<sup>-1</sup>) whereas males travelled at 2.4 km day<sup>-1</sup> (SE = 0.8 km day<sup>-1</sup>) on average.

The mean home range size of martens in the settlement phase (i.e. from the breakpoint up to 100 days) was 9.5 km<sup>2</sup> (SD = 10.6 km<sup>2</sup>, range = 0.2 - 65.6 km<sup>2</sup>,  $n = 26$ ; Fig. 2.3). Variance in range size was not significantly affected by sex, year of release, the interaction between sex and year of release, settlement time or settlement distance.

The preference of martens for broad habitat types after settlement and up to 100 days since release differed significantly between release years (GEE-GLM;  $\chi^2_3 = 55.2$ ,  $p < 0.001$ ). When broad habitat type preference was assessed separately for each year, pine martens did not display a strong habitat preference in year one, but in the second year martens preferred forest habitats and avoided agricultural areas and grassland (GEE-GLM;  $\chi^2_2 = 76.6$ ,  $p < 0.001$ ; Fig. 2.4a). Marten preferences for forest type also differed between years (GEE-GLM;  $\chi^2_5 = 17.15$ ,  $p = 0.004$ , Fig. 2.4b). When each year group was assessed separately, martens showed strong preference for felled areas in year one (GEE-GLM;  $\chi^2_4 = 28.9$ ,  $p < 0.001$ ; Fig. 2.4b), while in the second year, martens did not show preference for any forest types.

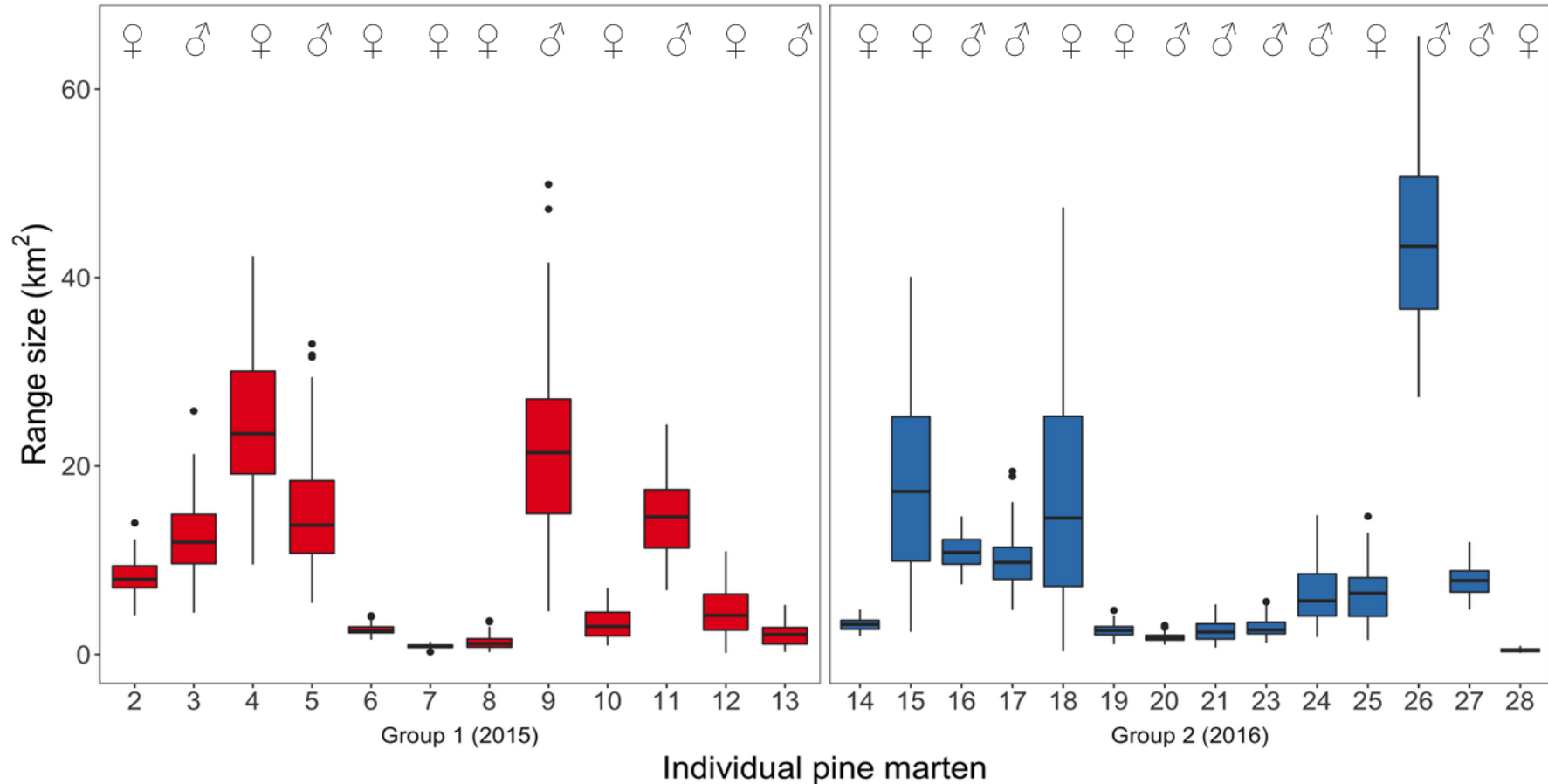


**Figure 2.1. Post-release movement of translocated pine martens *Martes martes* away from release sites over 100 days after release.** Each panel represents the movement of an individual marten. The green line shows a 'broken-stick' regression fitted to the data, representing a two-phase movement pattern. The purple line shows a linear regression fitted to the data representing continuous movement away from the release pen. The AICc values for each model are provided. When AICc=NA, a broken-stick regression could not be fitted due to scarcity of locations immediately after release. Animal number is shown in parentheses. Animals 1-13 were released in 2015 and 14-29 in 2016.

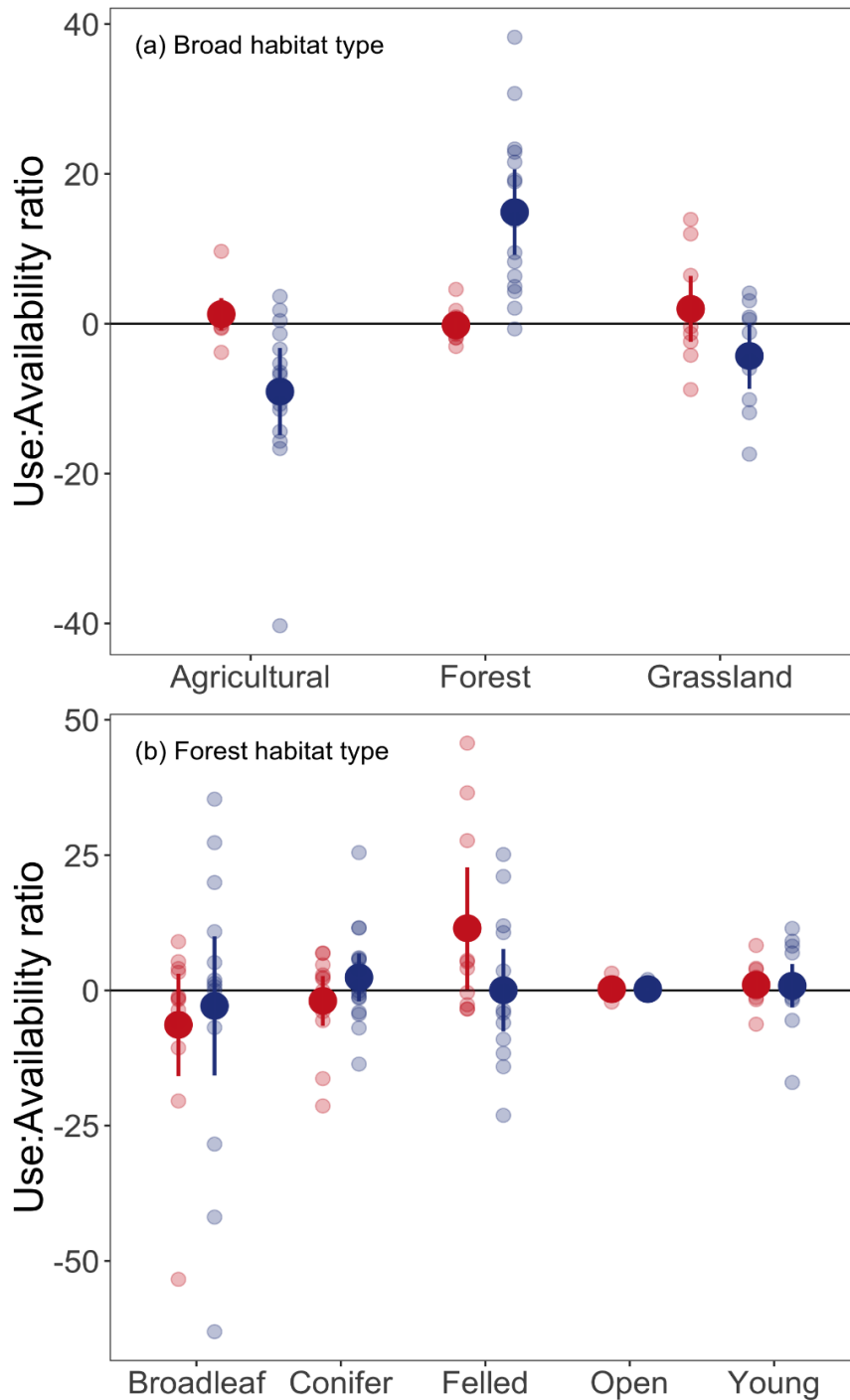


**Figure 2.2. Summaries of post-release movement of translocated pine martens away from release pens over 100 days after release. a)** Distance ( $d$ ) from release pen (km) at which pine martens switched from the ‘exploration’ phase and entered the ‘settlement’ phase during which they established stable home ranges. **b)** Time ( $t$ ) since release (days) at which pine martens switched from the ‘exploration’ phase and entered the ‘settlement’ phase during which they established stable home ranges. **c)** Rate ( $r$ , in km/day) that pine martens dispersed from their release pen before entering the settlement phase. **d)** Rate ( $r$ , in km/day) that female and male pine martens dispersed from their release pens. The first release group (2015) is shown in red and the second group (2016) is shown in blue. Females are shown in orange and males are shown in green. Raw data are shown in black.





**Figure 2.3. Home range size of translocated pine martens, calculated using locations recorded from the time of settlement up until 100 days post-release.** Tops and bottoms of the bars represent the 75<sup>th</sup> and 25<sup>th</sup> percentiles of the data, the black lines are the medians and the whiskers extend from their respective hinge to the smallest or largest value, no further than 1.5 times that of the interquartile range. Points outside this range are outliers. The first release group (2015) is shown in red and the second group (2016) is shown in blue. Individual pine marten numbers correspond to animals in Figure 2.1. ID 1, 22 and 29 have been excluded from range calculations due to an inadequate number of locations collected post-settlement.



**Figure 2.4. Habitat preferences of translocated pine martens released in year one (2015; red) and two (2016; blue).** Top plot shows broad-scale habitat preferences, bottom plot shows forest habitat preferences. Plots show the ratio of use to availability of habitat types plotted on the scale of the response. Mean values and 95% confidence intervals are shown in bold. Raw data for each marten are shown by small points. A value of 0 indicates use of a habitat in equal proportion to its availability. Positive values indicate preferential use of a habitat type in relation to its availability. Negative values indicate lower use of a habitat than expected in relation to its availability.

## **Discussion**

Post-release movement of translocated martens followed distinct patterns and the presence of previously released conspecifics altered the duration and extent of dispersal by individuals in a subsequent release. This in turn influenced home range location and resulting habitat use. Animals released in phases should thus not be expected to follow identical post-release strategies, but instead are influenced by the presence and location of conspecifics.

We observed a clear two-phase, post-release movement pattern undertaken by pine martens translocated from their core range in Scotland to mid-Wales. This pattern comprised exploration followed by settlement and was likely a result of initial searching of the new environment for denning and foraging habitat (Slough 1989; Sjoasen 1997; Stamps 2001; Moehrenschrager & Macdonald 2003). A switch to settlement suggests identification of adequate habitat in which to establish a territory. Post-release movement strategies differed between subsequent years of release, with animals travelling further and faster before settling in year two. Here, the main period of exploration predominantly occurred within the first two weeks post-release. Intensive tracking of animals within this initial time period is therefore clearly desirable to avoid loss of contact with dispersing animals. Preferences for broad-scale habitat and forest-type also differed between years. It is likely that conspecific density and habitat quality are major factors influencing these differences.

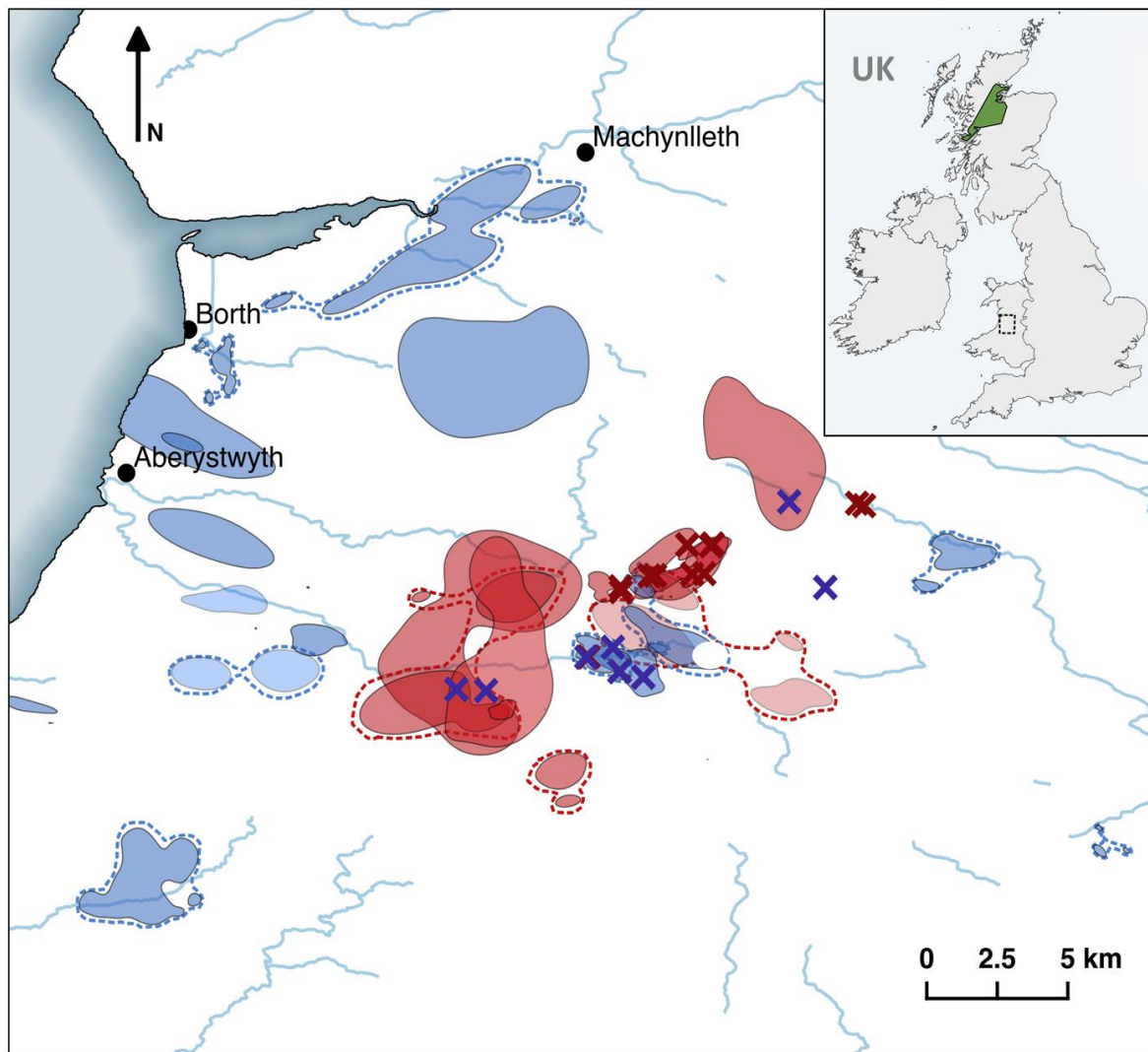
The initial retention of translocated individuals closer to their release sites is central to the long-term viability and establishment of a new population (Yott et al. 2011). Although they differed between years, in Wales the mean distances of pine marten dispersal prior to settlement (8km in 2015 and 14.0km in 2016) were comparable to those recorded for *Martes americana* translocations over similar time periods (0.4-75.3km within 4-161 days; Davis 1983, 0.4-45.7km within 1-64 days; Woodford et al. 2013). Year 1 individuals established territories near to their release sites (Fig. 2.5). Although consisting of large forestry blocks, these release sites are surrounded by pasture, moorland and farmland. Such areas were selected for marten release as they provided a diverse structural environment required for denning, combined with fields

and edge-habitat in which to forage, resulting in the use of habitat proportional to its availability. Within large compartments of commercially managed forestry, tree thinning and felling are common. The felled woodland, favoured by animals released in the first year (Fig. 2.4b), often comprises wind thrown trees or large areas of debris, and offers structural complexity utilised by martens for denning and foraging (Clevenger 1994; Caryl et al. 2012; Lombardini et al. 2015). Growth of new vegetation as a result of felling has been shown to increase diversity and biomass of rodent species, the primary food source of martens (Sidorovich et al. 2010; Caryl et al. 2012). In newly felled areas, martens have been found to respond to this through increased predation, not only on field voles *Microtus agrestis* but bank voles *Myodes glareolus* and wood mice *Apodemus sylvaticus* (Steventon & Major 1982; Sidorovich et al. 2010). The preferential use of these areas by martens in the first year of the releases may therefore be a result of high prey abundance in close proximity to denning sites.

As marten density in the release area increased as a result of territorial establishment by year one individuals, animals released under the same protocols and conditions in year two likely dispersed further in response to territory or site saturation and competition for resources (Yott et al. 2011; Woodford et al. 2013). A study on released otters similarly found that the movement (i.e. exploration) distance of individuals released into unoccupied areas was much lower than those released into areas containing conspecifics (Sjoasen 1997). Density-dependent dispersal (Massaro et al. 2017) is therefore a likely driver of greater settlement distance in second year animals. However, these second-year animals did settle faster than those released in the first year (Fig. 2.2b), possibly spending less time searching for appropriate habitat near to release sites and dispersing immediately out of the large forest blocks into empty territories. These individuals quickly settled in smaller forest fragments on the periphery of the core population (Fig. 2.5), suggestive of saturation around the release sites. The mosaic structures made up of non-commercial woodland, scattered within and around areas dominated by farmland, explain the broad-scale preferential use of forested habitat but lack of selectivity of forest type.

Movement of some individuals was unpredictable and, in both years, a small number of martens (six individuals in total; 15% of 39 animals) were lost after release. Four of these individuals were found again after a long period of absence, some having

travelled exceptionally long distances (e.g. one individual was relocated 103km away from its release site 172 days post-release). When a population is in flux, processes such as habitat preference and range size may be less predictable, demonstrated here as animals try to re-establish themselves, with a lack of mutually exclusive ranges in individuals released in year one (Fig. 2.5). High numbers of these long-distance dispersers may be detrimental to the viability of the translocated populations. With the next nearest established population of martens located in Kielder forest, over 300km away, the likelihood of new individuals arriving in the area and compensating for loss of highly dispersive translocated individuals is low (Mihoub et al. 2011). This long-distance dispersal has been observed in slightly higher proportions in other translocation studies of marten species (26%; Davis, 1983, 30%; Slough, 1989) and is often indicative of local territorial saturation (Yott et al. 2011). Here, the driving forces behind long-distance dispersal remain unclear, although it has been suggested that individual personality and stress levels may be influential (Clobert et al. 2009). The drivers of range size variation were also unclear and could not be attributed to sex, year of release or any post-release metrics. The home range sizes estimated for settled martens were, however, similar to those previously recorded for martens in source locations (5.6-23.6 km<sup>2</sup>; Caryl, 2008). On visual inspection, these range sizes of martens do show overall differences, with ranges being more defined and apparent in year two individuals who show distinct territorial formation akin to those typical of established populations (Powell 1979; Balharry 1993); Fig. 2.5). This may potentially be a result of stronger territorial distinction by established individuals in their second year, when sex-based differences in ranging become more apparent prior to mating and offspring being born in following years (Powell 1979; Erlinge & Sandell 1986; Slough 1989; Sjoasen 1997; Yott et al. 2011; Tolhurst et al. 2015).



**Figure 2.5. Map of home ranges of translocated pine martens released in 2015 (red) and 2016 (blue) in Wales.** Home ranges are 90% kernel density estimates. Individuals with multiple home range centres are grouped with dotted lines. Release pens, indicated by X, are shown for 2015 (red) and 2016 (blue). Rivers are indicated in blue. Inset map of UK indicates trapping locations in Scotland (green) and the release site area in Wales (dashed box).

The difference in post-release strategies by year one and year two animals in this study suggests that the role of conspecifics, particularly established residents, can influence post-translocation movement by released animals. In translocation projects, release of animals is frequently performed in phases due to logistical constraints (Richardson & Ewen 2016). There is often an assumption that individuals in initial and subsequent releases will behave in a comparable manner (Richardson & Ewen 2016). However, as shown in this study, the presence or absence of an established

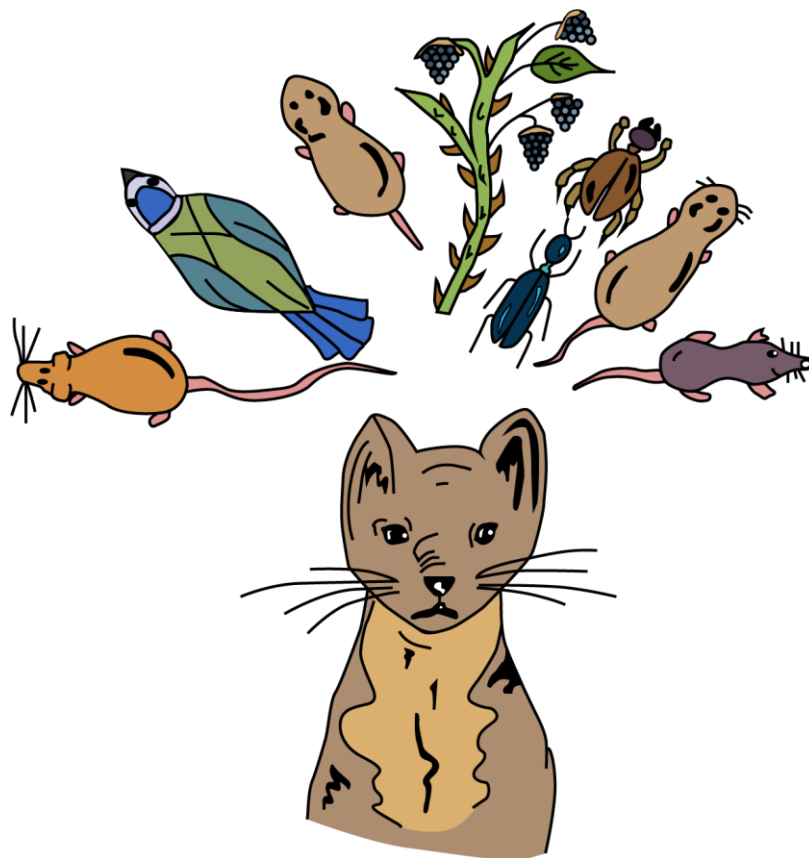
population can result in different dispersal strategies (Richardson & Ewen 2016). The response of released animals to conspecific presence and density should thus be central to reintroduction planning (Richardson & Ewen 2016). Reinforcement of social or colonial species can exploit conspecific attraction to aid the success of projects, either translocating animals in family units or releasing individuals into pre-established colonies (Ward & Schlossberg 2004). The presence of other individuals can indicate suitability of habitat as well as mate availability, having an anchoring effect on subsequently released animals (Ward & Schlossberg 2004). Even in mammals that are not obviously social or colonial, such as the pine marten, social information is still important in dispersal decisions. Translocation and release of animals therefore requires consideration of the social structure and demographic processes driving movement and ranging behaviour. In a translocated population however, this social structure is initially undefined and can result in unpredictable responses to conspecifics and increased dispersal or mortality, particularly if neighbours are unfamiliar (Shier & Swaisgood 2011; Richardson & Ewen 2016). Conspecific attraction might, however, improve the establishment of a release-site population and can be achieved through i) translocation of large numbers of individuals, such as in year one of this study, ii) translocation of neighbouring individuals from source sites (Ydenberg et al. 1988; Shier & Swaisgood 2011), although this may result in a higher level of relatedness amongst individuals, or iii) translocation of individuals into pre-established, low-density populations, such as in year two of this study (Richardson & Ewen 2016).





## Chapter 3

### **Dietary variation in pine martens *Martes martes* before and after a conservation translocation**



### **Chapter 3: Dietary variation in pine martens *Martes martes* before and after a conservation translocation**

#### **Abstract**

Adaptation and survival of translocated individuals to a new environment is a requirement for successful conservation reintroductions and diet is a key dimension of this adaptation. Through investigating the diet of animal populations in source and destination sites, and of individuals before and after translocation, we can better understand how translocated animals adapt and survive, improving the outcomes of reintroductions. Very few studies have investigated the diet of translocated animals before and after translocation. We translocated 39 pine martens *Martes martes* from Scotland, where resident populations are expanding in range and abundance, to Wales, an unoccupied part of their historic range. We investigated the diets of martens before and after translocation, using conventional hard-part analysis of collected scats, combined with stable isotope analysis of whisker samples from known individuals. We show that martens eat significantly fewer voles, berries and amphibians in Wales but more invertebrates, rabbits and rats. Martens in Wales were also found to consume grey squirrels *Sciurus carolinensis* (10% frequency of occurrence in scats), which they had not previously encountered, as grey squirrels are absent in the source locations in Scotland. Isotopic analysis of individual whiskers show that individuals retain their relative trophic position ( $\delta^{15}\text{N}$  value) after translocation, however all individuals appear to be feeding at a higher trophic level. This suggests this generalist population is composed of facultative specialists. Although voles appear to be a preferred prey group in both source and destination sites, martens are capable of prey-switching and feeding on locally abundant prey, including novel species, such as the grey squirrel, that are not present in source sites. This is of particular interest because of the importance of marten restoration for the future of grey squirrel management in the U.K. However, the impact of prey-switching should be considered in feasibility studies and mitigation planning for threatened prey species prior to translocations. The combination of dietary flexibility and individual specialisation displayed here in the form of facultative specialisation enables translocated animals to complement their preferred diet with abundant prey sources,

enhancing the probability of individual survival and, ultimately, the success of conservation translocations.

## ***Introduction***

In a period of climate change, increasing habitat fragmentation and urbanisation, an accelerated level of biodiversity loss is being experienced worldwide (Walther et al. 2002; Gaston 2005). Biodiversity losses can, in some cases, be mitigated establishing protected areas, *ex-situ* conservation measures such as captive breeding and translocations of species that have declined or been lost. Population restoration or reinforcement through the translocation of animals into regions of their historic range is now a common practice in conservation (Seddon 2010; IUCN/SSC 2013). The success, or otherwise, of such translocations is indicated by the establishment of self-sustaining populations and this favourable outcome depends upon the selection of locations with adequate habitat and sufficient resources (IUCN/SSC 2013). In many instances, characteristics for the selection of the 'best' or most suitable destination sites for restoration are based on knowledge of the species in nearby elements of its contemporary range. However, habitats are often limiting in some way and so using currently occupied habitat as the basis for future site selection could still miss important elements, particularly in territorial species where some individuals may be 'forced' into habitats they would otherwise not have chosen. It is therefore almost impossible to quantify all elements of a species' niche and thus prospects for identically matching pre- and post-release habitats are poor. As such, the responses of individuals to new habitats may differ from expectations. The behaviour of animals in refugia and their residual habitats may not be representative of that displayed in high-quality habitats, and translocation of individuals to part of the species' historic range might allow selection of different and/or better habitats and foods.

One of the key ways in which the ecology of translocated individuals might vary is through the exploitation of different food resources. If the resource bases of the pre- and post-release habitats differ, then one of the potential responses of introduced individuals could be to expand their realised niches and exploit these differences, particularly with respect to diet (Crego et al. 2018). The diet of resident species may

also change to incorporate an introduced species (Wanink & Goudswaard, 1994; Bilney et al., 2006). Introductions have thus been shown to have both positive and negative impacts on native or local flora and fauna in the recipient ecosystems (Atkinson et al., 2001; Traba et al., 2017), and these can occur through a number of mechanisms. For example, even the best-matched habitats are likely to differ with respect to relative and absolute abundance of different food resources. The specificity and flexibility of predator diet is therefore likely to influence the success of the translocation (Baker et al., 2001; Bodey et al., 2009). Populations of generalist species may be comprised of individuals that are either generalists (Type A generalists) or individuals that specialise on different things (Type B generalists) (Bearhop et al. 2004; Vander Zanden et al. 2010). Therefore, the type of generalist will be a factor in the outcomes of translocation for threatened species. If the translocated sample of animals comprises type A generalists, or a broad range of type B generalists, then we would expect broad translocation success and survival of individuals. However, if the translocated population comprises a restricted sample of type B individuals, we would expect some individuals to thrive and others to fail if their favoured resources are not readily available. Species that are dietary generalists often thrive by adapting to take the most abundant and easy to capture prey (Sidorovich et al. 2010; Medina et al. 2011), following the alternative prey hypothesis (Lack 1954). This opportunistic variation in prey selection based on availability, known as prey-switching (Murdoch & Oaten 1975), can be beneficial to fitness (Ben-David et al. 1997). Mesocarnivores, such as foxes, mustelids and feral cats, are often characterised by such variable diets and as a result have thrived as invasive species, with devastating impacts on native prey (King 1984). Thus, the impact of translocated animals on vulnerable or pest species not encountered in their source location may have unexpected knock-on effects in the recipient ecosystem, which may itself be of conservation or economic interest (Polak & Saltz 2011; Svenning et al. 2016).

In conservation terms, the restoration of native top predators has generally had positive knock-on impacts on ecosystem function (Ritchie et al. 2012), often through the control of animals perceived to a nuisance or pest: grey wolf *Canis lupus* reintroduction and the resulting control of large ungulate populations in Yellowstone National Park has enabled vegetation recovery (Ripple et al. 2001; Beschta & Ripple 2009). To facilitate detection of wolves, elk avoided scrub and remained in open areas,

enabling the growth and establishment of young saplings that had, in the absence of wolves, suffered from browser suppression (Ripple et al. 2001; Beschta & Ripple 2009). Furthermore, wolf recovery has also limited coyote *Canis latrans* numbers and ranging. In both instances these changes were not driven solely by direct predation but also by avoidance of wolves and the risk of encounters with wolves (Berger & Gese 2007). The reintroduction of mesocarnivores, as opposed to apex predators, is perhaps less likely to elicit such top-down ecological change, though, for reasons of their relatively great abundance, ecosystem impacts might nevertheless be widely felt. Restoration of mesocarnivore populations in the absence of apex predators can result in intensified impacts of foraging due to their 'fearlessness' of predation (Suraci et al. 2017). Effectively, this is a form of 'mesopredator release', allowing for rapid expansion of native mesopredator populations and associated impacts on prey populations (Prugh et al. 2009; Roemer et al. 2009). Although more often related to invasive, non-native mesopredators (Johnson et al. 2007), this has also been demonstrated by native species such as the coyote in the absence of wolves in North America (Crooks & Soule 1999).

The pine marten *Martes martes* is a mustelid carnivore that is native to the UK and which suffered population and range declines in the 19<sup>th</sup> and early 20<sup>th</sup> centuries, as a result of intensive predator control and habitat loss (Langley & Yalden 1977). However since the 1990s, the species has begun to recolonize its former range from its refugia in the Scottish Highlands (Sainsbury et al. 2019). Although populations have spread to the central belt of Scotland and been re-established as far south as Dumfries and Galloway (Croose et al. 2013), the pine marten has yet to re-establish in England and Wales. Surveys in 2013 and 2014 (Croose et al. 2013; Macpherson 2014) found no evidence of populations in England and Wales, aside from small numbers in Northumberland, Shropshire and Hampshire, the latter two of which are most likely the result of illicit releases (Sainsbury et al. 2019). As a result, we undertook a project to reinforce the marten population in Wales, with the aim of establishing a viable population in the region (Macpherson 2014).

Pine martens are somewhat adaptable carnivores with regards to diet, hunting technique and activity schedule (McDonald 2002; Birks 2017). This variation is driven largely by temporal fluctuations in the abundance of their primary rodent prey (Helldin

1999). In recent years, there has been an increased focus on the ecology of pine martens due to their potential role in controlling the invasive non-native grey squirrel *Sciurus carolinensis* (Sheehy & Lawton 2014; Sheehy et al. 2018). Grey squirrels are of particular concern to the forestry industry, due to their tendency to strip bark and the damage this causes to timber quality and yield (Mayle et al. 2009). Thus far, grey squirrel control methods, including poisoning, trapping and shooting, have been unsuccessful in reducing grey squirrel abundance and the resulting tree damage at anything other than local spatial and temporal scales. However, studies in Ireland and Scotland (Sheehy & Lawton 2014; Sheehy et al. 2018) have shown promise, whereby in areas of high and increasing pine marten density, grey squirrel densities are low or declining. This, in turn, is thought to benefit the native red squirrel *Sciurus vulgaris*, which has suffered major declines as a result of competition and disease transmission from the non-native grey squirrel (Rushton et al. 2006). Predation of squirrels by pine martens, which has been demonstrated to varying degrees across their range (Storch 1990; Zalewski 2005; Sidorovich et al. 2010; Sheehy et al. 2014), is therefore of primary interest for conservationists and foresters alike.

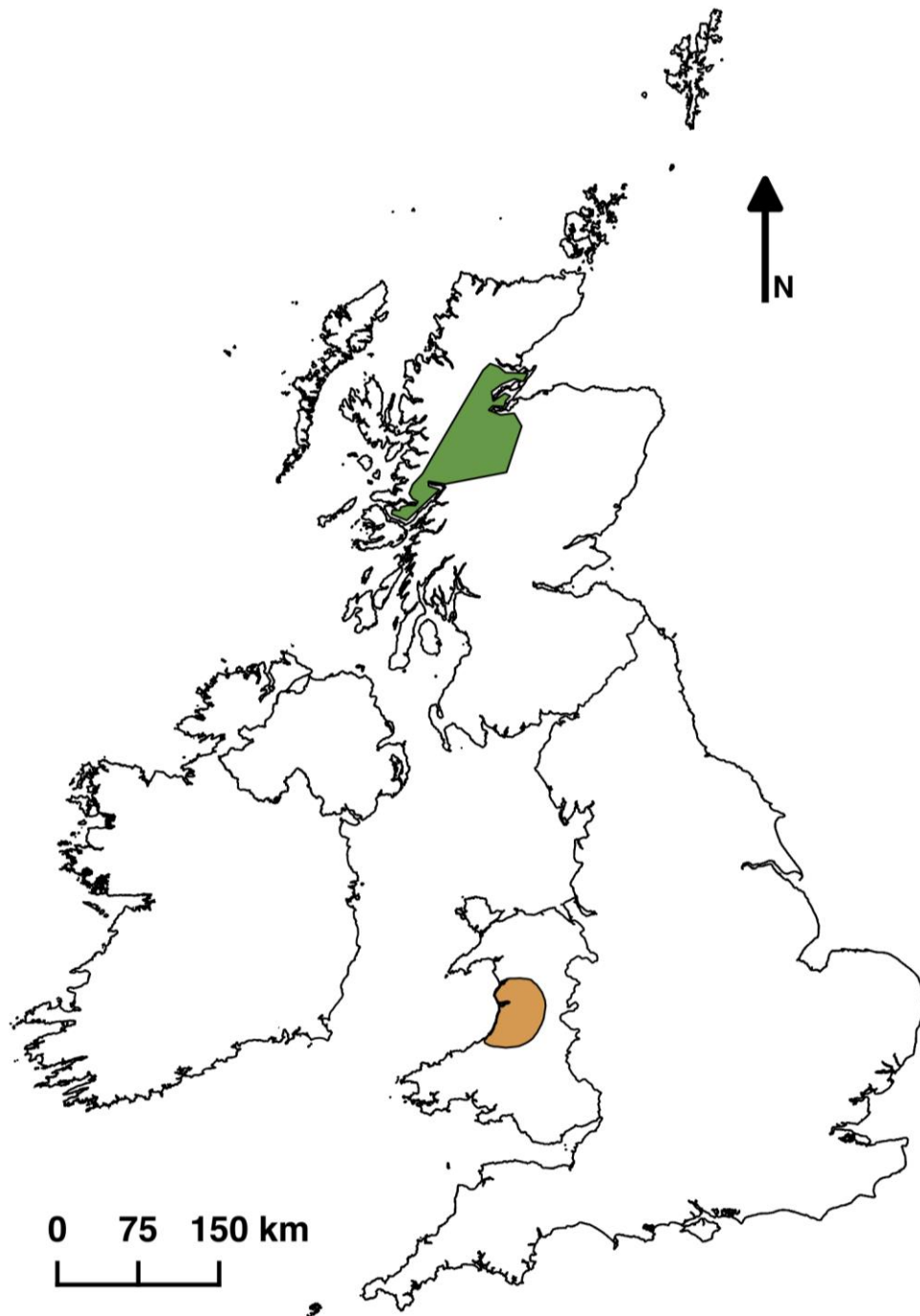
We have taken advantage of the pine marten restoration project in Wales (Macpherson 2014) to study variation in the diet of translocated mesocarnivores in their source and release sites. We were able to document diet composition at the level of the individual and the population, before and after their translocation. We translocated wild-caught animals, sourced from resident marten populations in Scotland, where they co-occur with red squirrels, to create a new population in an unoccupied region in Wales, with no nearby red squirrels but a long-established grey squirrel population (Lucas 1997). Through a combination of conventional analysis of undigested hard parts and stable isotope analysis of tissue from martens and their prey, we have documented dietary variation in both environments. Although the assessment of post-translocation diet is frequently used to assess predator impact on the recipient ecosystem (Koprowski 1994; Baker et al. 2001; Ripple et al. 2014), it is rarely compared to the diets of populations at source locations. This assessment of pre- and post-translocation diet at population and individual levels is therefore an unusual approach in the review of a translocation. Analysis of pine marten scats provided a ‘snapshot’ overview of population-level dietary composition of unknown

individuals and qualitative detail to enable interpretation of stable isotope data. Stable isotope analyses of marten whiskers using carbon and nitrogen isotopes provide an insight into individual-level differences and longer-term diets. We expected that if martens are Type A generalists, there would be little evidence of dietary consistency across locations but a high level of variance in both locations, as all individuals should consume what is most abundant. This would be reflected in differing prey occurrences in marten scats and differing niche breadths. However, if martens are Type B generalists, we expect the majority of individuals to retain similar diets and to maintain a degree of dietary specialisation at either end of the translocation. This would result in low levels of isotopic variance, i.e. small individual niche breadth before and after translocation, and a high degree of correlation between mean isotopic values.

## **Materials & Methods**

### *Study sites*

Sample collection was undertaken in source sites in the Scottish Highlands and destination sites in mid-Wales (Fig. 3.1). Habitat in both locations was dominated by commercial conifer plantations, largely comprising Sitka spruce *Picea sitchensis*, interspersed with Norway spruce *Picea abies*, Douglas fir *Pseudotsuga menziesii*, larch *Larix kaempferi*, *L. eurolepis* and lodgepole pine *Pinus contorta*. Commercial plantations also incorporated smaller areas of plantation and naturally regenerating mixed deciduous woodland, comprising sessile oak *Quercus petraea*, beech *Fagus sylvatica*, rowan *Sorbus aucuparia*, birch *Betula* spp. and willow *Salix* spp., and were surrounded by agricultural land, primarily marginal, unimproved and semi-improved grassland for livestock grazing.



**Figure 4.1. Pine marten scat survey and whisker collection sites from 2015-2018.** Scat collection and pine marten source sites in Scotland are indicated in green. Scat collection and pine marten release sites in Wales are indicated in orange.



### *Scat collection and analysis*

Pine marten scats were collected at source sites in Scotland in March in 2015, 2016 and 2017. Scat surveys comprised a 1.5km transect within every 4km<sup>2</sup> in regions thought to contain marten populations (Survey method from The Vincent Wildlife Trust). DNA was extracted from a subset of all scats (n = 569) collected in Scotland from 2015-2016 and tested for pine marten DNA to determine if scat identification was correct (See methods in O'Meara et al., 2014; C. Powell & C. O'Reilly, Waterford Institute of Technology, *unpublished data*). These analyses confirmed that all identifiable scats came from pine martens (n = 432), with none being assigned to any other small carnivore species. Remaining scats were of insufficient quality to identify (n = 137). A sample of 255 scats, collected from six main sites in Scotland (102 from 2015, 18 in 2016 and 135 in 2017; Fig. 3.1), were used in analysis of marten diet in source populations. In recipient sites in Wales, scats were collected from around release and den sites and opportunistically from forestry tracks and baited camera traps after martens were released. Formalised scat transect surveys were not feasible due to the low density of animals and apparent absence of territorial marking. A total of 181 scats collected in Wales (4 from 2015, 17 from 2016, 108 from 2017 and 52 from 2018) were used. All were assumed to be from translocated individuals, as earlier surveys had found no evidence of a resident population (Macpherson 2014). Following collection, all scats were frozen at -20°C until being processed.

For processing, scats were first soaked in water and biological detergent solution for 24 hours before being broken apart over a 0.5mm sieve. Remains were washed thoroughly and stored in 70% ethanol prior to examination. Hard-parts (i.e. teeth and jaws, bone fragments and seeds) were examined using a binocular dissection microscope to identify prey remains to the lowest possible taxon group using reference keys (Day 1966; Teerink 1991; Wolfe & Long 1997; Yalden & Morris 2003). It was not possible accurately to identify bird remains to species, therefore the presence of feathers was used to indicate only the presence of birds as a Class. Seeds, berries and invertebrate remains were identified using field guides and reference samples collected from sites. For analysis, species were grouped into major food categories, based on taxonomic, ecological or morphological features (i.e. size). Pine marten scats are dominated by hair and a sub sample of scats from each country (n = 22 from each country) were

sampled for hair (n = 24 hairs per scat). Imprints of hair were made into clear nail polish on microscope slides. These were then examined under 400x magnification and, if high enough quality to assess, identified to species level (Teerink 1991). Only 3 scats (<7%) within this sub-sample contained the hair of more than one prey item. Other studies have suggested that scats from species of a similar size, such as ferrets (Bodey et al. 2011), represent one complete prey item. We found that 81% of scats analysed for hair (36 out of 44 scats) contained hair that matched the bone fragments found in the same scat. The remaining 8 scats did not contain any bone fragments with which to compare the hair samples. This investigation would suggest that bone fragments are representative of the range of prey consumed. We present diet composition with frequency of occurrence (FO), representing number of instances of each prey type, where identification of one prey type in one scat represents one occurrence. We also calculate the percentage frequency of occurrence (%FO), which represents the occurrence of each prey group as a proportion of all occurrences. We calculated niche breadth B, using Levins' (1968) measure:

$$B = \frac{1}{\sum p_i^2}$$

where  $p_i$  is the proportion of scats containing prey group  $i$ . The measure is then standardised (onto a scale of 0-1) to enable comparison between different sample sizes from each country:

$$B_A = \frac{B - 1}{n - 1}$$

The higher the value of  $B_A$ , the more diverse the diet is considered to be.

## **Stable isotope sample collection and analysis**

### *Sampling martens*

Pine martens were live-trapped in September-November 2015, 2016 and 2017 in Scotland using live-capture traps (Tomahawk 205, Tomahawk Live Trap, Hazelhurst, USA). Two whiskers were plucked from each captured marten ( $n = 49$ ), while they were anaesthetised for fitting radio-collars prior to translocation from Scotland to Wales. 39 of these animals were then translocated to Wales in 2015 and 2016. The remaining 10 individuals were surplus to requirement and were re-released at capture locations. Two whiskers were taken again from 21 (9M, 12F) animals in Wales when they were either re-trapped to remove radio collars 8-10 months after their release ( $n = 19$ ) or were found dead ( $n = 2$ ). When recaptured for collar removal, animals were not anaesthetised and samples were cut with scissors as close to the whisker base as possible, rather than plucked. Not all individuals had been recaptured in Wales by the time of this study ( $n = 18$  remained uncaptured), therefore we have not included post-translocation samples from all translocated animals.

### *Reference prey collection*

To account for spatial and temporal variation in marten isotopic signatures, reference prey samples based on scat contents were collected to enable adjustment of marten samples to a common baseline. Prey samples were collected in source and release sites during the months preceding whisker sampling, ensuring isotopic signatures of foods were spatially and temporally matched to those assimilated into the marten whiskers (Inger & Bearhop 2008). In Scotland, samples were collected approximately eight weeks prior to marten capture and translocation (July-August in 2015, 2016 and 2017). In Wales, samples were collected in release site woodlands in the spring following release of martens (March-April 2016 and 2017), but prior to re-trapping to remove radio-collars in May-July. To collect small mammal prey, 40 Longworth traps (Penlon Ltd., Abingdon, UK) were set in a grid formation in marten trapping (Scotland) or release sites (Wales) for two days. Traps were filled with hay, baited with commercial dried food for rodents and fly pupae for shrews, and checked twice daily. Up to 10 specimens of each species per site were euthanised for use in

stable isotope analysis, further individuals were released at point of capture. Small mammal carcasses were stored at -20°C.

### *Sample preparation*

Whisker samples (one from each capture event) were rinsed in distilled water to remove any oil and dirt and left to air dry (Robertson et al. 2013). Small mammal samples were defrosted and a section of muscle was taken from the right hind leg of each animal. All samples were then freeze-dried for 36 hours to remove any residual moisture. Whiskers were weighed, measured and cut into sections weighing approximately 0.7 mg each. Sections were then cut into several smaller pieces and decanted into tin cups. Each whisker provided a mean of 2 sections (SD = 0.8, range = 1-4). The growth rate of marten whiskers could not be measured directly but was considered to be comparable to that of badgers *Meles meles* (Robertson et al. 2013) and stoats *Mustela erminea* (Spurr 2002), which have been estimated to grow at 0.43mm and 0.6mm per day, respectively. These values were used to estimate the mean time period represented by each whisker. Of the martens sampled, the mean whisker length was 52mm (range = 26-76) and was therefore estimated to represent approximately 3-4 months (87-122 days). The limited number of whisker sections did not provide an adequate number of sections to compare diet through time and account for seasonal effects. Furthermore, whisker samples taken from animals in Wales do not all reflect the same time period, as animals were recaptured opportunistically over a 2 month period. Freeze-dried prey muscle samples were homogenised into a fine powder using a pestle and mortar. Approximately 0.7mg of each sample was decanted into tin cups and sealed for simultaneous carbon and nitrogen stable isotope analysis. We determined the masses of the stable isotopes of carbon and nitrogen using elemental analysis-isotope ratio mass spectrometry. Both isotope ratios are expressed as  $\delta$  values in parts per mil (‰), representing the ratio of the heavy to light isotope based on the international standard for each element (atmospheric nitrogen, N<sub>2</sub>, for  $\delta^{15}\text{N}$  and Vienna Pee Dee Belemnite VPDB for  $\delta^{13}\text{C}$ ). Precision of measurements was estimated to be  $\pm 0.1\text{‰}$  calculated from standards run within batches of samples. The incorporation of carbon and nitrogen from foods into metabolically inert tissues, such as whiskers, enables the preservation of a dietary isotopic record at the time of tissue formation (Crawford et al. 2008). The breadth of carbon sources being utilised is indicated

by the ranges of  $\delta^{13}\text{C}$ , while  $\delta^{15}\text{N}$  signatures broadly represent the trophic levels at which consumers are feeding (Post 2002; Bearhop et al. 2004; Inger & Bearhop 2008).

## **Statistical analysis**

### *Scat content analysis*

We used a resampling approach to identify differences in pine marten scat content between Scotland and Wales. We generated null distributions by creating 10,000 pseudo-samples of diet in Wales, with sample size of 181, based on the composition of sample of scats from Scotland. The probability of sampling each prey item in Wales was based on their percentage frequency of occurrence (%FO) in the Scottish dataset. We then compared the observed %FO value generated from Welsh scats to the predicted %FO distributions generated from Scottish data. We generated exact p-values by comparing the observed %FO values to the null distributions generated using the resampling approach. Each p-value therefore represents the proportion of the frequency histogram (for the null distribution) found below the observed %FO value. The observed consumption of each species group in Wales was considered to be significantly different from the predicted values in Scotland if the observed %FO in Wales lay outside the 95% confidence limits.

### *Stable Isotope analysis*

We inspected the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of marten whiskers in relation to those of their prey (Fig. 3.4). Prey groups, whether based on ecological function or taxonomic divisions, were not well differentiated, therefore exact dietary composition could not reliably be assessed using mixing models (Phillips et al. 2014). Furthermore, after adjustments using trophic discrimination factors (TDFs), which are calculated based on the phylogeny and dietary ecology of consumers and generated in SIDER (Healy et al. 2018; -4.41‰ for  $\delta^{15}\text{N}$  and -2.88‰ for  $\delta^{13}\text{C}$  for all marten samples), some marten signatures fell outside of the isotopic ranges occupied by the prey items collected. This suggested that either i) there was spatial or temporal heterogeneity between prey and predator samples that we had not captured or, ii) there were prey sources that we had not sampled or, iii) the trophic discrimination factors generated for this species were

incorrect. As a result, we focussed analyses on the marten whisker signatures only. We analysed variation in marten  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in three ways; (1) a between-country population analysis to assess variation in isotope values between source and destination, sites while controlling for variation between years, (2) a between location, within-individual correlation in mean isotope values per whisker to assess consistency (specialisation) in individuals between Scotland and Wales and (3) a between location within-individual correlation in the standard error of the mean isotope values per whisker, to assess within-individual variation in isotope values in Scotland relative to those in Wales.

The between-country population analysis (analysis 1) included all martens that were trapped throughout the entire study in both Scotland ( $n = 49$ ) and Wales ( $n = 21$ ). This model comprised a linear mixed effects model with a Gaussian error distribution and a random effect of individual ID nested within country, since multiple whiskers and whisker sections were treated as repeat measures of individual martens. Country of capture, sex, weight, age (juvenile, sub-adult or adult), translocation year (2015 or 2016) and a sex\*weight interaction were explanatory variables. The interaction term was included to account for the pronounced sexual size dimorphism seen in martens. Model selection was performed using an information theoretic framework using the *R* package '*MuMIn*' (Barton 2018). Model performance was assessed using Akaike's information criterion corrected for small sample size (AICc). Models within  $\Delta\text{AICc} \leq 2$  of the top model were included in the top model set (Burnham & Anderson 2004), averaged to identify the main explanatory variables and to calculate effect sizes and 95% confidence intervals (Burnham & Anderson 2004). If only one model was in the top set then these results are reported. Variables in averaged models with 95% confidence intervals that did not overlap zero were considered significant. The relative importance (RI) of each variable and the full model averages are reported as these are deemed more conservative (Grueber et al. 2011). The explanatory power of full averaged models was estimated with Nagelkerke  $R^2$  defined by Nakagawa and Schielzeth (2013) in the package '*MuMIn*' (Barton 2018). The marginal  $R^2$  represents the percentage of variance explained by the fixed effects alone and the conditional  $R^2$  represents the explanatory power of fixed and random effects combined.

For analyses 2 and 3, only martens with samples from both Scotland and Wales were used. This gave a paired before and after translocation comparison for each individual. Only individuals whose whiskers could be divided into more than 1 section, and therefore generate mean and standard error (SE) values ( $n = 15$ ), were analysed. For both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  we used Pearson's product moment correlation coefficient ( $r$ ) to test if isotopic position of an individual in Scotland was correlated with its isotopic position once translocated to Wales, relative to other translocated individuals. The closer the correlation coefficient to 1, the more closely correlated the values and the more consistent an individual's isotopic position before and after the translocation.

Isotope values of individual Scottish and Welsh martens were adjusted to a common baseline to control for spatial and temporal variation of the isotope signatures of food sources. Plots of food sources (Fig. 3.4) suggested that the mean isotopic baseline of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  differed between countries. Therefore to enable comparison of individuals between countries, we established a baseline for each country using the isotope signature of a commonly eaten prey animal (Post 2002), the field vole *Microtus agrestis*. Field voles were used as they were frequently captured and eaten in both Scotland and Wales. An overall baseline mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  was first generated using all field vole samples from Scotland and Wales. The baseline mean of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for each country was then generated using samples from each country. This baseline mean of each country was then subtracted from the overall mean baseline. This gave the distance of each country mean from the mean overall isotopic baseline. This country-specific distance was then subtracted from each individual marten whisker value to give an adjusted  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ . The resulting value represents the relative position of each marten from the isotopic baseline of their country and enables comparison between countries. All statistical analyses were performed using *R* version 3.5.2.

### *Ethical Statement*

The study was approved by The University of Exeter Animal Welfare and Ethical Review Board and under licences from Scottish Natural Heritage and Natural Resources Wales and from The Home Office under the Animals (Scientific Procedures) Act.

## Results

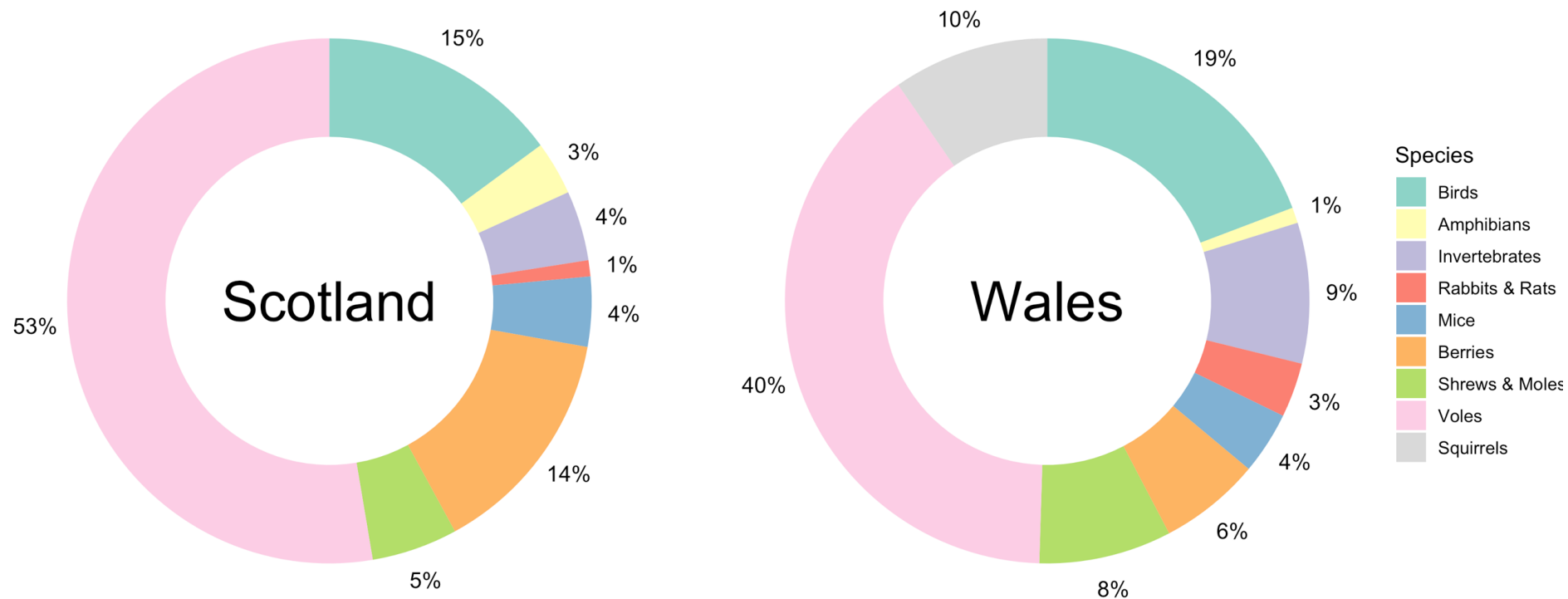
### *Hard-part analysis*

A total of 436 scats were analysed, 352 of which contained identifiable remains (Table 3.1). The standardised Levins' measure of niche breadth revealed that martens in Wales ( $B_A = 0.43$ ) exhibited a broader dietary niche than those in Scotland ( $B_A = 0.26$ ; Table 3.1). The percentage frequencies of occurrence (%FO) of a number of prey items in marten scats in Wales was significantly different from those in Scotland (Fig. 3.2, Table 3.1). Among key components of marten diets, voles, comprising field voles *Microtus agrestis* and bank voles, were the most dominant item in both locations, but comprised a significantly smaller ( $p < 0.001$ ) proportion of items in Wales (40%) than in Scotland (53%). Squirrel remains were only found in marten scats from Wales, where they amounted to 10% of identifiable prey occurrences ( $p < 0.001$ ). Bird remains, in the form of feathers, comprised a similar proportion of items in Wales (19%) and Scotland (15%), as did mice (Wales 4%, Scotland 4%). Among the less frequent prey categories, shrew remains also occurred at a similar proportion (Wales 8%, Scotland 5%), whereas invertebrate remains appeared with significantly greater frequency in Wales (9%) than in Scotland (4%;  $p < 0.001$ ) as did medium-sized mammals (rats and rabbits; Wales 3%, Scotland 1%,  $p < 0.001$ ). By contrast, berries were found less frequently in Wales (6%) than in Scotland (14%;  $p < 0.001$ ), as were amphibians (Wales 1%, Scotland 3%,  $p < 0.02$ ).

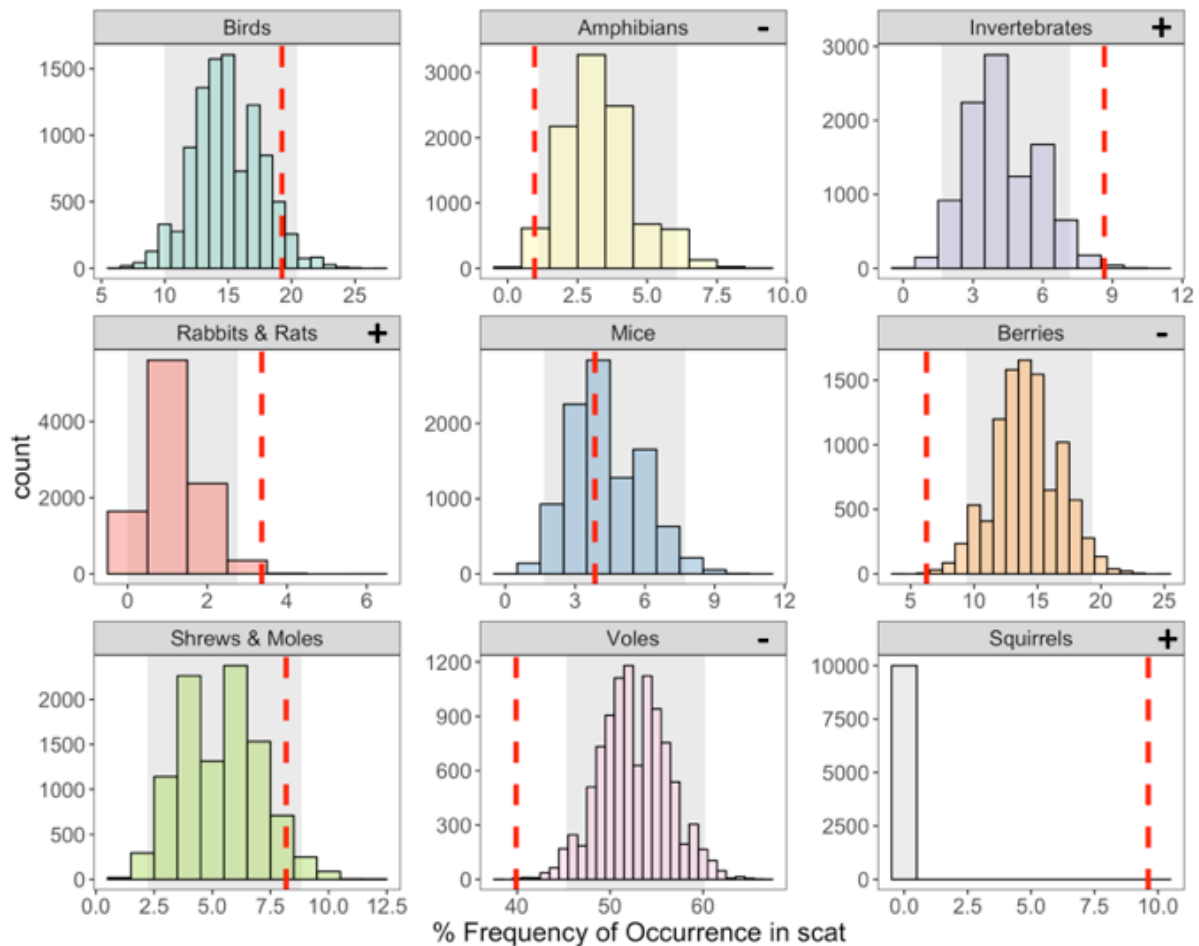


**Table 3.1. Results of examination of pine marten scat contents from Scotland (source sites) and Wales (release sites) collected between 2015 and 2018.** Species are grouped based on taxonomic, ecological or morphological features (i.e. size). Squirrels have not been grouped with 'medium-sized mammals' due to the interest in their role in marten diet as well as differing diet to rabbits and rats. Totals of prey groups are given above individual species values.

Prey item	Scotland		Wales	
	FO	%FO	FO	%FO
<b>Voles (total)</b>	<b>159</b>	<b>52.6</b>	<b>83</b>	<b>39.9</b>
<i>Myodes glareolus</i>	17	5.6	3	1.4
<i>Microtus agrestis</i>	73	24.2	46	22.1
Vole spp.	69	22.8	34	16.3
<b>Mice (total)</b>	<b>13</b>	<b>4.3</b>	<b>8</b>	<b>3.9</b>
<i>Apodemus sylvaticus</i>	3	1.0	3	1.4
<i>Mus musculus</i>	0	0.0	3	1.4
Mouse spp.	10	3.3	2	1.0
<b>Shrews and Moles (total)</b>	<b>16</b>	<b>5.3</b>	<b>17</b>	<b>8.2</b>
<i>Sorex minutus</i>	5	1.7	2	1.0
<i>Sorex araneus</i>	4	1.3	6	2.9
Shrew spp.	5	1.7	5	2.4
<i>Talpa europaea</i>	2	0.7	4	1.9
<b>Medium size mammals (total)</b>	<b>3</b>	<b>1.0</b>	<b>7</b>	<b>3.4</b>
<i>Rattus norvegicus</i>	1	0.3	5	2.4
<i>Oryctolagus cuniculus</i>	2	0.7	2	1.0
Squirrels <i>Sciurus</i> spp.	0	0.0	20	9.6
Amphibians	10	3.3	2	1.0
Invertebrates	13	4.3	18	8.7
Birds	45	14.9	40	19.2
Berries	43	14.2	13	6.3
Total no. of identified prey items	302		208	
<b>Total no. of scats examined</b>	<b>255</b>		<b>181</b>	
No. of scats containing unidentifiable items	47		37	
No. of scats containing bones & teeth	184		124	
No. of scats containing hair only	24		20	
No. of scats analysed for hair	22		22	
<b>Levins' standardised niche breadth</b>	<b>0.26</b>		<b>0.43</b>	



**Figure 3.2. Diet composition of pine martens derived from scats in Scotland (left) and Wales (right).** Values represent the percentage frequency of occurrence (%FO) of each prey group in each country – a breakdown of these values is also provided in Table 3.1. Prey groups are represented by colours.

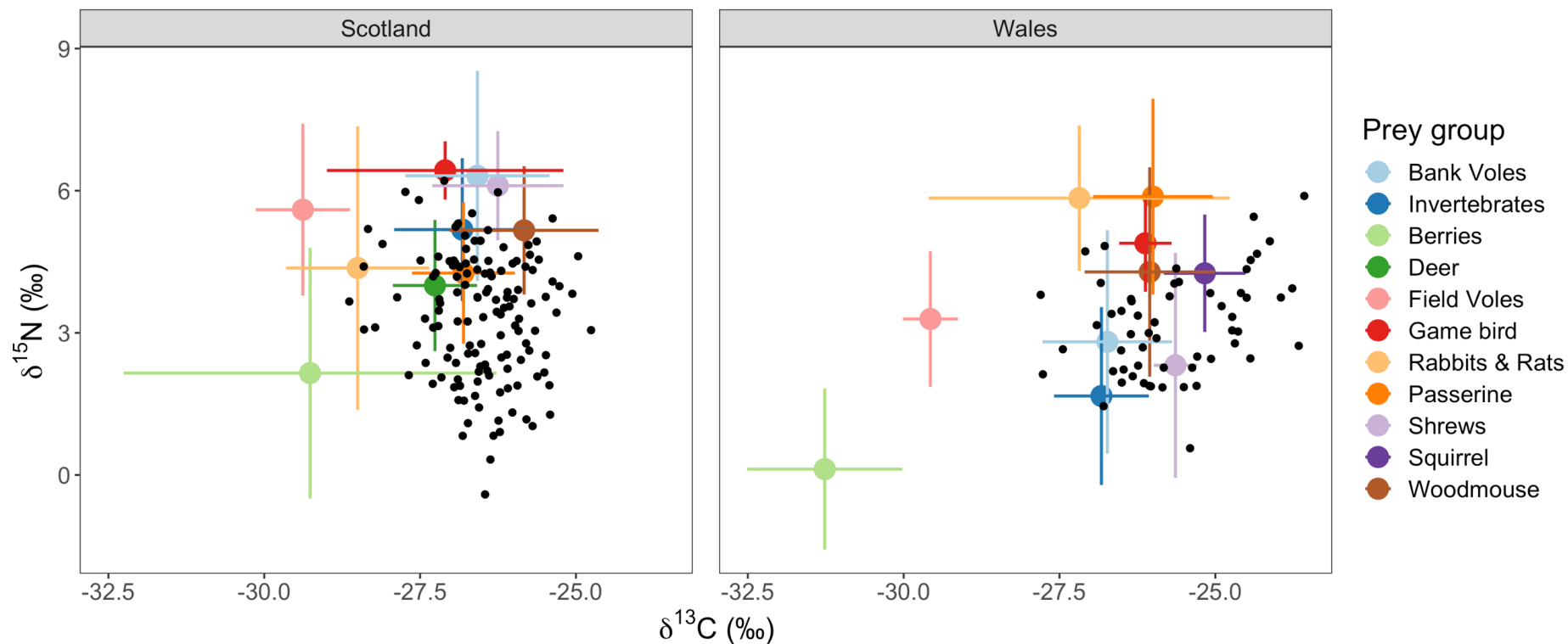


**Figure 3.3. Comparison of the relative importance of prey categories in diet of translocated pine martens in Wales, compared to resident martens at source sites in Scotland.** Observed percentage frequency of occurrence %FO of each prey category in Welsh marten scats is indicated with a red dotted line. Predicted distribution of the %FO of each prey category based on the %FO of each prey category in Scottish marten scats is shown as a histogram, derived from bootstrapping with replacement. The range of the 95% quantile of the predicted %FO is shown in grey shading behind each distribution plot. Prey items which were consumed less than predicted are marked with '-' in the top right of each plot and those which were consumed more than predicted are indicated with a '+'. The %FO is given on the x-axis and the number of bootstrapped samples out of 10,000 samples is given on the y-axis.

### *Stable Isotope analysis*

In analysis of the stable isotope values of all individuals captured (Model 1), the null model was in the top model set for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ .  $\delta^{15}\text{N}$  values of marten whiskers did not vary significantly by sex, weight, the interaction between sex and weight, age, translocation year or country of capture.  $\delta^{13}\text{C}$  values of marten whiskers were significantly greater for translocated martens in Wales than in Scotland (Table 3.2), but were not affected by any other terms in the model. For both isotopes, models explained a large proportion of the variance when encompassing the random effect of individual marten ( $R^2c$ ; Table 3.2). However, the marginal  $R^2$ , which does not take into consideration the nested random effect of individual marten within country, showed the fixed effects had poor explanatory power alone ( $R^2m$ ; Table 3.2). This suggests that unmodeled differences between individuals explained the majority of variation in marten isotope values. Further analysis of a subset of individuals sampled in both countries, adjusted to a common baseline, enabled comparison of diet within individuals ( $n = 15$ ; 7M 8F). There was a significant correlation between the isotope values of individuals in Scotland and in Wales for mean  $\delta^{15}\text{N}$  ( $r = 0.65$ ,  $p = 0.009$ , Table 3.2; Fig. 3.5) but not mean  $\delta^{13}\text{C}$  ( $r = 0.37$ ,  $p = 0.179$  Table 3.2) or standard error of the mean  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$  ( $\delta^{15}\text{N}$ :  $r = -0.30$ ,  $p = 0.271$ ,  $\delta^{13}\text{C}$ :  $r = -0.22$ ,  $p = 0.439$ ; Table 3.2). Adjustment of marten isotopic signatures using mean field vole values accounted for differences in the isotopic baseline in both countries. The mean  $\delta^{13}\text{C}$  values for field voles in Scotland was  $-29.4\text{‰} \pm 0.17$  SE in Scotland and  $-29.6\text{‰} \pm 0.20$  SE in Wales. The mean  $\delta^{15}\text{N}$  values were  $5.60\text{‰} \pm 0.40$  SE in Scotland and  $3.29\text{‰} \pm 0.64$  SE in Wales. These differences could also be observed when prey sources were plotted together (Fig. 3.4). This baseline adjustment of marten values revealed that, as well as mean  $\delta^{15}\text{N}$  values being correlated, values were also, on average, over 2‰ higher in Wales (Scotland mean:  $6.26\text{‰} \pm 0.34$  SE, Wales mean:  $8.61\text{‰} \pm 0.26$  SE; Fig. 3.5). To investigate the potential dietary composition of martens using whiskers, prey groups were plotted in isotopic space (Fig 3.4). To account for trophic enrichment of consumer tissues, a result of the retention of heavier isotopes during consumer metabolism (Kelly et al. 2012), pine marten whisker values were adjusted using Trophic Discrimination Factors (TDFs) calculated in SIDER (Healy et al. 2018) based on marten phylogeny and ecology (Fig 3.4). Values produced ( $-4.41\text{‰}$  for  $\delta^{15}\text{N}$  and  $-2.88\text{‰}$

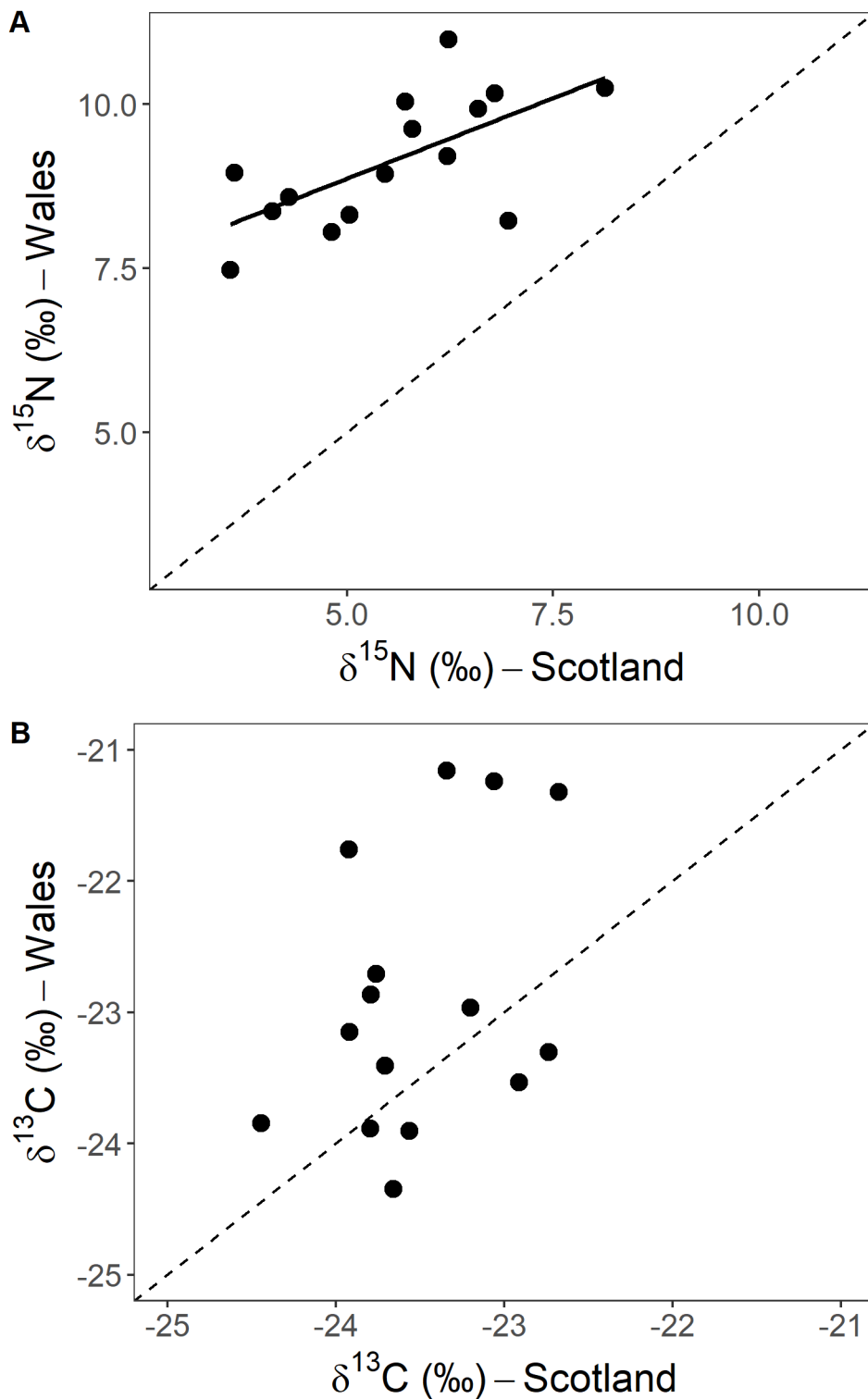
for  $\delta^{13}\text{C}$ ) were comparable to those of badger, red fox *Vulpes vulpes* (Kelly et al. 2012) and sea otter *Enhydra lutra nereis* (Newsome et al. 2009). However, due to unclear partitioning between prey groups, dietary reconstruction using isotopic data was not possible.



**Figure 3.4. Isotopic signatures of food sources and pine marten whiskers in source (Scotland) and release (Wales) sites.** Marten whiskers are adjusted using trophic discrimination factors (TDFs) generated in SIDER (-4.41‰ for  $\delta^{15}\text{N}$  and -2.88‰ for  $\delta^{13}\text{C}$ ; black points) to account for enrichment at higher trophic levels. Prey sources are represented by mean  $\pm$  standard deviation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

**Table 3.2. Models assessing the importance of biotic and abiotic variables on the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  in pine marten whiskers, and the correlation between Scottish and Welsh samples from the same pine marten.** For linear mixed effects models, the effect size, 95% confidence interval (CI) and relative importance (RI) of each variable retained in the top averaged model are given. The fit of the averaged model is represented by the conditional  $R^2$  ( $R^2\text{c}$ ) and marginal  $R^2$  ( $R^2\text{m}$ ). For Model 2 and 3, Pearson's correlation coefficient  $r$ , and the associated  $p$ -value are reported. Results in bold are significant.

Model Name	Full model	Analysis/test used	Average model result					
			Variable	Effect size	95% CI	RI	$R^2\text{c}$	$R^2\text{m}$
Model 1	$\delta^{15}\text{N} \sim \text{sex} * \text{weight} + \text{age} + \text{country} * \text{year} + (\text{ID}/\text{country})$	Linear mixed effects model	Year	-0.69	-1.14, 0.29	0.6	0.639	0.078
	[Top model] $\delta^{15}\text{N} \sim \text{year} + \text{age} + (\text{ID}/\text{country})$		Age	-0.23	-0.98, 0.52	0.3		
	$\delta^{13}\text{C} \sim \text{sex} * \text{weight} + \text{age} + \text{country} * \text{year} + (\text{ID}/\text{country})$ [Top model] $\delta^{13}\text{C} \sim \text{country} + (\text{ID}/\text{country})$	Linear mixed effects model	<b>Country</b>	<b>0.61</b>	<b>0.28, 0.95</b>	<b>1</b>	<b>0.529</b>	<b>0.043</b>
Model 2	<b>mean Scottish <math>\delta^{15}\text{N}</math> ~ mean Welsh <math>\delta^{15}\text{N}</math></b>	Pearson's product-moment correlation	<b><math>r = 0.65</math>, <math>p = 0.0009</math></b>					
	mean Scottish $\delta^{13}\text{C}$ ~ mean Welsh $\delta^{13}\text{C}$		$r = 0.37$ , $p = 0.179$					
Model 3	SE of mean Scottish $\delta^{15}\text{N}$ ~ SE of mean Welsh $\delta^{15}\text{N}$	Pearson's product-moment correlation	$r = -0.30$ , $p = 0.272$					
	SE of mean Scottish $\delta^{13}\text{C}$ ~ SE of mean Welsh $\delta^{13}\text{C}$		$r = -0.21$ , $p = 0.439$					



**Figure 3.5. The correlation between isotopic  $\delta^{15}\text{N}$  signatures (A) and  $\delta^{13}\text{C}$  (B) of individual martens in Scotland and Wales, scaled to a common baseline.** Common baseline values were based on variation in field vole  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values, and pine marten whisker values in each country were adjusted accordingly. Values are not adjusted using a trophic discrimination factor (TDF). Each point represents an individual marten. Scottish  $\delta^{15}\text{N}$  values (A) were significantly correlated with Welsh values for each individual ( $r = 0.65$ ,  $p < 0.01$ ; Table 3.2), this correlation is represented by a solid black line. There was no significant correlation between  $\delta^{13}\text{C}$  values therefore no line has been added.



## ***Discussion***

At a population level, pine marten diet before and after translocation from Scotland to Wales was found to differ substantially. In Wales, marten diets were more diverse than in Scotland and consisted of significantly smaller proportions of voles, berries and amphibians but greater proportions of rabbits and rats, invertebrates and squirrels, the last of which was not available in Scotland (Table 1; Fig 3.2 & 3.3). As a result, after translocation, the majority of individuals appeared to be feeding at a higher trophic level (Fig. 3.5) This demonstrates that as a species, pine martens are dietary generalists that are able to vary their diets in relation to changing prey availability. Martens studied before and after translocation retained their dietary specialisations relative to one another, suggesting that at an individual level they are dietary specialists (Type B generalists; Bearhop et al., 2004). However, the recorded change in trophic level reveals that this specialisation is not completely rigid and that specialist individuals can display a degree of dietary flexibility, likely through the consumption of abundant species to complement their dietary preferences.

At a population level, the carbon sources that martens are utilising differ between Scotland and Wales. Carbon isotope ratios ( $\delta^{13}\text{C}$ ) vary spatially, driven by the photosynthetic pathways of primary producers, therefore  $^{13}\text{C}$  may be enriched or depleted due to variation in vegetation type and the associated photosynthetic metabolisms as well as climatic conditions (Marra et al. 2000; Bearhop et al. 2004; Layman et al. 2007). For example,  $\delta^{13}\text{C}$  is often used to differentiate between marine and terrestrial plant sources. Here, as a result of the spatial shift, individuals did not maintain consistent  $\delta^{13}\text{C}$  position between countries, even when controlling for the between-country variation in isotopic baselines. This is likely driven by such climatic differences and variation in vegetation type. However,, analyses of martens that were sampled before and after translocation found that individuals maintained their relative trophic position ( $\delta^{15}\text{N}$  values). Furthermore, adjusting for baseline differences,  $\delta^{15}\text{N}$  values in Wales were almost one trophic level higher (2.5-5‰ increase in  $\delta^{15}\text{N}$  with each trophic level; Bearhop et al., 2004) than in Scotland. This highlights that, although flexible in their overall diets as a population, individual martens appear to consistently feed at a similar trophic position relative to other individuals within the population, even

when experiencing different environmental conditions. This would imply a degree of sustained foraging specialisation (Type B generalists) and/or dietary preferences by individuals, similar to that seen in badgers *Meles meles* (Robertson et al. 2014), turtles *Caretta caretta* (Vander Zanden et al. 2010) and guillemots *Uria lomvia* (Woo et al. 2008). Robertson et al. (2014) found that badgers within the same social group occupied different dietary niches, even though resource availability was the same. This was thought to be driven by intraspecific competition but also determined by the size of the social group and the composition of their territory (Robertson et al. 2014). It is therefore possible that social and territorial factors may also drive marten specialisation, such that more dominant individuals may occupy 'prime' territories, resulting in younger or subordinate animals settling in less optimal habitat where prey sources are more variable or less favourable.

Martens in Wales exhibited greater niche breadth than those in Scotland, indicative of a broader diet. This would suggest that they are facultative specialists (Glasser 1982), i.e. a combination of a Type A and Type B generalist. More specifically, each individual displays a degree of dietary specialisation or preference which constitutes a substantial proportion of their diet. The remaining part of their diet is supplemented by prey that is locally or seasonally abundant, particularly when preferred prey are in low abundance (Glasser 1982; Shipley et al. 2009). This flexible specialisation enables efficient foraging and can reduce competition with conspecifics through differing prey preferences (Shipley et al. 2009). Other dietary studies on *Martes* species have shown that when the preferred small rodent prey are in low abundance, larger mammals such as rabbits and squirrels, as well as insects and berries play a more important role in this predators' diet, particularly during winter and spring (Lockie 1960; Zalewski et al. 1995; Caryl 2008; Paterson & Skipper 2008). A combination of intraspecific competition, as newly released martens establish territories, and varying prey availability in Wales may thus be contributing to the broader niche breadth observed in Welsh martens (Fig 3.2, Table 3.1). The temporal variation in sample collection should also be considered. The collection of Welsh samples over a longer time period to those collected in Scotland may contribute to dietary variation recorded. Martens have been demonstrated to vary their diet seasonally and therefore findings of this study should be interpreted with this in mind. Similar

dietary behaviour can be found in black footed ferrets *Mustela nigripes*, which show dietary specialisation in prairie dogs *Cynomys* spp., however adjust their degree of specialisation subject to abundance of this prey source (Brickner et al. 2014). Canada lynx *Lynx canadensis* also display this plasticity to tolerate the cyclic prey abundance of the snowshoe hare *Lepus americanus* (Roth et al. 2007). This allows the predator species to become 'decoupled' from the cyclicity of its preferred prey and consume more abundant prey sources (Roth et al. 2007).

We also showed how these differences in diet arose between Scottish and Welsh marten populations. Martens in Wales showed a reduced consumption of berries and voles (Fig. 3.2 & 3.3), both of which had lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values than other prey sources (Fig. 3.4). The replacement of these low  $\delta^{15}\text{N}$  prey types in the Welsh marten diet with larger mammals such as squirrels, rabbits and rats seen in scats (Fig. 3.2 & 3.3, Table 3.1), as well as marginally more birds and shrews (Fig. 3.3, Table 3.1), may be contributing to the increase in trophic level ( $\delta^{15}\text{N}$ ) observed (Fig. 3.5). These prey animals have a more varied diet than field voles, incorporating a variety of plant matter and, particularly with regards to squirrels, may have very different carbon signatures due to their nut-based diet (Ben-David et al. 1997). The marginal increase in bird and rabbit consumption may also contribute to this trophic level shift. However, we were unable to reconstruct detailed marten diet using isotopic data from prey sources due to unclear partitioning between prey groups (Fig. 3.4). When animals are nutritionally stressed, i.e. experiencing starvation,  $\delta^{15}\text{N}$  has been shown to be enriched by 0.5-2‰, with  $\delta^{13}\text{C}$  remaining relatively unaffected (Newsome et al. 2009). Therefore it may be possible that the nutritional and physiological state of pine martens post-translocation is contributing to the elevated  $\delta^{15}\text{N}$  values observed in Wales. However, the body condition of recaptured pine martens was comparable, if not better than when they were translocated (VWT, *unpublished data*) and so it is unlikely that nutritional stress is a contributing factor. The reproductive status, sex and/or weight of individuals may also be influencing this apparent trophic shift, however population-level analyses did not detect an effect of sex and weight on isotopic signatures, and the sample size of recaptured animals did not allow for more detailed assessment of these effects.

In this study, marten diet was generally comparable to previous studies of the species across their Eurasian range, which found small rodents, namely field vole, bank vole and wood mouse *Apodemus sylvaticus*, to dominate diet throughout the year (Gurnell et al. 1994; Zalewski 2005; Caryl 2008; Sidorovich et al. 2010). Field voles, the primary constituent of marten diet in both Scotland and Wales (Fig. 3.2, Table 3.1), undergo cyclic fluctuations in parts of their range (Lambin et al. 2000), as well as seasonal fluctuations where populations are lower over winter (Putman 2000). This results in a marked spatial and temporal variation in the availability of a key food source for martens. The varying availability of this prey item means that martens which specialise purely on field voles are at a disadvantage, and thus a degree of dietary flexibility will likely provide a fitness advantage over more specialised individuals.

A species which is readily available in Wales but absent from most parts of northern Scotland is the invasive grey squirrel. The importance of grey squirrels in pine marten diets is of particular interest, given the potential for restored marten populations to effect change in grey squirrel populations (Sheehy & Lawton 2014; Sheehy et al. 2018) and, thereby reduce their impacts on forestry interests and on native red squirrel populations. Our translocation of martens was from an area with only red squirrels (Bryce 1997; Sheehy et al. 2018) to an area with only grey squirrels (Lucas 1997). No evidence of predation of red squirrels was found in Scottish samples, while predation of grey squirrels was recorded on multiple occasions Wales. Negative correlations between the distributions of martens and grey squirrels and positive correlations between martens and red squirrels (Sheehy & Lawton 2014; Sheehy et al. 2018) have provided compelling indications that the presence of martens could be used to control grey squirrel populations to the benefit of red squirrel populations. However, the mechanisms for this relationship are not clear and may encompass predation, as is apparent here, and non-lethal behavioural effects, as indicated by Chapter 4, and most likely, combinations of the two. We have identified similar levels of grey squirrel consumption by translocated martens in Wales (10% FO in scats) as by resident martens in Ireland (10% FO in scats; Sheehy et al., 2014). Squirrel consumption had also previously been documented in Russia and Scandinavia, where red squirrels comprised a high proportion of marten scats, particularly during winter (8.1-29.7% FO of prey items; Zalewski, 2005, 7-50% FO in scats; Storch, 1990,

1.2-1.6% FO in scats; Sidorovich et al., 2010). Grey squirrels have not yet invaded these red squirrel ranges, and therefore are not available as a prey source. There are substantial red squirrel populations in Scotland (Bryce 1997), within the range of pine martens (Sheehy et al. 2018), but red squirrel remains were not detected in any marten scats during this study and were similarly scarce in previous studies (0% FO in scats; Gurnell et al., 1994, 0.4% of prey items; Halliwell, 1997). In Wales, predation of grey squirrels may therefore be occurring for a number of reasons, including: i) relatively low small rodent abundance, ii) high abundance of grey squirrels, and iii) ease of capture of grey squirrels within dreys (Zalewski 2005; Pulliainen & Ollinmäki 2014). Although impacts of predation by martens on squirrel survival at a population level may not yet be detectable in Wales (Chapter 4), grey squirrel movement and foraging behaviour appear to be impacted by this risk of predation (Chapter 4 & 5). The potential ramifications of marten predation for current grey squirrel management strategies are substantial, however the long-term ecological effects of this in the area around the reintroduction site require further investigation. With time, squirrel predation by pine martens may contribute to, and drive, similar landscape-scale patterns to those documented in Ireland and Scotland (Sheehy & Lawton 2014; Sheehy et al. 2018).

There are however additional considerations, given the dietary flexibility of reintroduced martens revealed by this study. While, the introduction of martens to areas with an abundant pest species, such as grey squirrels, may be beneficial for establishing a marten population and controlling an invasive species (Sheehy & Lawton 2014), it could have negative implications for species of conservation concern, such as hazel dormouse *Muscardinus avellanarius*, pied flycatcher *Ficedula hypoleuca*, black grouse *Lyrurus tetrix* and certain bat species (Macpherson 2014). In regions where 'at risk' species are present (unlike in our destination sites in Wales), the opportunistic dietary habits of martens may prove detrimental to their populations and generate conflict between different conservation interests. This may be of particular concern for predator species that show preference for prey with cyclic dynamics, not only with regard to predation of vulnerable species, but also for the resilience of re-establishing predator populations to low prey abundance. In the context of species translocation, dietary flexibility is of particular interest and concern during initial

years when reintroduced carnivore populations may still be establishing. Translocation of dietary specialists could result in poor translocation success, subject to the degree and flexibility of specialisation. This may be of particular relevance if reintroducing dietary specialists that have been reared in captivity as part of a breeding programme. Evidence suggests that reintroductions of captive-reared animals have a low success rate (Griffith et al. 1989). Preconditioning these animals to the prey that will be available to them on release can enhance post-release predation skills and survival (Biggins et al. 1999). However, if translocating animals from the wild, selecting a broad range of individuals from different habitats, which may therefore have different dietary preferences, may enhance the success of individual survival and population establishment post-translocation, as well as spread predation pressure across multiple prey groups. The impact of a facultative specialist on prey populations must therefore be carefully considered. Consumption of a readily preferred prey group may be beneficial from a species control perspective, however the ability of predators to switch or specialise could also be detrimental. If a locally abundant and protected species becomes a source of preference for some individuals, the impact of their predation may be substantial. However, if anticipated, these negative impacts of predation can be mitigated through protecting areas of importance, using exclusion techniques (Hayward & Kerley 2009) and monitoring at-risk populations.

This study demonstrates that dietary studies combining hard-part analyses and stable isotope methods provide a multi-faceted approach to understanding species diet at both a population and individual level. Populations of generalists can be made up of individual specialists that could affect the success of individuals after a translocation event. However, specialisation is not necessarily rigid and individuals displaying facultative specialisation are able to maintain a degree of dietary preference, which is then supplemented by readily available prey. Such opportunistic predation can be detrimental to at-risk prey populations, however it may also be beneficial in the control of invasive, non-native species. Consideration of the degree of dietary flexibility, the retention of any dietary preferences, as well as the resulting predation impacts of translocated animals are thus vital aspects of any translocation and should be incorporated into species reintroduction planning.

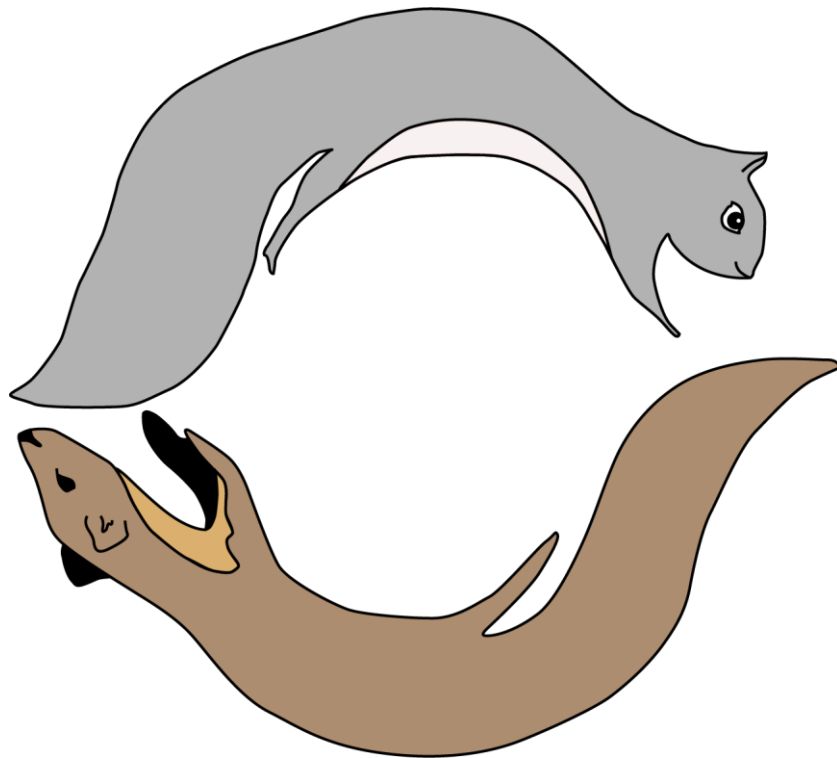






## Chapter 4

**Translocated native pine martens *Martes martes*  
affect space use by invasive non-native grey  
squirrels *Sciurus carolinensis***



## **Chapter 4: Translocated native pine martens *Martes martes* disrupt short-term space use by invasive non-native grey squirrels *Sciurus carolinensis***

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### **Abstract**

Predators can shape the distributions and dynamics of their prey through direct and indirect mechanisms. Where prey animals are regarded as pests, the augmentation of predator populations might offer a potential tool in their management. Declines in invasive non-native grey squirrel *Sciurus carolinensis* populations in Ireland and Scotland have been related to an increase in range and density of native pine marten *Martes martes* populations. These reductions in grey squirrel abundance have, in turn, been linked to recovery of native red squirrels *Sciurus vulgaris*. Taking the opportunity presented by a conservation translocation of pine martens from Scotland to Wales, we investigated the short-term effects of exposure to translocated martens on the space use and survival of resident grey squirrels. Grey squirrel range size and daily distance travelled increased significantly with increasing exposure to martens but we found no effect of marten exposure on the recapture probability (i.e. apparent survival) of the sampled squirrels within the study timeframe. This is suggestive of contemporary non-lethal effects changing the ranging or foraging regimes of squirrels, due either to predator avoidance and/or earlier lethal effects associated with a reduction in intraspecific competition. Synthesis and applications. Our evaluation mimics the conditions experienced by grey squirrels at the front edge of natural recovery of pine marten populations and presents the first direct evidence that pine marten translocations could play an influential role in the dynamics of invasive non-native grey squirrel populations. Translocations of native predators, undertaken primarily for biodiversity conservation, could

therefore find additional application in managing the ecological and economic impacts of invasive non-native prey.

## **Introduction**

The direct effects of a predator on its prey are often obvious, however indirect effects can play an equally influential role on prey demography and distribution (Brown, Laundre, & Gurung 1999; Preisser, Orrock, & Schmitz, 2007). In a 'landscape of fear', cues to predator activity can elicit behavioural changes in prey species (Laundré, Hernández, & Altendorf, 2001; Suraci, Clinchy, Dill, Roberts, & Zanette, 2016) that manifest in anti-predatory behaviours, including modifications of space use, that often come at the expense of foraging and reproduction (Heithaus *et al.*, 2007; Suraci *et al.*, 2016). Regulation of prey populations, their behaviour and ecosystem impacts, can stem from fear-mediated responses (Jacob & Brown, 2000; Ripple & Beschta, 2004). Raccoons *Procyon lotor*, for example, exert impacts on potential prey animals by reducing the time they spend foraging (Suraci *et al.*, 2016). Prey animal fitness can also be linked to anti-predator responses; Green turtles *Chelonia mydas* generally avoided areas of high tiger shark *Galeocerdo cuvier* predation risk, but those in poorer body condition took greater risks to exploit areas of higher forage quality. These condition-dependent decisions affected not just turtle fitness but extended to alteration of seagrass community composition (Heithaus *et al.*, 2007). Thus, fear of predators not only affects fitness of prey but can also result in trophic cascades with ecosystem effects.

Diversity in the responses of prey animals to their predators (Parsons *et al.*, 2017) is related to the forms that cues to predation risk can take. These range from direct evidence of predator presence through sounds and scents (Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005; Suraci *et al.*, 2016), to the association of risk with particular habitat types (Heithaus *et al.*, 2007; Lima *et al.*, 1985). The variability and complexity of non-lethal effects of predation and predator presence can therefore make the relatively simple concept of a landscape of fear difficult to demonstrate or quantify, particularly when lethal and non-lethal effects co-occur (Polis, 1991).

The direct and indirect effects of predators upon their prey may result in comparable population effects, i.e. reduced abundance of prey animals, and so patterns observed at landscape scales might not distinguish mechanistic drivers. By investigating the mechanisms underlying observed patterns relating the distributions and abundances of predators and their potential prey at finer temporal and spatial scales, we might predict and understand landscape scale trends (Levin, 1992). This study therefore takes advantage of a unique situation in which predator abundance, and hence the risk environment of prey animals, has been manipulated and monitored on a fine scale.

The manipulation of predator-prey relationships has long been used as a method of population control. In some circumstances, biological control agents provide a 'natural' method of managing problem species, reducing the need for ongoing human interventions (Atkins, Redpath, Little, & Amar, 2017; Wanger *et al.*, 2010). However, the introduction of predators has often led to unexpected outcomes, many of which have been detrimental to non-target, native species (Doody *et al.*, 2009; Parkes & Murphy, 2003; Simberloff & Stiling, 1996). Although the use or restoration of native predators to control non-native prey is relatively untested, it has potential in invasive species control. In North America the native blue crab *Callinectes sapidus* limited the abundance and range of the introduced European green crab *Carcinus maenas* through predation (DeRivera, Ruiz, Hines, & Jivoff, 2005), while in Indonesia, the endemic Celebes toad *Ingerophrynus celebensis* negatively affected invasive ant *Anoplolepis gracilipes* populations through predation, thereby enhancing native ant abundance (Wanger *et al.*, 2010). In these cases, the density of the native predator was an important factor in their impact on the invasive prey. More importantly, the differing evolutionary histories of native predator and invasive prey have resulted in a spectrum of ineffective anti-predatory responses by naïve prey, from failure to recognise predation risk to anti-predatory responses that do not enable predator evasion (Salo *et al.*, 2007; Sih *et al.*, 2010; Wanger *et al.*, 2010).

The recovery of the native pine marten *Martes martes* in the U.K. and Ireland, after an extended period of decline and near-absence (Langley & Yalden, 1977; Sainsbury *et al.* 2019), has been hailed as an advance in controlling invasive non-native grey squirrel *Sciurus carolinensis* populations (Sheehy & Lawton, 2014; Sheehy, Sutherland, O'Reilly, & Lambin, 2018). Grey squirrels are classified as

a pest in the UK due to the damage they cause to timber through bark-stripping (Kenward & Parish, 1986), as well as competing with, and spreading infection to, native red squirrels *Sciurus vulgaris* (Rushton *et al.*, 2006). In regions of Ireland (Sheehy & Lawton, 2014) and Scotland (Sheehy *et al.*, 2018) where pine martens have been recovering for a substantial period and now live at high, medium and even low densities, grey squirrel populations have been negatively affected. The resulting lower densities of grey squirrels have in turn been associated with increases in red squirrel populations, thereby indirectly linking pine marten recovery to that of red squirrels. To date, the mechanistic basis of these observations remains unknown. Where they co-occur, grey squirrels, along with other native squirrel species, feature in the diets of both the American marten *Martes americana* and the ecologically and taxonomically similar fisher *Pekania pennanti* (Arthur *et al.*, 1989; Hales, Belant, & Bird, 2008). However, range overlap between grey squirrels and these arboreal mustelid predators is somewhat limited and the grey squirrel thus largely evolved in an environment containing primarily terrestrial and aerial predators, and has been exposed to arboreal mustelids at only the limits of their native range. It might be expected that grey squirrels are therefore unlikely to demonstrate effective anti-predatory responses to arboreal mustelids in either their native or non-native ranges. As a result, this prey species population is likely to suffer directly from the native predator's recovery. Understanding the grey squirrels' response to perturbations, such as introducing a novel predator, is therefore important in predicting the impact of increasing pine marten populations on the future status of grey squirrels in their non-native range.

The translocation of pine martens as part of a species reinforcement program has created a unique opportunity to investigate the responses of resident, non-native grey squirrels to the arrival of native but newly establishing pine martens. By simultaneously tracking martens and squirrels we were able to record how the distribution of the martens influenced the spatial behaviour of the squirrels. We predicted that in areas experiencing higher pine marten activity, grey squirrels would 1) occupy restricted home ranges, due to increased vigilance and reduced foraging or roaming behaviours which are associated with the presence of other predators (Lima *et al.*, 1985) 2) show little shift in the location of their home range and 3) move less per day in order to reduce their encounter rate with martens by restricting their ranges, as suggested by findings from Sheehy & Lawton (2014).

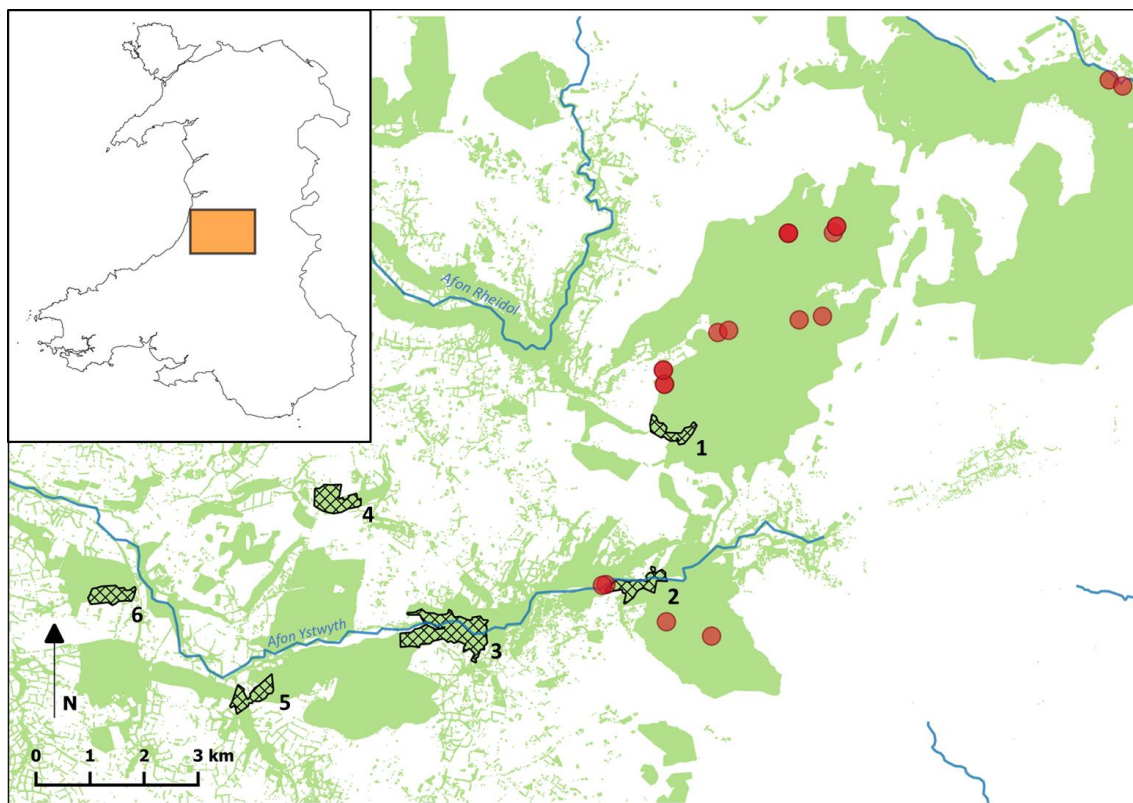
We would also expect grey squirrels to 4) exhibit lower survival, when compared to squirrels in areas with lower pine marten density as a result of direct predation.

## **Materials & Methods**

The study was undertaken in Mid-Wales, UK in six similar broadleaf (>80% broadleaved trees) and mixed broadleaf (>50% broadleaved trees) woodland compartments (National Forest Inventory, 2016) (Fig. 4.1, Table 4.1). In all compartments there was minimal understorey and a closed canopy. Tree species composition on all sites was similar, comprising mature beech *Fagus sylvatica*, sessile oak *Quercus petraea* and silver birch *Betula pendula*, interspersed with low numbers of conifer trees, comprising European larch *Larix decidua* and lodgepole pine *Pinus contorta*. The study compartments were surrounded by large blocks of similar commercial conifer woodland (comprising >80% coniferous trees) and marginal upland farmland, largely comprising semi-improved and unimproved grasslands. Sites were selected based on their similarity in habitat, i.e. primarily broadleaf woodland with relatively open understorey, which was a favourable habitat for grey squirrels and their proximity to marten release sites. The six compartments had a mean area of 32.9ha (Range 17.9-77.0ha) and were >3km apart. Given the mean range size of grey squirrels in the U.K. is <5ha (Gurnell *et al.*, 2001; Lawton & Rochford, 2007; Wauters *et al.*, 2002), each compartment was assumed to host independent populations (Fig. 4.1). Grey squirrels had been established in this area of mid-Wales for over 60 years (Lucas, 1997) and the sites had no record of grey squirrel culling, through trapping or poisoning, in the last 20 years. The nearest population of native red squirrels was 20km to the south.

Between September and December 2015, squirrel traps were positioned on the ground and pre-baited for seven days before being set for 7-12 days and checked every morning and evening. Trap density was approximately 0.9 per hectare, with an average of 24 traps per woodland (Table 4.1). Adult squirrels were tagged with a subcutaneous passive integrated transponder (PIT: Avid Identification Systems Inc.) to enable identification on recapture. Adult squirrels over 500g were fitted with collars equipped with GPS loggers (modified i-gotU GT-120,

MobileAction Technology, Taiwan) configured to record locations at hourly intervals and VHF beacons (Biotrack, UK) to enable confirmation of residency and recovery of the GPS unit by recapturing the squirrel after three weeks. GPS units successfully recorded between 5 and 24 days (SE 0.9 days) of movement data. A subsample of trapped individuals were collared (87%), remaining individuals were only tagged and juveniles, or individuals below 500g were excluded from all tagging or collaring. Locations taken within one hour of collar application (Delehanty & Boonstra, 2009) and 12 hours before collar removal were removed from the dataset. As a further part of data cleaning, individual points recorded further than 2km from the edge of the trapping woodland block were considered spurious and removed ( $n = 12$  of 8598 points). This conservatively allowed for movement out-with woodland patches based on evidence that when woodland habitat is unavailable, or during dispersal, squirrels have been found to remaining within approximately 400m of the nearest habitat patch (Stevenson *et al.*, 2013).



**Figure 4.1. Locations of pine marten release sites and grey squirrel trapping sites in mid-Wales.** Release sites are shown as red dots and grey squirrel trapping sites 1-6 as hatched areas. Insert shows location in Wales. Woodland is indicated in green.

Between September and November 2015, 20 pine martens were trapped in the Scottish Highlands, equipped with VHF radio collars (Biotrack, Wareham) and transported to three release sites in Wales (Fig. 4.1). They were, held individually in soft release pens for up to 5 days, released, tracked and located 1-7 times per week for up to 10 months following release. Locations were triangulated from bearings using LOAS 4.0 (Ecological Software Solutions). Bearings that did not converge were excluded. Systematic scat surveys, undertaken as transects between 2011 and 2015, had found no evidence of pine martens in the region and the translocated martens were considered to be the only ones in the area (Macpherson *et al.*, 2014).

### *Squirrel ranging*

We derived four measures of squirrel ranging; home range (90% Kernel Density Estimate – KDE, as used by Borger *et al.*, 2006) and core range (50% KDE) sizes (km<sup>2</sup>), daily distance travelled (km) and home range centroid shift (m). Range sizes were calculated using the R package ‘adehabitatHR’ (Calenge, 2006) using reference smoothing parameter ‘h-ref’ (Borger *et al.*, 2006; Laver & Kelly, 2008). We ensured there were sufficient data for all squirrels to have reached the asymptote of a home-range area curve before including them in analysis (Laver & Kelly, 2008) and one squirrel was consequently excluded (see Supporting Information). We checked for spatial autocorrelation by plotting the semi-variance of location positions against time lag between each location using the R package ‘ctmm’ (Calabrese, Fleming, & Gurarie, 2016; Fleming *et al.*, 2014). Variograms were visually inspected to ensure they reached an asymptote and there was no observable patterning. None displayed spatial autocorrelation and all were retained.

The mean daily distance (km) travelled was estimated using ‘distm’ in the R package ‘geosphere’ (Hijmans, Williams, & Vennes, 2017) by summing the straight-line distances between consecutive locations across the whole of the squirrel’s collaring period. Home range shift (Janmaat, Olupot, Chancellor, Arlet, & Waser, 2009) was the Euclidean distance (m) between the centroids of the home ranges in the first and last weeks of tracking using gCentroid (R package ‘rgeos’; Bivand, Rundel, Pebesma, Stuetz, & Hufthammer, 2017).



### *Marten exposure*

For each squirrel, we extracted locations of all pine martens during the same monitoring period, plus the week prior to account for exposure before squirrels were collared. Marten locations were used to create a density surface (Sims, Witt, Richardson, Southall, & Metcalfe, 2006) using the package 'adehabitat' (Calenge, 2006). The surface comprised grid cells (100x100m) and the size and composition of the grid remained constant. The kernel density estimates of marten locations were then generated using increasing bandwidth resolutions (h) of 0.5, 1, 2 and 3km which enable the effect of one point to extend through more adjacent cells, with increasing bandwidth size (see Appendix 1). The home range of each squirrel was then mapped onto its matched marten density surface. The underlying marten densities in each cell within this squirrel range were then extracted and summed to give the total 'marten exposure' (martens per km<sup>2</sup>) for each squirrel. The number of individual martens present in the whole landscape, i.e. the number of animals that had been released by the start date of individual grey squirrel monitoring, was calculated to account for the increasing likelihood of a squirrel-marten encounter over time.

### *Apparent survival*

We estimated apparent survival for squirrels in relation to pine marten exposure at each woodland site, rather than at an individual squirrel level, as some PIT tagged squirrels were not collared, preventing the calculation of marten exposure for these individuals across their home range. We used a measure of recapture probability as a proxy for squirrel survival. The encounter histories for all PIT tagged squirrels were used and individual apparent survival was scored as 1 if an individual was caught in both the first and second trapping period, and 0 if it was only caught in the first. Trapping duration and interval between trapping periods were unequal. To make sites comparable, we sampled, with replacement, 5 days on which trapping occurred. This was the lowest duration of trapping in one period at one site. We resampled 1000 times and calculated the proportion of iterations that each individual had an apparent survival of 1. For every squirrel we had an indication of its likelihood of being recaptured in the second trapping period, if a) it was captured in the first trapping period and b) had that trapping period lasted 5 days. Marten exposure was estimated as above, but in this analysis we used the maximum grey squirrel home range size recorded

over the entire study area (25.5 ha), centred on the centroid of the squirrel trap line. This was taken as the most conservative characterisation of marten exposure for each woodland.

### ***Statistical analysis***

To test the effect of marten exposure on grey squirrel ranging, we fitted a series of generalised linear models to three responses: home range (90% KDE) size (ha), core range (50% KDE) size (ha), and mean daily distance travelled (km). Response variables were log-transformed to normalize their distribution and models used a Gaussian error structure. We included sex of the squirrel, marten exposure and number of martens as fixed effects and included the interaction between sex and marten exposure. All explanatory variables were standardised to have a mean of 0, and SD of 0.5 (for continuous variables). Sex was rescaled to have a lower value of -0.5 and upper value of 0.5 (Gelman, 2008). Each of these models was fitted four times using the estimates of marten exposure calculated at the four spatial bandwidths. One squirrel had exceptionally high levels of marten exposure and on close inspection of a Cook's distance plot, this individual had high leverage and was removed from analyses (see Supporting Information for analyses including this outlier). We evaluated the performance of models using Akaike's information criterion corrected for small sample size (AICc) and all models within  $\Delta\text{AICc} \leq 2$  of the top model were included in the top model set (Burnham & Anderson, 2004). Model selection used the package 'MuMIn' (Barton, 2018). Full model averages were then used to identify main explanatory variables and generate effect sizes and 95% confidence intervals (Burnham & Anderson, 2004; Grueber, Nakagawa, Laws, & Jamieson, 2011). If 95% confidence intervals of variables did not overlap zero, variables were deemed significant. The relative importance (RI) of each variable within the top model set was also used. The explanatory power of full averaged models was then estimated using a likelihood-ratio based pseudo- $R^2$  where a value of 1 represents 100% of variance explained by the model.

### ***Apparent survival analysis***

A high number of squirrels were not recaptured in the second trapping period, resulting in zero-inflated indices of apparent survival. Therefore we used a zero-

inflated beta-binomial Bayesian model to test the relationship between marten exposure and apparent survival. This approach simultaneously fits two processes to the data, one that models whether apparent survival is zero or not, and another which models survival if greater than zero. Models were fitted in 'stan' (Carpenter *et al.*, 2017) using the R package 'brms' (Burkner, 2015). Marten exposure was a fixed effect. Parameter values were estimated using Markov-chain Monte-Carlo (MCMC) methods, using 'brms' defaults for priors and initial values. Four chains were run for 2000 iterations of which 1000 were discarded as burn-in. MCMC chains for all parameters converged ( $R\text{-hat} < 1.01$ ) and had an effective sample size greater than 2000. From the remaining MCMC chains, we calculated the mean estimate and 95% credible intervals. The statistical significance of the effect of all model parameters was determined by the 95% credible interval not overlapping zero.

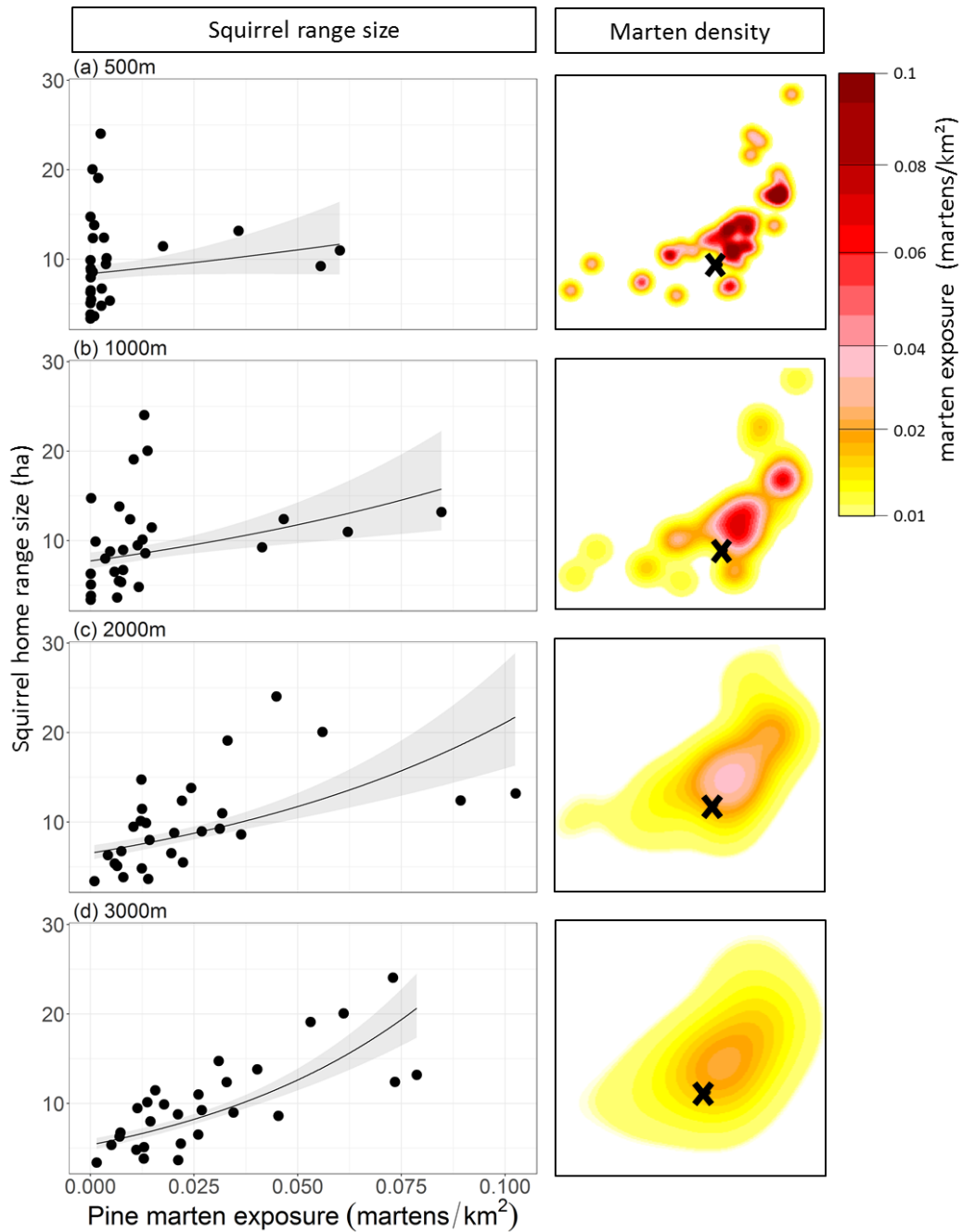
#### *Ethical statement*

This study was approved by the University of Exeter Animal Welfare and Ethical Review Board and licenced by the Home Office, Scottish Natural Heritage and Natural Resources Wales.

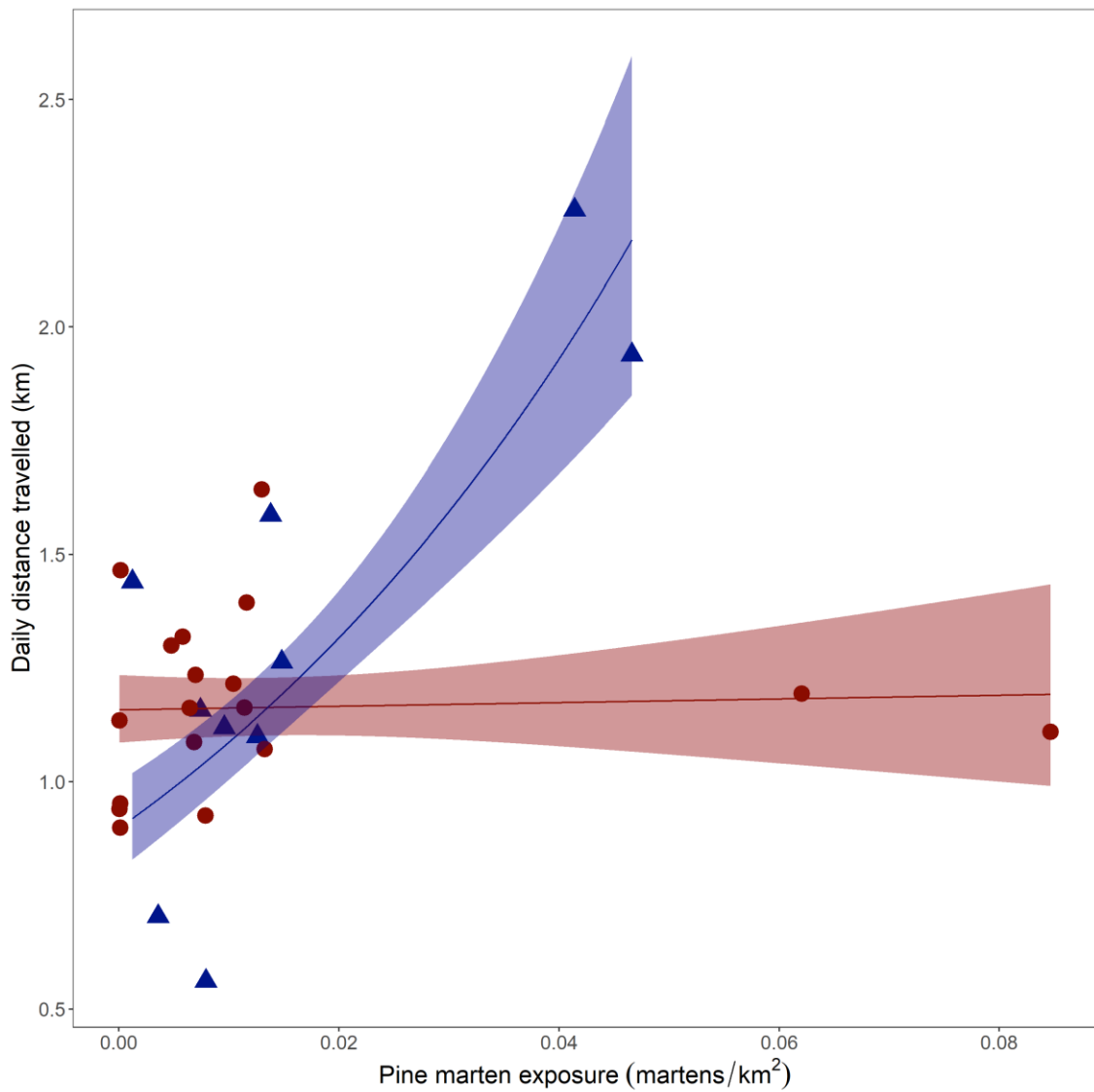
### **Results**

A total of 53 individual squirrels were collared over a 90 day period, 37 of which were recaptured, 16 collars were not recovered due to VHF antenna damage, animals dispersing, collars detaching in inaccessible dreys or mortality of animals in areas where they could not be relocated. Eight recovered collars could not be used due to GPS logger loss or failure. Ranging data from 29 squirrels (18F and 11M) were therefore suitable for analysis. These squirrels were tracked for a mean duration of 16 days (SE 0.9 days, range 5-23) and the mean number of locations per individual was 265 (SE 17, range 82-437). Mean home range (90% KDE) was 10.4ha (SE 1.1ha) and the mean core range (50% KDE) was 2.0ha (SE 0.2ha). Models of space use included 28 squirrels, after exclusion of an outlier (Tables 4.2 & 4.3, Fig. 4.2). When marten exposure was considered at larger scales ( $h \geq 2000\text{m}$ ; Table 4.1) but not at a finer scale ( $h \leq 1000\text{m}$ ), home and core ranges increased significantly as marten exposure increased (Table 4.3; Fig. 4.2). The daily distance travelled was also significantly and positively related to

marten exposure (Tables 4.2 & 4.3), though this effect was only detectable at larger spatial scales ( $h \geq 1000\text{m}$ ). There was a significant interaction between sex and distance travelled at the 1000m bandwidth. Males showed increased daily distance travelled with higher marten exposure, whereas females did not (Tables 4.2 & 4.3, Fig. 4.3). There was no significant effect of marten exposure on shift in home range centroids (Table 4.3) at any spatial scale, though exposure was retained in the top model set and model estimates were consistently positive, providing some suggestion that greater marten exposure may be associated with greater shifts in range centroids. Sex was retained in all top model sets as a main effect, though it did not appear to account for significant differences in range size or shifts. Survival analysis included 61 PIT tagged squirrels that were captured four times on average (SD 2.7, range = 1-11); 16 squirrels were captured only once. The number of consecutive trap days at sites ranged from 5-17 and the mean interval between the first and second trapping period was 37 days. There was no significant effect on apparent squirrel survival of exposure to martens for either the zero inflated (Estimate = 0.19, 95% credibility interval = -0.19-0.66) or beta-binomial (Estimate = -0.05, 95% credibility interval = -0.15-0.08) parts of the model and the 95% credible intervals overlapped zero for both estimates.



**Figure 4.2. Relationships between grey squirrel home range sizes and pine marten exposure (martens/km<sup>2</sup>).** Home ranges are 90% Kernel Density Estimates (KDEs). (a)-(d) represent the different bandwidths used (500, 1000, 2000 & 3000m) in calculation of marten exposure. Panels on the right show example maps of the pine marten density surface at each bandwidth for an individual squirrel with its 90% home range represented by a black cross. Darker colours represent higher marten density and thus higher levels of exposure experienced by an individual squirrel in that location.



**Figure 4.3. Effect of variation in exposure to translocated pine martens on daily distance travelled by grey squirrels.** Sexes respond differently to pine marten exposure, male squirrels are shown as blue triangles and females as red circles. Pine marten exposure (martens per km<sup>2</sup>) is calculated using a bandwidth of 1000m.

**Table 4.1. Description of the six woodland compartments used for grey squirrel trapping and the number of squirrels caught and used in analyses.**

Site	Compartment Area (ha)	No. of traps	Trap density	No. of individual squirrels trapped	Nearest marten release pen (km)	No. of squirrels in analysis (M:F)	Dominant tree species
1	17.9	36	2.02	8	0.7	1:1	<i>F. sylvatica</i> <i>B. pendula</i>
2	25.7	22	0.86	8	0.4	0:8	<i>F. sylvatica</i> <i>P. contorta</i>
3	77.0	25	0.32	10	2.6	3:2	<i>F. sylvatica</i> <i>P. contorta</i>
4	30.5	18	0.59	10	5.0	3:3	<i>F. sylvatica</i> <i>Q. petrea</i> <i>L. decidua</i>
5	23.5	19	0.81	10	6.7	2:1	<i>F. sylvatica</i> <i>Q. petrea</i> <i>L. decidua</i>
6	22.8	24	1.05	15	8.9	1:3	<i>F. sylvatica</i> <i>L. decidua</i>

**Table 4.2. Summary of models of variation in exposure to introduced native pine martens upon the space use of invasive non-native grey squirrels.** Full averaged models include terms from models in the top model set, where  $\Delta AIC_c \leq 2$ . Terms in the averaged models included the effect of variation in local density of translocated pine martens within the squirrel home range (exposure), the number of martens that had been released into the landscape (martens), squirrel sex and an interaction exposure\*sex. For each squirrel behaviour variable, four models were run; one for each pine marten kernel bandwidth used to estimate marten density (500, 1000, 2000 and 3000m). Significant effects are where 95% confidence intervals do not cross zero (see Table 4.3) and are shown in bold.  $R^2$  represents the likelihood-ratio based pseudo- $R$ -squared value for the model.

Response	Marten bandwidth (m)	Full averaged model	$R^2$
<b>Core range (50% KDE)</b>	500	sex + martens + exposure	0.147
	1000	sex + martens + exposure	0.207
	2000	sex + martens + <b>exposure</b>	0.402
	3000	sex + martens + <b>exposure</b>	0.626
<b>Home range (90% KDE)</b>	500	sex + martens + exposure	0.100
	1000	sex + martens + exposure	0.148
	2000	sex + <b>exposure</b>	0.327
	3000	sex + <b>exposure</b> + exposure*sex	0.636
<b>Daily Distance travelled (km)</b>	500	sex + exposure + exposure*sex	0.213
	1000	sex + <b>exposure</b> + <b>exposure*sex</b>	0.385
	2000	sex + <b>exposure</b> + exposure*sex	0.308
	3000	sex + <b>exposure</b> + exposure*sex	0.314
<b>Centroid Shift</b>	500	sex	0.058
	1000	sex + exposure	0.073
	2000	sex + exposure	0.132
	3000	sex + exposure	0.153



**Table 4.3. Effects of variation in exposure to introduced native pine martens upon the space use of invasive non-native grey squirrels.** For each behavioural variable, four models were run; one for marten exposure (martens/km<sup>2</sup>) calculated at each pine marten kernel bandwidth (500, 1000, 2000 and 3000m). Estimates of effect sizes are from Generalised Linear Models (Table 4.2). For each squirrel space use metric the averaged standardised effect size across the top model set, lower and upper 95% confidence limits and relative importance (RI) of marten exposure is shown at each kernel bandwidth size. NR indicates pine marten exposure was not retained in the top model set. In one instance (daily distance, bandwidth 1000m), results are given for males and females separately because the effect of variation in marten exposure significantly interacted with the effect of squirrel sex (Figure 4.3).

Kernel bandwidth	Mean marten exposure (martens/km <sup>2</sup> )	Core (50%) range			Home (90%) range			Daily distance travelled (km)			Centroid shift (m)		
		Estimate	Confidence Limits	Relative importance	Estimate	Confidence Limits	Relative importance	Estimate	Confidence Limits	Relative importance	Estimate	Confidence Limits	Relative importance
500m	0.007 ± 0.003	0.03	-0.20, 0.26	0.45	0.03	0.18, 0.24	0.2	0.10	-0.13, 0.32	0.6	NR	-	-
1000m	0.014 ± 0.004	0.29	-0.25, 0.83	0.66	0.18	-0.25, 0.62	0.6	(M) 1.03 (F) 0.28	0.41, 1.66 0.09, 0.47	1 1	0.05	-0.32, 0.42	0.18
2000m	0.025 ± 0.005	0.66	0.27, 1.05	1	0.56	0.21, 0.90	1	0.25	0.01, 0.42	1	0.24	-0.46, 0.94	0.46
3000m	0.028 ± 0.004	0.83	0.51, 1.14	1	0.76	0.48, 1.03	1	0.25	0.05, 0.45	1	0.29	-0.46, 1.04	0.52

## **Discussion**

Using the unique opportunity presented by a conservation translocation of pine martens, our study sheds light on some of the likely processes underlying the landscape-scale responses of non-native prey, grey squirrels, to the return of a native predator (Sheehy & Lawton, 2014; Sheehy *et al.*, 2018). We found that, contrary to our predictions of diminished ranging, squirrel range size and daily distance travelled increased with increasing exposure to the novel predator. We found that male and female grey squirrels increased the daily distances they travelled to different extents in response to marten exposure, potentially reflecting the typical wider ranging behaviour of males (Gurnell *et al.*, 2001). An increase in ranging behaviour may be a strategy utilised by squirrels to enable them to tolerate and respond to marten exposure without shifting their home range location. These differences in space use were observed over even brief time periods, during which new martens were still being released into the area, suggesting that the impact of pine martens in a landscape may be manifest almost immediately after their reintroduction to, or dispersal into, the region. Our results complement the observations of landscape-scale negative correlations between grey squirrel abundance and pine marten presence (Sheehy & Lawton, 2014; Sheehy *et al.*, 2018). Contrary to expectations, particularly in view of the observed behavioural changes, we saw no relationship between squirrel survival and marten exposure. Perhaps this is unsurprising given the relatively short time frame and small sample size, resulting in a small chance of detecting differences in mortality rates.

These findings might be interpreted in a number of ways. First, we could infer that pine marten presence does not directly affect the behaviour of surviving grey squirrels but that the observed changes are driven by changes in intraspecific competition. This may be a result of pine marten predation of grey squirrels in surrounding areas, prior to the study, or of un-monitored individuals, which in turn has changed the territorial and social environment for surviving individuals. Alternatively, there may be an immediate, fear-mediated response, contrary to the prediction arising from Sheehy *et al.*'s (2018) models, which suggested grey squirrels were naïve to the presence of pine martens. In this scenario, we propose

that grey squirrels are able to detect and identify the martens as a threat and consequently change their behaviour. This change could be permanent or plastic, resulting in either long-term population level changes or merely temporary behavioural changes which, after an initial period of disruption, return to 'normal'. The presence of such a landscape of fear would suggest that the prey species exposed to this novel threat then used the landscape differently to individuals not facing the new threat, or changed their behaviour in areas of high perceived predation risk (Apfelbach *et al.*, 2005; Jacob & Brown, 2000; Rosell, 2001). Due to the timing of this study we are only able to compare grey squirrel behaviour across a spectrum of exposure to newly introduced martens, as opposed to a clear before-after-control-impact design. While the distribution and movement of prey can be dramatically altered by the presence of a predator (Heithaus & Dill, 2006), the temporal and spatial scales at which these changes occur depends upon the system being studied. Valeix *et al.* (2009) found that African herbivores displayed varying spatial and temporal habitat shifts in response to lion predation risk; grazers had limited habitat providing their required resources and did not alter their distribution while browsers altered their distribution to encompass the available alternative feeding habitats. In the face of high predation risk, a trade-off is made between resource acquisition and safety from predation (Lima *et al.*, 1985) and these trade-offs may occur on a small scale, through behavioural changes while feeding (Laundré *et al.*, 2001; Suraci *et al.*, 2016), and on a large scale, through spatial expansions and shifts to alternative feeding areas (Heithaus & Dill, 2006; Maillard & Fournier, 1995; Valeix *et al.*, 2009). The findings of our study are consistent with the latter of these responses, suggesting squirrels are extending, rather than shifting, their ranges in response to predation risk. The duration of such behavioural responses is thus also important to consider. Behavioural plasticity may allow for a temporary change in squirrel space use during a time of novel perturbations, but a return to 'normal' ranging behaviour once this novel predator becomes 'familiar' (Bateman & Fleming, 2014). Such plastic or habituation responses in squirrels have been demonstrated by fox squirrels *Sciurus niger* across urban and rural gradients (McCleery, 2009).

One explanation for differences in space use by squirrels is a change in range utilisation and foraging regime. Behaviour may be altered for the avoidance of

predation in time (Griffin, Griffin, Waroquiers, & Mills, 2005), space (van Beest, Vander Wal, Stronen, Paquet, & Brook, 2013) or both. Some species under elevated risk of predation display higher vigilance and reduced time spent foraging at a particular location (Heithaus & Dill, 2006; Laundré, *et al.*, 2001; Maillard & Fournier, 1995; Valeix *et al.*, 2009). Here, with increasing predation risk and reduced foraging returns, the trade-off between safety and resource acquisition becomes biased towards safety (Laundré *et al.*, 2001; van Beest *et al.*, 2013; van der Merwe & Brown, 2008; ). Consequently, increased vigilance and movement would likely reduce time foraging at single patches and increase the number of patches exploited, elevating the daily distance travelled between patches and range sizes.

Squirrel range size is a function of season, habitat quality and density of conspecifics (Lawton & Rochford, 2007; Wauters *et al.*, 2002) and the link between marten density and quality of grey squirrel habitat warrants attention. It is conceivable that, within the ostensibly similar habitats of these six woodland compartments, martens selected habitats that were poor for grey squirrels. In such a scenario, squirrels that were resident where martens spent more time would require larger home ranges to acquire sufficient resources. Studies of marten habitat preference suggest that woodland was preferred over other locally available habitats, such as grassland, though this preference was not tied to woodland type but to structural complexity and cover within the woodland; moreover, marten habitat selection operates at a scale that is an order of magnitude, or more, greater than that for squirrels (Caryl, 2008 & 2012; Pereboom *et al.*, 2008). Grey squirrels show preference for mixed broadleaf forests (Gurnell *et al.*, 2001; Kenward, 1986) and our study sites were selected on this basis. The habitats surrounding the broadleaf and mixed broadleaf woodland compartments of our study, were predominantly grasslands and mixed-age conifer plantation, interspersed with areas of clear-fell and dense understorey, where we would expect to find naturally low densities of grey squirrels. Marten habitat preference might nevertheless be influencing squirrel density in surrounding habitats and thus altering the overall squirrel population dynamics through a change in population density and composition. Incorporation of fine-scale habitat composition in future assessments of grey squirrel and pine marten ranging may shed some light on the potential for such relationships. The

effect of season and the associated reproductive and dispersal behaviours of squirrels may play a role in variation in space use as squirrels might display different ranging behaviours in the latter months of the year, towards the end of the period of this study. Our analyses suggest that the effects of marten exposure were independent of sex effects, except in one model of daily distances, where there was a significant interaction between sex and exposure. In relation to dispersal, the tracked animals were resident during the observation period, and we have shown that they did not shift their range centroids. Thus, reproductive and dispersal behaviours are unlikely to have introduced a systematic bias with respect to variation in marten exposure. Again, future work at appropriate spatial and temporal scales could consider the potential for effects on dispersing animals as well as residents.

The impact of marten exposure on grey squirrel space use was calculated over a range of different spatial scales, by using different bandwidths for marten ranges (Fig. 4.2) to capture the high mobility of the predator (Caryl, 2008; Zalewski et al., 1995) and effectively “allow” the effect of pine martens to be felt over a wider area. Pine marten ranges are highly variable, depending on habitat quality and conspecific density (Powell, 1979) and are likely larger for translocated animals that are exploring new landscapes. As models incorporated the greater potential extent of pine marten influence (through increasing bandwidths), we identified a more consistent effect on squirrel behaviours.

This study presents an initial insight into the fine-scale, short-term effects that a recovering native predator can have on its invasive, non-native prey. Our results suggest that even shortly after translocation and while living at low densities, pine martens affect grey squirrel behaviour. However, exact timing of onset, duration and persistence of such changes remains unknown. We utilised a conservation translocation to simulate the natural range expansion of recovering marten populations and their use as a native agent of biological control. Our main methodological approach was not that of a capture-mark-recapture (CMR) study, therefore the trapping periods were not consistent across sites, and so larger studies of density and survival across habitat types may provide an insight into direct, lethal effects of marten presence. There is now a need to understand the wider implications of such behavioural changes for grey squirrel populations over

longer time periods and whether this might help explain the downstream consequences for red squirrel populations described in Ireland and Scotland (Sheehy et al., 2014, Sheehy et al., 2018) and for forestry economics. The re-establishment of martens may alter the abundance, behaviour and/or distribution of grey squirrel populations, not only in initial stages, as shown here, but over longer time periods, as shown in Ireland and Scotland.

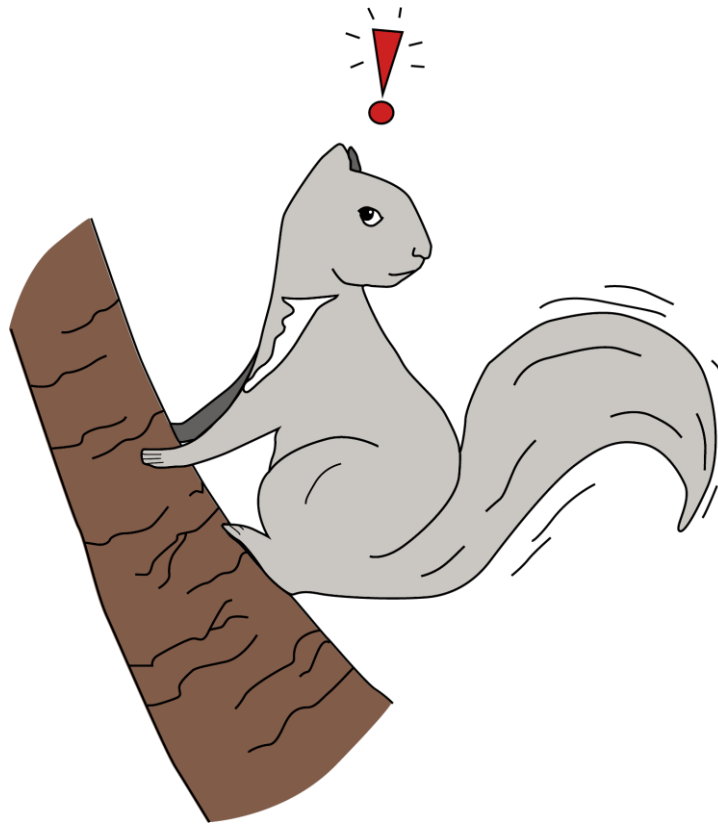






## Chapter 5

### **Behavioural responses of resident non-native grey squirrels *Sciurus carolinensis* to the presence of translocated native pine martens *Martes martes***



## **Chapter 5: Behavioural responses of resident non-native grey squirrels *Sciurus carolinensis* to the presence of translocated native pine martens *Martes martes***

### ***Abstract***

Predators can influence the dynamics of their prey by direct, usually lethal, and indirect, usually non-lethal, mechanisms. Risks of predation can alter the behaviour of prey animals, and spatial variation in such risks can create a 'landscape of fear' in which predators can have heterogeneous effects on prey fitness. We have investigated the impact of a translocated native predator, the pine marten *Martes martes*, on the behaviour of the invasive non-native grey squirrel *Sciurus carolinensis*. Using a giving-up density (GUD) framework and observations of squirrel behaviour, we compared the foraging behaviour of grey squirrels at paired feeding stations, near to and distant from trees, in woodlands with and without translocated pine martens. The volume of food remaining in feeding trays at the end of foraging periods was measured to determine when squirrels 'gave-up' foraging under these different conditions of risk. We found that the proportion of trays fully depleted by squirrels was significantly lower overall and trays had significantly more food remaining after a foraging session, in woodlands where pine martens were present than in those where they were absent. This suggests a fear-mediated response to increased predation risk. Squirrels did not show any differences in their foraging at trays near to or distant from trees, but exhibited differences in fear-associated behaviours in these locations, with such behaviours increasing with time near to trees and decreasing with time far from trees. This suggests that predation risk in woodlands is driven by multiple factors such as and the threat of predation by other species as well as the pine marten. Differences driving variation in food consumption, such as vigilance or head-down behaviours, could not be detected in behavioural observations, but we conclude that differences in when squirrels 'gave-up' foraging are the result of a pine marten avoidance strategy. Reductions in foraging time in woodlands with resident pine martens may have detrimental impacts on grey squirrel fitness. We have demonstrated that the impacts of pine martens on grey squirrels extend beyond direct predation into non-lethal, fear-

mediated effects. Furthermore, fear in predator-prey interactions might be incorporated into management strategies for pest species and considered as part of feasibility studies for predator translocations.

## ***Introduction***

The structure and function of communities are influenced by predator-prey interactions (Lima 1998). Predation is regarded as a key driving force of community level population dynamics, though in some cases the non-lethal effects of predators can be greater than the direct effects of predation (Lima & Dill 1990; Brown 1999; Brown et al. 1999; Creel & Christianson 2007). When faced with the risk of predation, prey animals often have to prioritise safety over other activities such as reproduction and foraging. The trade-off between ensuring safety and undertaking other activities could result in reduced energy intake, reduced reproductive effort or increased predation risk (Brown et al. 1999). This in turn may have a negative impact on the overall fitness and demography of prey that can be comparable at a population level to the lethal effects of predation (Lima & Dill 1990; Brown et al. 1999; Lima & Bednekoff 1999; Creel & Christianson 2007). Quantifying the non-lethal effects of predators, and the 'landscape of fear' (Brown 1999) that they create, is thus key to understanding the role of fear in predator-prey relations.

The 'landscape of fear' created by the presence of a predator can not only influence behaviour and demography of prey animals, but also the wider ecological community, indicating its potential as a tool in wildlife management (Creel & Christianson 2007; Laundré et al. 2014). Practical applications of the landscape of fear have been demonstrated experimentally through the manipulation of apparent predation risk in order to manage nuisance species. For example, the negative impacts of raccoon *Procyon lotor* foraging on lower trophic levels in the absence of predators was decreased using the playback calls of larger carnivores in the form of domestic dog *Canis lupus familiaris* barks (Suraci et al. 2016). Importantly, the role of fear will only remain impactful if associated with true experience or risk of predation. Creation of a true 'landscape of fear'

requires behavioural conditioning, in which the suggested presence of a predator is associated with exposure to, or attack by that predator. This has been demonstrated in the use of Harris' hawks *Parabuteo unicinctus* to reduce the abundance of the pest species, Egyptian geese *Alopochen aegyptiaca* on golf courses. The vigilance displayed by remaining geese continued to be higher in the presence of hawk-associated vehicles even when hawks were absent (Atkins et al. 2017). Although scarce, it is clear from studies that have manipulated the 'landscape of fear' that it could be exploited in an applied setting, with significant implications for both management and conservation.

The complexity of interactions involved in the 'landscape of fear' has meant that design, implementation and demonstration of fear and its effects as a tool in wildlife management, as opposed to behavioural research, is challenging. When fearful, there are a variety of anti-predator strategies that might enable prey animals to persist, by altering the areas that they use or the way they behave. In some instances, prey animals improve their risk perception and become habituated to the presence of particular predators and threats (Deecke et al. 2002; Rodriguez-Prieto et al. 2009). Studies have also found physiological changes in prey animals such as an increase in stress hormones (Sheriff et al. 2010) or reduction in reproductive hormones under increased predation risk (Boonstra et al. 1998; Creel & Christianson 2007). Alternatively, anti-predator behaviours can comprise a shift in range away from areas or times where predators are present to avoid peak predator activity (Moreno et al. 1996; Lima & Bednekoff 1999; Jacob & Brown 2000; Heithaus & Dill 2006; Gehr et al. 2017). These avoidance strategies may not always be possible and individuals may have to make a trade-off between resource acquisition and safety (Brown 1999). Safety can be improved by an increase in vigilance (Brown 1988, 1999; Apfelbach et al. 2005; Watson et al. 2007), reduced handling time of food or foraging in a less exposed location (Brown 1999; Ripple et al. 2001; Brown & Kotler 2004). Although this may be beneficial over short time periods, increased vigilance detracts from other fitness-related activities and can be detrimental at an individual and population level (Brown 1999; Ripple et al. 2001; Creel & Christianson 2007; Watson et al. 2007).

Investigation of antipredation strategies can be undertaken through tracking studies, behavioural observations and foraging experiments. One approach used to quantify risk as perceived by animals is to use a 'Giving-Up Density' (GUD) framework (Brown 1988, 1999; Jacob & Brown 2000; Bedoya-Perez et al. 2013). The fundamental principle of this is that foragers will give-up feeding in a patch when food supply reaches a density, the GUD, at which the benefits gained from the food being received no longer outweigh the risk being taken to obtain it (Jacob & Brown 2000). This process of optimal foraging is a primary principle of the marginal-value theorem (Charnov 1976), which predicts that a forager will harvest a depletable resource patch for as long as the benefits outweigh the costs. These costs can include predation risk, food availability and physiological constraints (Bedoya-Perez et al. 2013), all of which can be manipulated, and the variation in GUD measured under an experimental framework. GUD studies use a depletable food resource, which is measured before and after a foraging bout. The GUD represents the density of food at which the animal 'gives-up' foraging and leaves the resource patch (Jacob & Brown 2000; van der Merwe & Brown 2008). Higher foraging costs are incurred when the threat of predation is high, foragers will quit patches sooner and the resulting amount of food left, i.e. the GUD, will be higher (Brown 1988). The decision of when to cease foraging therefore provides a valuable insight into prey animals' perceptions of risk in their environment. GUD can be used to compare the risk of predation in different habitats and microhabitats. If two foraging patches have the same energetic value and foraging costs, any variation in GUD can be attributed to predation risk (van der Merwe & Brown 2008). This variation across an environment enables us to map animal perceptions of the 'landscape of fear' (Brown & Kotler 2004; van der Merwe & Brown 2008) and manipulation of this landscape therefore holds potential in establishing if there is a detrimental effect of predator presence on prey foraging behaviour. If these effects are detrimental at a prey population level, the role of predators could be incorporated into wildlife management strategies.

A potential application of the 'landscape of fear' in wildlife management is in understanding the control of the invasive grey squirrel *Sciurus carolinensis* in the UK, through the restoration and recovery of a native carnivore, the pine marten *Martes martes*. Grey squirrels are widely perceived by people as a pest species, responsible for disease transmission to native red squirrels *Sciurus vulgaris*

(Rushton et al. 2000; McInnes et al. 2006) and tree damage (Mayle et al. 2009), and as a result there is significant ecological and economic interest in their eradication. Following recent studies in Ireland and Scotland (Sheehy & Lawton 2014; Sheehy et al. 2018), the pine marten has been identified as a potential influence upon the distribution and abundance of grey squirrels. Surveys found increased pine marten density and long-term residency were correlated with grey squirrel declines and, in turn, with higher numbers of red squirrels (Sheehy & Lawton 2014; Sheehy et al. 2018). The direct causes of these changes in relation to marten presence have yet to be fully understood. Squirrels of both species are known prey of the pine marten (Ben-David et al. 1997; Putman 2000; Sheehy et al. 2014, Chapter 3), and though not generally their primary food source, squirrels will be consumed opportunistically and are therefore at risk of predation (Putman 2000; Sheehy et al. 2014, Chapter 3). The use of predators as biological control agents is a method typically utilised to control pest species (Symondson et al. 2002; Paz et al. 2013). Lethal control of grey squirrels, although capable of limiting populations at local scales, has been largely unsuccessful in reducing the density and spread of the species at a national level, in part due to a combination of challenges of funding and logistics as well as inconsistent culling practices on a local and regional scale (Schuchert et al. 2014). However, grey squirrel management continues to be widespread (Mayle et al. 2007; Schuchert et al. 2014). The control and reduction of UK grey squirrel populations nevertheless remains a major challenge for both conservationists and foresters that would benefit from additional and alternative approaches. The recent conservation translocation of the pine marten to mid-Wales (Macpherson 2014) presents a unique opportunity to investigate the roles of this native predator through not only lethal effects, but also the potential creation of a 'landscape of fear' for grey squirrels.

Here, we aimed to determine whether pine martens create a landscape of fear for grey squirrels. We assessed the perceived predation risk through behavioural observation and quantification of foraging decisions made by grey squirrels using a standardised feeding experiment. We implemented a 'Giving-Up Density' (GUD) framework in combination with behavioural observations to quantify risk perception and response within different micro-habitats (foraging station level) and macro-habitats (woodland-level). The use of GUD studies on squirrels has

been successfully used to quantify local predation hazards, anthropogenic impacts and diet selection (Lima & Valone 1986; Bowers et al. 1993; Bowers & Breland 1996), however we have no understanding of how grey squirrels respond to pine marten predation risk in particular. Since squirrels are not social foragers, they generally rely on proximity to cover to evade predation (Lima et al. 1985; Newman & Caraco 1987; Bowers et al. 1993). Studies have shown that squirrel patch use varies as a result of predation risk (Newman & Caraco 1987), with areas near to cover being preferred, and therefore more heavily depleted, compared to sites distant from cover (van der Merwe & Brown 2008). We thus expected higher levels of food depletion (i.e. low GUD) and visitation in locations near to trees, with lower levels of fear-associated behaviours and vigilance (Arenz & Leger 2008). In woodlands where there were resident martens, we expected to see lower levels of food depletion (i.e. high GUD) and visitation, accompanied by high levels of fear-associated behaviour and high proportion of time spent vigilant (Brown & Kotler 2004).

## ***Materials & Methods***

### *Study area*

The study was conducted in May-June 2017 in six mixed broadleaf and conifer plantation woodlands in mid-Wales. Three sites were known to have pine martens present on the basis of radio-tracking translocated and released martens, camera trapping and/or scat collection, while three other sites had no such evidence of marten presence. Martens had been translocated as part of a pine marten recovery project, aiming to restore marten populations in Wales and England (Macpherson 2014). All martens in the region were recently translocated individuals that had been radio-collared for post-release monitoring. Populations of grey squirrels were well established across all woodland sites, and none of these woodlands had recent records of red squirrels. The distances between sites was between 2.5km and 17.5km, and the composition and structure of these woodlands was similar throughout, reducing the potential for spatial and climatic variation.

### *Giving-up density experiment*

Eight GUD feeding stations were established in the six woodlands ( $n = 48$  stations). Each station comprised a pair of trays ( $n = 96$  trays), one in a 'near' location, at the base of a tree (mean  $\pm$  SE =  $25 \pm 2$ cm from a tree, range = 3-286cm) and one in a 'distant' location, in more open ground away from cover ( $356 \pm 12$ cm from a tree, range = 129-883cm). The mean distance between trays, within a pair was  $639\text{cm} \pm 13\text{cm}$  and stations within a woodland site were at least 30m apart. Each station comprised a plastic seed tray (L 38 x W 24 x H 5cm, approximately 4.6L) with a plastic-coated mesh grid of 5 x 5cm squares placed on top, which could be moved up and down but not removed, preventing foraging squirrels from kicking contents out of the tray. This also meant that foraging was made more difficult without having to increase the volume of foraging substrate. Bases of trays were perforated to enable drainage and were pinned to the ground using ground hooks to prevent tipping. Trays were left in-situ throughout the study. Prior to commencement of the study, feeding station sites were pre-baited for a minimum of seven days using peanuts, whole maize and cobnuts. These encouraged the squirrels to feed at these locations on the ground and were checked daily for signs of squirrel feeding. Three days prior to the study commencing, plastic trays used in the GUD study were filled with bait and left at the feeding station locations, enabling habituation by the squirrels to feeding in the trays and reducing neophobic responses that might influence GUD in the early days of the trial. A foraging mixture of peanuts and sieved, coarse sand was added to each tray on a daily basis. The mixture comprised 25g of whole peanuts mixed evenly into 2.5L of sand. Volumes were based on pilot studies and allowed for space below the tray brim, preventing sand from being kicked out during foraging. Foraging mixtures were added to trays before first light (at approximately 4am) prior to squirrels beginning to forage, and collected six hours later (at approximately 10am). The remaining foraging mixture from each tray was then sieved through a soil riddle (grid 1 x 1cm) to separate the remaining whole and large peanut fragments from the sand. The experiment was only undertaken on predominantly dry days, preventing water-logging of foraging stations and ensuring conditions were well suited to grey squirrel foraging.



### *Foraging behaviour observations*

All visitation by squirrels to the trays was recorded using motion sensitive infra-red trail cameras (Bushnell Trophy Cam HD). These were set to record 60 second videos with a one second interval throughout the active hours of the study. The camera set-up was standardised at all trays. Cameras were mounted on wooden stakes 2m from the tray on a north-south axis, reducing glare at dawn. Videos recorded during each six hour session were watched to identify the number of visits made by a) squirrels and b) non-target species. The latter were retained and used in statistical models to account for food depletion not associated with grey squirrels (Bedoya-Perez et al. 2013). The number of videos containing squirrels was used as a proxy for squirrel visitation rate. Individual squirrels were not identified during this study and the GUD was attributed to the last squirrel to have foraged at that site. If the last forager observed was not a squirrel, then trays were excluded from the analysis as the GUD, which is determined by the last forager, was not representative of squirrel foraging. However an exception was made if the last foraging bout after a squirrel was made by a small passerine as, after close observation of videos, their impact on remaining food was deemed negligible. Sessions in which cameras malfunctioned and squirrel visitation could not be quantified were excluded from any analyses ( $n = 194$ ). Only data for all trays meeting these inclusion criteria were used in GUD analysis ( $n = 286$  sessions), however video footage of all squirrel behaviour from all trays was included in behavioural analyses.

### *Giving up densities (GUDs)*

Giving-up density was successfully recorded for 8 foraging stations with paired trays per day across six woodland sites for 5 days ( $n = 480$  trays). Squirrel visitation could not be quantified at a number of trays ( $n = 78$ ) due to camera malfunction and these trays were excluded from any analyses. Of the trays with full video footage ( $n = 402$ ), those with a squirrel ( $n = 262$ ) or a small passerine ( $n = 24$ ) as the last forager to deplete the station were included in GUD analyses ( $n = 286$ ). Trays that did not have small passerines or squirrels as the last forager ( $n = 116$ ) were excluded from GUD analyses.

Videos were analysed by 13 trained observers using BORIS event-recording software (Friard & Gamba 2016) to identify foraging and vigilance-based behaviours. Behavioural categorisation was based on previous squirrel behavioural studies and initial observations of videos to ensure behaviours were distinct enough to categorise (Lurz et al. 2005; Makowska & Kramer 2007; Partan et al. 2010; Table 5.1). In each 60 second video, the duration of squirrel presence and the duration and/or frequency of behavioural states were recorded (Table 5.1). Each video was treated as a separate observation for behavioural analyses since squirrels were not individually identifiable, however we address some of this non-independence in foraging analyses by including tray as a random factor in analyses. Videos with poor light levels were discarded as observations could not be made confidently. Continuous behaviours were grouped as either 'foraging-focussed', predominantly head-down, or 'vigilance-focussed', predominantly head-up, behaviours (Table 5.1). The proportion of time spent performing these behaviours at each tray, each day, was then calculated by dividing the duration of these behaviours by the total time the squirrel was present. The number of 'fear'-associated behaviours (Table 5.1) was also counted and summed for each tray each day. Videos were randomly allocated to observers and observations were carried out blindly. Between-observer consistency (inter-rater reliability, IRR; Hallgren, 2012) was estimated by comparing five selected videos that all observers watched to assess the level of agreement between observers. The intra-class correlation coefficient score of agreement generated was 0.98 (95% CI = 0.95 - 0.99), where 1 was 100% agreement. Therefore, we did not control for observer ID in analyses (Kaufman & Rosenthal 2009; Gamer et al. 2010; Hallgren 2012).

### **Statistical Analysis**

We used generalised linear mixed models (GLMMs) to analyse variation in giving up densities and squirrel behaviour. Following Forstmeier and Schielzeth (2011), we report the full model due to all terms being of interest and the importance of non-significant results for our hypotheses. For all models, we estimated their explanatory power with Nagelkerke  $R^2$  as defined by Nakagawa and Schielzeth (2013), where the value (between 0 and 1) represents the proportion of variance explained by the fixed effects alone (marginal  $R^2$ ), as well as the fixed effects plus the random effects (conditional  $R^2$ ). Terms were deemed significant if 95%

confidence intervals did not cross zero. Nagelkerke  $R^2$  values were calculated in the package *MuMIn* (Barton 2018). All statistical analyses were performed using *R* version 3.5.2.

We investigated variation in the giving-up density in a two-step process. First, we tested whether a tray had been fully depleted or not, scoring trays with 1 if they were fully depleted and 0 if there was food remaining after a foraging session (Depletion model). Depletion was modelled using a GLMM with a Binomial error distribution. Second, we tested what affected the volume of food remaining in trays that were not fully depleted (GUD model). GUD was log-transformed and modelled using a linear mixed model (LMM) with Gaussian errors using the '*lme4*' package (Bates et al. 2015) to meet assumptions of homoscedasticity and normality of residuals. Both depletion and GUD models contained explanatory variables of marten presence (present or absent), location (near or distant), day (1-5), and all possible two-way interactions (Table 5.2). Day was centred to assist in model output interpretation. The number of videos that contained non-target species was also included as a covariate to control for any additional effect on food depletion. Random effects of tray ID, nested within site, were also included.

**Table 5.1. Description of squirrel behaviours recorded during foraging.** Individual behaviours are categorised into *Foraging-focussed* – predominantly head-down behaviours, *Vigilance-focussed* – predominantly head-up behaviours and *Fear-associated behaviours* for behavioural analyses.

Behaviour	Description
Foraging behaviours	
<i>Foraging</i>	Head below plane of shoulders. Squirrel is looking for food/digging. May be caching food.
<i>Sitting eating</i>	Bipedal eating: head is above plane of shoulders. Sitting, body motionless, head or eyes may be scanning. Sitting or standing on hind legs holding food and eating or chewing.
<i>Quadrupedal eating</i>	Head is at or above plane of shoulders. On all fours or three legs with one leg raised chewing. Body motionless. Head or eyes may be scanning.
Vigilance behaviours	
<i>Bipedal vigilance</i>	Stops current behaviour, on hind legs, not manipulating food/chewing. May be holding food in hands or in mouth but not chewing. May be raised on hind legs.
<i>Quadrupedal vigilance</i>	Stops current behaviour, head above plane of shoulders, four legs on ground, sometimes one front leg is raised. May be holding onto edge of tray with one or more limbs.
<i>Grooming</i>	Scratches or grooms self.
Fear-associated behaviours	
<i>Tail flag</i>	Tail waved with high vigour, longer duration, above the axis of the back, usually up over the head, involves most of the tail in movement.
<i>Foot stamping</i>	Shifts from foot to foot.
<i>Retreat</i>	Sniffs tray but backs away or moves in direction not towards tray.

**Table 5.2. Variables used to explain squirrel foraging behaviours and predictions of how they will affect giving-up density and behaviours undertaken.**

Predictors	Levels	Prediction
Marten presence	Present/ Absent	The presence of pine martens in the woodland will affect the volume of food consumed and the behaviours displayed in trays due to different risk of predation in each location
Location	Near/ Distant	The location of the tray near to or distant from a tree will affect the volume of food consumed and the behaviours displayed in trays due to different levels of risk in each location
Day	Day 1-5	The day of experiment (1-5) will affect the volume of food consumed and the behaviours displayed in trays due to habituation to feeding in trays over time
Marten presence x Location	Present + Near, Present + Distant, Absent + Near, Absent + Distant	The location of the tray near to or distant from a tree combined with the risk of pine marten predation (marten is present/absent) will affect the volume of food consumed and the behaviours displayed in trays due to different levels of risk and predation in each location
Marten presence x Day	Present + Day 1-5, Absent + Day 1-5	The presence of pine martens in the woodland will affect the volume of food consumed and the behaviours displayed in trays due to different risk of predation in each location, however this will vary with time due to habituation to feeding in trays
Location x Day	Near + Day 1-5, Distant + Day 1-5	The location of the tray near to or distant from a tree will affect the volume of food consumed and the behaviours displayed in trays due to different levels of risk in each location, however this will vary with time due to habituation to feeding in trays

### *Behaviour while foraging*

We then constructed four behavioural models. We first tested what influenced the number of visits to a tray (Visitation model) with the number of squirrel videos recorded per tray per day as a proxy for visitation rate. We then analysed the number of fear-associated behaviours displayed (Fear model) and the proportion of time spent undertaking ‘foraging-focussed’ and ‘vigilance-focussed’ behaviours (Foraging and Vigilance models respectively). All four models contained marten presence, location, day, and all possible two-way interactions as fixed effects (Table 5.2) and nested random effects of tray ID within site. Visitation and Fear models were negative binomial GLMMs modelled using the ‘*lme4*’ package (Bates et al. 2015), with the Fear model containing an offset to account for the total time that the squirrel was present (log-transformed duration of squirrel presence; Francis et al., 2018). Day was centred in both models. A high number of squirrels displayed either no foraging or no vigilance during their foraging bouts resulting in zero-inflated behaviour proportions. Foraging and Vigilance models therefore comprised zero-inflated beta-binomial models. These models simultaneously fit two modelling processes, one which models if the squirrel performed the behaviour or not, and one which models the proportion of time spent doing that behaviour if it was greater than zero. Zero-inflated beta-binomial models contained the full set of explanatory variables (fixed and random effects) in both parts of the model. Zero-inflated beta binomial models were fitted using Bayesian inference in ‘*stan*’ (Carpenter et al. 2017) using the *R* package ‘*brms*’ (Burkner 2015). Parameter values were estimated using Markov-chain Monte-Carlo (MCMC) methods, using ‘*brms*’ defaults for the priors and initial values. Four chains were run for 2000 iterations of which 1000 were discarded as burn-in. MCMC chains for all parameters converged ( $R\text{-hat} < 1.01$ ) and had an effective sample size greater than 2000. From the remaining MCMC chains we calculated the mean estimate and 95% credible intervals. The statistical significance of the effect of all model parameters was determined by the 95% credible interval not overlapping zero.

## **Results**

### *Giving-up densities (GUDs)*

The proportion of trays that were fully depleted differed between sites with and without pine martens. 29 trays were fully depleted across the entire study, 22 of these were in sites without martens. At sites where martens were not found, the proportion of trays that were fully depleted increased with the day of experiment. All model estimates are presented in Table 5.3. At sites with martens, the proportion of fully depleted trays was lower overall (estimate averaged over time = 0.05; 95% Confidence Interval [CI] = 0.0004 - 0.09) than sites without martens (estimate averaged over time = 0.16; 95% Confidence Interval [CI] = 0.11 - 0.21). The proportion of trays fully depleted changed differently through time where martens were present compared to where they were absent. Full depletion decreased with time in the presence of martens (slope = -0.03, 95% CI = -0.06 - 0.00; Table 5.3; Fig. 5.1a), whereas in sites without martens, depletion increased with time (slope = 0.05, 95% CI = 0.01 - 0.08; Table 5.3, Fig. 5.1a). The marginal  $R^2$  for the global Depletion model was 0.15, increasing to 0.22 when the variation explained by tray and site effects was included.

**Table 5.3. The effect of pine marten presence, location in relation to cover, and day of experiment on squirrel foraging behaviours.** The baseline of 'Marten' is marten absence and the baseline of 'Location' is distant from cover. Models (Generalised Linear Mixed Models – GLMMs) comprise Depletion: the proportion of trays that were fully depleted, GUD: the volume of food remaining after the last individual has foraged, Visitation: the number of visits to each tray and Fear: the number of fear behaviours displayed at each tray. The values provided comprise the model estimate with the 95% confidence interval in parentheses. Below the dotted line are results of zero-inflated beta binomial models where the values comprise the model estimate (lower 95% credible interval, upper 95% credible interval). Models comprise Vigilance: was vigilance behaviour performed (Y/N) and if it was, what proportion of time was spent vigilant, and Foraging: was foraging behaviour performed (Y/N) and if it was, what proportion of time was spent foraging. The explanatory power of models is detailed by the marginal  $R^2$ , representing the proportion of variance explained by the main effects of the model. The conditional  $R^2$  which incorporates the variance explained by the random effect is given in parentheses.

<i><b>Model</b></i>	<i><b>Predictors</b></i>						
	Marten	Location	Day	Marten x Location	Marten x Day	Day x Location	$R^2$ ( $R^2_c$ )
<i>Depletion</i>	-1.79 (-3.74, -0.16)	0.19 (-0.87, 1.24)	0.28 (-0.22, 0.77)	-0.25 (-2.50, 2.00)	<b>-1.35 (-2.26, -0.43)</b>	0.24 (-0.43, 0.91)	0.15 (0.22)
<i>GUD</i>	1.25 (0.10, 2.40)	-0.05 (-0.78, 0.69)	-1.09 (-1.38, -0.79)	-0.16 (-1.15, 0.83)	<b>0.85 (0.51, 1.20)</b>	0.17 (-0.18, 0.51)	0.18 (0.49)
<i>Visitation</i>	0.15 (-0.21, 0.50)	<b>0.40 (0.12, 0.67)</b>	-0.005 (-0.10, 0.11)	-0.31 (-0.67, 0.05)	-0.07 (-0.19, 0.05)	0.02 (-0.10, 0.13)	0.03 (0.25)
<i>Fear</i>	0.35 (-0.06, 0.77)	-0.25 (-0.56, 0.06)	-0.13 (-0.27, 0.01)	-0.05 (-0.45, 0.36)	-0.05 (-0.20, 0.09)	<b>0.25 (0.12, 0.38)</b>	0.08 (0.23)
<i>Vigilance (Y/N)</i>	0.36 (-0.11, 0.84)	-0.11 (-0.18, 0.40)	-0.03 (-0.04, 0.10)	0.01(-0.23, 0.24)	0.02 (-0.05, 0.10)	-0.06 (-0.13, 0.02)	0.06
<i>Vigilance (Proportion of time)</i>	-0.10 (-0.30, 0.09)	-0.15 (-0.35, 0.06)	0.00 (-0.06, 0.05)	0.09 (-0.09, 0.25)	0.00 (-0.05, 0.06)	0.01 (-0.04, 0.07)	0.06
<i>Foraging (Y/N)</i>	-0.08 (-0.97, 0.75)	0.16 (-0.26, 0.59)	0.07 (-0.03, 0.18)	-0.17 (-0.50, 0.18)	0.09 (-0.02, 0.20)	-0.10 (-0.20, 0.01)	0.15
<i>Foraging (Proportion of time)</i>	0.11 (-0.09, 0.33)	0.04 (-0.13, 0.21)	0.0 (-0.04, 0.05)	0.04 (-0.10,-0.19)	0.01 (-0.04, 0.06)	-0.01 (-0.06, 0.03)	0.15



Of the trays not fully depleted ( $n=257$ ), GUD ranged from 0.01-25g (mean = 5.58g). At sites without martens, the GUD was lower overall (0.46g, 95% CI: 0.29-0.72) compared to sites where martens were resident, where GUD was significantly higher overall (1.13g, 95% CI: 0.76-1.69). Marten presence also affected the relationship through time and where martens were present, the GUD declined rapidly with time (slope = -1.02, 95% CI: -1.32--0.72;  $n = 114$ ) compared to where martens were absent and the GUD decreased less with time (slope = -0.17, 95% CI: -0.45 -- 0.11;  $n = 143$ ; Table 5.3; Fig. 5.1b). Whether a tray was in a location near to, or distant from a tree, and its interaction with other variables was not significant. The marginal  $R^2$  for the global GUD model was 0.18, rising to 0.49 when the variation explained by tray and site effects was included.

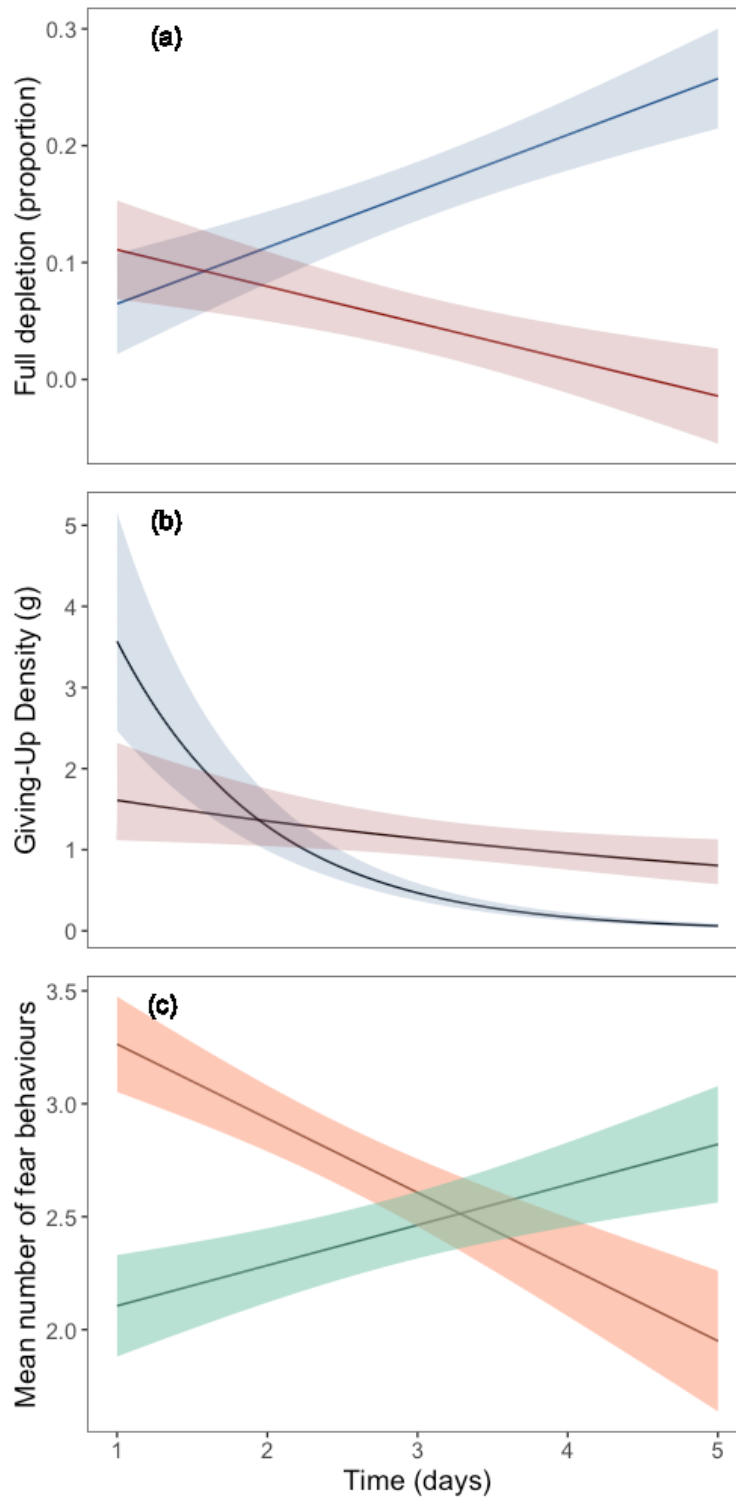
### *Visitation*

There was large variation in visitation rates between trays (1-79 times in a single day). The visitation rate to trays near cover (18.5 visits per day, 95% CI: 15.6 - 22.0) was significantly higher than that for trays further away (14.6 visits per day, 95% CI: 12.2 - 17.5; Table 5.3). Visitation rate was not affected by the presence or absence of pine martens or the day of the experiment. There was a large amount of variance not explained by the model (marginal  $R^2 = 0.03$ ), however on inclusion of the random effects (tray nested within site) the model fit was improved (conditional  $R^2 = 0.25$ ; Table 5.3), suggesting this variable explains a large proportion of the variance.

### *Behaviour while foraging*

After removal of unobservable footage, the number of one minute videos analysed was 9988, comprising 166 camera trap hours. The number of fear-related behaviours ranged from 1-25 per minute. Initially, the number of fear behaviours were similar, however in distant trays, the number of fear behaviours declined with day of experiment (slope = -0.33, 95% CI: -0.54 - -0.11; Table 5.3; Fig. 5.1c). In near trays the number of fear behaviours increased slightly with day of experiment (slope = 0.18, 95% CI: -0.01-0.37; Table 5.3; Fig. 5.1c). Whether the site contained pine martens or not had no effect on the numbers of fear-related behaviours displayed (Table 5.3). The Fear model did not explain a large proportion of the variation in fear behaviours (marginal  $R^2 = 0.08$ ), however the random effect of tray nested within site was important (conditional  $R^2 = 0.23$ ).

Within the Foraging model, the display of any foraging behaviours at all, namely foraging, sitting eating or quadrupedal eating, in one minute videos (zero-inflated portion of model) was unaffected by tray location, the day of experiment or marten presence or by the interactions between variables (Table 5.3). Furthermore, if squirrels were foraging, the proportion of time spent foraging (beta-binomial portion of model) was not explained by these variables (Table 5.3). The Foraging model was a reasonable fit to the data (Bayes- $R^2 = 0.15$ ). The same was found within the Vigilance model with regards to non-foraging focussed behaviours, namely bipedal vigilance, quadrupedal vigilance and grooming, however this model explained the data less well (Bayes- $R^2 = 0.06$ ; Table 5.3).



**Figure 5.1. The effect of marten presence and tray location on grey squirrel foraging:** a) The proportion of trays fully depleted when pine martens are absent (blue) versus when they are present (red) with day of experiment b) The Giving-Up Density (g) when pine martens are absent (blue) versus when they are present (red) with day of experiment c) The number of fear-associated behaviours displayed per minute, in trays near to (green) and distant from (orange) trees, plotted against day of experiment- excluding trays where no fear behaviour was displayed. All plots comprise modelled outputs. Model fit is quantified by  $R^2$  values in Table 5.3.

## ***Discussion***

Pine marten presence was associated with a fear response by grey squirrels, reducing their depletion of provisioned food resources over time (Fig. 5.1). This is suggestive that a 'landscape of fear' exists, where the presence of a predator affects the behaviour of prey, in a way which is detrimental to prey fitness. However, this effect was not apparent in behavioural observations of squirrels during foraging bouts. Current evidence suggests that the presence of martens negatively impacts the population density of grey squirrels over large spatial and temporal scales (Sheehy & Lawton 2014; Sheehy et al. 2018). The process underlying this squirrel-marten relationship is still not fully understood and aside from direct predation (Chapter 3), it is possible that pine martens may shape the grey squirrels' landscape of fear. Previous work on this squirrel population (Chapter 4) has demonstrated that in the presence of martens, grey squirrel range size and daily distance travelled is higher, which was suggested to be a predator avoidance strategy, combined with a reduction in grey squirrel density as an outcome of earlier predation.

The proportion of fully depleted trays and the giving-up density (GUD) in relation to marten presence was found to interact with time. By the final day of the study, fewer trays were fully depleted by squirrels in sites where martens were resident (Fig. 5.1a). Of the trays not fully depleted, more food remained in sites where pine martens were present, i.e. GUD was higher overall (Fig. 5.1b). This reduced resource depletion in sites where martens had been reintroduced may result from a combination of lethal and non-lethal effects. As well as a potentially lower number of foragers due to direct predation (lethal effects; Chapter 3), squirrels may undertake shorter foraging bouts as they move around more to avoid predation (non-lethal effects; Chapter 4). As a result, less food would be consumed and the depletion of a food source would be expected to take longer (Brown 1999; Carthey & Banks 2018). Furthermore, predator detection strategies, such as vigilance, would be costly to food acquisition and drive the earlier quitting rate observed in marten-occupied sites. We therefore expected these fear-induced feeding modifications to be detectable in foraging footage. However, our behavioural observations did not find such differences. This may be a result of an inadequate video length (one minute) to capture the true

combinations of behaviours in full foraging bouts by single individuals. Vigilance periods themselves may not differ in relation to marten presence but their frequency might (i.e. interscan duration; Beauchamp and Ruxton, 2016; Bednekoff and Lima, 1998), an aspect that we were unable to measure due to each one minute video being treated as a separate observation. Alternatively, behavioural changes by squirrels in the presence of martens may be too subtle to detect in videos, particularly due to the categorisation of behaviours required for observations undertaken by multiple people. The laterally facing position of the eyes on squirrel species' heads do not enable the determination of an individual's gaze (Arenz & Leger 2008; Hirschler et al. 2016) and subtle changes in head and body position, not associated with traditional vigilance positions, may enable changes in predator detection (Arenz & Leger 2008; Fernández-Juricic et al. 2011).

Food density has also been shown to influence the amount of foraging and the degree of vigilance displayed by foragers, regardless of predation risk (Beauchamp 2009). This can mask or confound risk effects at high food densities and only become apparent when food availability passes a lower threshold. In this study, the proportion of trays fully depleted at the start of this study was similar in woodlands with and without martens (Fig. 5.1a), potentially due to the appearance of patches of high food abundance during a time when natural food availability is low (Beauchamp 2009). Initially, squirrels may be trading-off safety for food acquisition, however this depletion was found to change differently with time in woodlands with and without martens (Fig. 5.1a & b). In marten occupied woodlands, this prioritisation of food appeared to decline with time. Here, food consumption may be traded for safety, demonstrated by fewer trays being fully depleted over time as predicted by the marginal value theorem (Charnov 1976). Habituation to feeding in trays may also contribute to this variation in GUD and depletion over time, suggesting that in woodlands without martens, habituation occurred much more rapidly (Fig. 5.1a & 1b).

The presence of martens did not significantly affect the locations in which squirrels elected to forage (i.e. near to or distant from trees; Table 5.3). Tray location was, however, associated with higher numbers of fear behaviours early in the study, with more fear behaviours observed at trays distant from cover

during this period (Fig. 5.1c). In squirrels, tail flagging and foot stamping (Table 5.1) are both behaviours linked to aggression and alarm, often associated with predator or intruder presence (Lurz et al. 2005; Digweed & Rendall 2009). In addition to the reintroduced pine marten, the red fox *Vulpes vulpes* and goshawk *Accipiter gentilis*, are important predators of grey squirrels in the UK, contributing to predation risk on the ground and from above respectively. The display of fear behaviours declined with time in distant trays and increased with time in trays near to trees (Fig. 5.1c), suggesting that there may be a degree of habituation occurring and that risk is perhaps realised at a different rate in near and distant trays. These fear-associated behaviours are likely driven by multifaceted predation risks from aerial, terrestrial and arboreal predators, therefore having no specific marten-associated effect on GUD.

We found that fear of predation by pine martens is a likely factor in observed changes in the foraging behaviour of grey squirrels, suggesting that martens create a 'landscape of fear' for the grey squirrel. The reduction in foraging by squirrels may be a contributing element of the local (Chapter 4) and landscape scale (Sheehy & Lawton 2014; Sheehy et al. 2018) patterns observed, where grey squirrel movement is increased and densities are reduced in the presence of martens. In periods of low food availability for squirrels, the effects of reduced food consumption, driven by fear, may be accentuated. As a result, if squirrels are unable to acquire adequate resources prior to winter months and before bud-burst in spring, their fitness may be compromised and a reduced level of survival may be observed. When combined with unexpected perturbations such as low temperatures, high levels of predation or disease outbreak (Gurnell 1996; Karels et al. 2000; Rushton et al. 2006), poor fitness can have significant effects on populations. When evaluating the prospect of pine marten impact on grey squirrels, this study demonstrates that their influence can extend beyond solely lethal effects. Fear of martens could therefore have an effect on squirrels at a population level over time (Suraci et al. 2016; Lurgi et al. 2018). The continued pressure of fear, and the resulting reduction in fitness, might also reduce the capacity of squirrel populations to recover after an intense culling event. A strategy that optimises low-level pressure on populations has been effective in invasive mammal control in Australia, as demonstrated on rabbits *Orytolagus cuniculus* (Wells et al. 2016), following a 'press and pulse' approach (Bender et

al. 1984; Lurgi et al. 2018). In the rabbit system, the 'press' was in the form of rabbit haemorrhagic disease or myxomatosis, putting long-term, low-level pressure on the population, and 'pulses' were periods of baiting and warren ripping, characteristic of unexpected perturbations (Lurgi et al. 2018). A similar multifaceted approach to squirrel control, which incorporates the non-lethal, fear-related effects of martens as a background level 'press' on grey squirrel populations, could play a role in reducing the density of grey squirrels below a critical level. This could, in turn, limit disease risk for red squirrels (Rushton et al. 2006), as well as decrease the amount of labour-intensive trapping and killing currently required.

Understanding the impact of predator presence on the fine- and broad-scale behaviour of prey is important in teasing apart landscape-scale patterns in species distribution. The giving-up density framework removes the need to observe individual behaviour and provides a directly quantifiable comparison of foraging under different conditions. In this instance we demonstrate that the impact of pine martens extends beyond direct predation into non-lethal, fear-mediated effects, altering grey squirrel foraging. With mounting interest in predator restoration in the UK and elsewhere, clarifying both lethal and non-lethal predator-prey processes is vital in predicting predator impacts. Here we have demonstrated that marten presence initiates a fear response in grey squirrels, however before widely advocating use of pine martens as a biological control agent, we should ideally understand the population-level impact of these fear induced changes. A reduction in grey squirrel density as a result of lethal and non-lethal effects may alter broad-scale population dynamics such as survival, reproduction, individual dispersal and immigration and this in turn may influence effects on bark-stripping behaviour and native red squirrels. Discovering the mechanisms, such as the role of fear, underlying predator-prey interactions can help conservationists manage expectations of stakeholders and develop strategies that enhance the effects of predator restoration. It is unlikely that predator restoration alone will be a 'silver-bullet' in invasive species eradication, however the lethal and non-lethal effects they introduce may both play a crucial part in any management framework.





## Chapter 6

### **Discussion**

## Chapter 6: Discussion

### Overview

Ecological restoration is a key component of worldwide conservation (Svenning et al. 2016). However, it is important that the processes underlying ecosystem function are understood before species and habitat composition are altered through human intervention. Carnivore restoration particularly, raises considerable interest and concern due to the potentially influential impacts that predators can have on ecosystems (Ritchie et al. 2012), and the social and economic effects this may have (Root-Bernstein et al. 2018). Although there are examples of carnivore restoration from North America (Estes & Palmisano 1974; Ripple et al. 2001) and Fennoscandia (Ludwig 2007), the re-introduction of carnivores is a relatively new strategy in the UK, but is now widely discussed, especially in the context of the reintroduction of charismatic apex predators. Currently, their restoration is still many years away. However, restoration of mesopredator populations is occurring naturally, by virtue of range expansion (Sainsbury et al. 2019), and the assisted re-colonisation and recovery of these species is a key priority in UK conservation (e.g. the European Unions' Habitat Directive 1992). With this in mind, the restoration of pine marten populations in mid-Wales is an attempt to use translocation to restore one of these recovering carnivores at a regional level. Understanding the ecological impacts of this restoration at an individual and population scale is central to guiding future conservation planning for this species. Given the relationship that pine martens have displayed with the native and invasive squirrel species in this region (Sheehy & Lawton 2014; Sheehy et al. 2018), there was a need to further investigate the processes driving the landscape-scale patterns observed between them.

This thesis investigates the potential mechanisms underlying the landscape-scale declines in grey squirrel abundance that have been documented in areas with pine martens (Sheehy & Lawton 2014; Sheehy et al. 2018). I investigated the spatial and behavioural ecology of translocated pine martens and resident grey squirrels in mid-Wales using biotelemetry, dietary analyses and behavioural experiments. Specifically, I described the post-translocation movement of pine

martens introduced from Scotland to Wales, revealing that the presence of conspecifics can drive post-release movement patterns (**Chapter 2**). I documented pine marten diet before and after translocation and found that individual martens have a degree of dietary specialisation, which they retain after translocation. Furthermore, martens in their new environment in Wales have a more diverse diet, which includes grey squirrels (**Chapter 3**). I explored the impact of pine marten presence on grey squirrel space use and behaviour using telemetry techniques, finding that in areas where grey squirrels experienced greater levels of exposure to pine martens, squirrels had larger home ranges and moved around more on a daily basis (**Chapter 4**). Finally I constructed foraging experiments and undertook behavioural observations on grey squirrels, showing that in the presence of martens, grey squirrels abandoned foraging sooner and as a result their food intake was reduced (**Chapter 5**).

Here, I review the findings of my thesis in relation to the two main themes of this work: factors affecting the successful translocation and restoration of carnivores, and the potential role of predators in wildlife management, resulting from predator-prey interactions. I will discuss the implications of my work for future conservation and management planning and suggest further research that can build on the foundations provided in this thesis.

## ***Restoration***

Predator population restoration requires a number of considerations prior to implementation. Animals must be moved into appropriate locations comprising adequate habitat and a suitable prey base (IUCN/SSC 2013). The behaviour of translocated animals can reveal if feasibility studies and release site selection have appropriately addressed the requirements of the species (Letty et al. 2007). Such that the retention and survival of individuals at release sites would indicate the suitability of reintroduction sites with regards to habitat and prey availability (Armstrong & Seddon 2008). Translocation may even provide better habitat and prey conditions than found in the species' source location. In **Chapter 2 and 3**, the translocation of martens from their core range in Scotland to an unoccupied part of their historic range in mid-Wales provided insight into the response of this species to translocation. These chapters revealed some of the factors influencing

movement, habitat and dietary selection of this recovering predator, as well as their potential impact on release site ecosystems.

#### *Reintroduction of the pine marten - Movement*

The 'Pine Marten Recovery Project' undertaken by the Vincent Wildlife Trust aimed to establish a population of martens in mid-Wales, which would facilitate the recolonization of Wales and western England by the species. The presence of conspecifics appeared to be an important aspect of translocation success and site residency, and is an important consideration for management and planning of future translocations. This translocation was undertaken in multiple phases (**Chapter 2**), allowing us to investigate the difference between individuals introduced into unoccupied regions (year one) and individuals introduced to areas where there were established populations (year two). Animals introduced in year two dispersed further from release sites but settled faster, suggesting that they used the social information provided by settled conspecifics in their settlement decisions. Therefore once a population becomes established in an area, further reintroductions to that area may become more straightforward and predictable, with the loss of individuals to long-distance dispersal events perhaps less likely (e.g. (Stamps 2001; Ward & Schlossberg 2004). This work demonstrates that phased introductions of wide-ranging, solitary mesocarnivores in large numbers is effective in reducing unnecessary loss of translocated individuals through dispersal and associated mortality. Post-release differences between cohorts is informative in not only how a species will behave when introduced into empty habitats (i.e. true reintroduction; IUCN/SSC 2013), but how individuals may respond to release into territories occupied by residual populations (i.e. reinforcement; IUCN/SSC 2013). When reintroducing solitary individuals, the species' social system and individuals' interactions with conspecifics are thus important to consider with regards to territoriality, competition and breeding.

#### *Reintroduction of the pine marten - Diet*

In **Chapter 3** I investigated the dietary response of these martens to translocation. Although martens are considered to be generalist predators, individuals did show a degree of specialisation, retaining their relative trophic position across the translocation. This dietary specialisation however, was not limiting and overall, the translocated population of martens showed a broader

dietary niche in Wales compared to Scotland. Source and release sites were broadly comparable with regards to habitat composition however the variation in diet would suggest a differing prey base. With regards to future marten reintroductions, these findings would suggest that perfect matching of prey bases and habitat types is not vital. At an individual level, the differing prey availability in the release area likely led to prey-switching by martens to readily abundant species to complement their dietary preferences, a characteristic of facultative specialists. The retention of such behavioural strategies after an environmental change such as translocation are important in buffering environmental variation, through flexibility, and also reducing competition between individuals, through specialisation. The degree of dietary specialisation demonstrated here, and its retention over a translocation event, also indicates the value of considering individual variation in reintroductions. The translocation of generalist species may focus on a group of animals and consider their overall responses (e.g. (Moehrensclager & Macdonald 2003; Woodford et al. 2013; Spinola et al. 2018), however this group is comprised of individuals whose behavioural strategies and personalities may differ. Therefore, considering the effect of individual variation, such as dietary specialisation and behavioural traits, for example boldness and aggressiveness, can contribute to our understanding of post-translocation outcomes (Clobert et al. 2009).

A further finding of this work was the prominence of grey squirrels in pine marten diet so soon after reintroduction to Wales (10% Frequency of occurrence). Confirmation of the lethal effect of marten re-introduction on grey squirrels provides support to previous suggestions that this recovering carnivore could play a role in pest management (Stockstad 2016; Hodgetts 2017). The role of native predator restoration in the reduction in invasive or abundant species has been documented in other systems such as recovery of otters and decline of invasive mink in England (McDonald et al. 2007), dingo suppression of invasive foxes and cats in Australia (Letnic et al. 2012) and wolf recovery leading to reduced distribution and density of elk in North America (Ripple et al. 2001).

#### *Reintroduction of other predators*

I focused on the pine marten, a recovering carnivore that is native to, and was resident in, the UK. However, the reintroduction of this species could be seen as

a gradual step towards quantifying the ecological and social feasibility of, and working out the most effective strategy for, apex predator reintroduction in the UK. The long-term success of conservation strategies require public support and acceptance. Without addressing the governance and social perception of conservation interventions, failure is likely, particularly with regard to controversial projects involving carnivores (Dickman 2010; Ritchie et al. 2012). Predator population restoration in the UK, and worldwide, is occurring at a greater frequency than ever before (Seddon 2010). This is partially driven by advances in captive breeding programmes, monitoring technology and better understanding of species requirements. The positive ramifications of predator reintroduction, such as pest control, can enhance public opinion and support for such projects, such that the proposed restoration of dingo populations in Australia for this purpose has been received with relative enthusiasm (van Eeden et al. 2019). In Scotland, the social feasibility of the restoration of predators such as lynx and wolves has also documented a lower level of resistance than anticipated, with a main motivation of support owed to deer control (Nilsen et al. 2007). However predator restoration does raise concerns regarding safety, economic loss and management (Kleiven et al. 2004). Nevertheless, attempts of predator restoration still continue and are partially driven by an increased drive to 'fix' or 'undo' human-driven declines of predator populations and degradation of entire ecosystems (Scherer 1994; Sandom et al. 2013). This self-imposed obligation to return landscapes to a pre-disturbance state can lead to poor conservation decisions being made with little consideration of how much environments have changed (Jackson & Hobbs 2009). In a human-dominated landscape, it is unrealistic to expect that all species present prior to disturbance will behave and thrive in an identical manner when reintroduced. The correct social and environmental conditions must be in place for such restoration projects to be successful. Reintroductions, whether for species recovery alone or with the intention of restoring particular ecosystem processes, should be based on a solid understanding of both species-specific, and broad ecological requirements and impacts. The knowledge generated in this thesis contributes to our understanding of ecological processes occurring in a small part of a larger trophic cascade. Thus, the time scales of restoration projects, especially when involving long-lived predators, must be incorporated into planning as the positive and negative impacts of predator restoration may take many years to become evident. Even in

systems where reintroduced predators have become established (Estes & Palmisano 1974; Ripple et al. 2001), the cascading effects are still emerging and ecosystem dynamics and food webs continue to change (Pace et al. 1999; Ripple & Beschta 2012).

## ***Predator-prey interactions***

### *Cascading effects*

Predator restoration can have far-reaching impacts on ecosystems, and this can be manifest through different trophic cascades, across multiple spatial and temporal scales. These can be positive and negative. The impact of predators can, through a series of processes, alter vegetation structure and soil nutrients (Kardol & Wardle 2010) as well as alter predator-prey dynamics at various trophic levels (Ritchie et al. 2012). More recently, the trophic cascade concept has incorporated the impact of non-lethal effects of predator presence; the idea of prey species existing in a 'landscape of fear'. The landscape of fear generated by predators can shape predator-prey dynamics as much as the lethal effects of predation (Laundré et al. 2010). Although the behaviour of sciurid species has been studied in a number of contexts relating to risk and fear (Lima et al. 1985; Partan et al. 2010; Jayne et al. 2015), the effect of pine martens has not yet been investigated. In **Chapter 4 and 5** I quantified these effects of fear through studies on space use and foraging of grey squirrels in the presence of pine martens.

In **Chapter 4** I demonstrated that variation in levels of exposure to translocated pine martens did not affect apparent survival and home range location of grey squirrels, but was related to differences in ranging behaviour. With increasing exposure to martens, squirrel range size and daily distance travelled increased significantly, suggesting a reduced density and a change in ranging patterns by squirrels. I hypothesised that this may be driven by either predator avoidance (non-lethal effects) and/or competitive release as result of marten predation (lethal effects). Then, in **Chapter 5**, I showed that grey squirrels gave up foraging sooner in sites containing pine martens. This is likely a result of a trade-off between safety and resource acquisition, which is more prominent in marten-occupied woodland. As a result, squirrels have a reduced energy intake, which

may be detrimental to fitness and survival at a population level. The conditions experienced by squirrels in this study are comparable to those at the front edge of natural pine marten recovery, where pine martens are occupying new habitats in low numbers and grey squirrel populations are well-established. In combination, **Chapter 4 and 5** reveal the existence of a 'landscape of fear', where the presence of a predator alters the behaviour of its prey (Laundré et al. 2010). This landscape is manifest very shortly after marten introduction, even when these predators remain at low densities relative to established populations in Ireland and Scotland. Fear forms an important aspect of predator-prey dynamics and can drive substantial declines in prey populations, beyond those caused by lethal effects alone (Boonstra et al. 1998). Fear, and the stress hormones it produces, can have detrimental effects on reproduction and immune responses of species, potentially leading to reduced reproductive output (Sheriff et al. 2009) and increased disease susceptibility (Clinchy et al. 2013). The long-term ramifications of fear and reduced foraging displayed by grey squirrels in the presence of martens have yet to be investigated and studies into such physiological impacts, life-history consequences and the population-level implications may enable further predictions to be made about long-term grey squirrel dynamics in the presence of a recovering predator.

### ***Implications & future directions***

In this thesis I investigated the relationship between pine martens and grey squirrels to understand the processes driving landscape-scale spatial patterns (Sheehy & Lawton 2014; Sheehy et al. 2018). Although I did not find any immediate effects of martens on apparent grey squirrel survival, the presence of grey squirrels in marten diet (**Chapter 3**), changes in space use by grey squirrels indicative of reduced conspecific density and potential avoidance behaviour (**Chapter 4**) as well as reduced foraging behaviour in marten-occupied woodland (**Chapter 5**) would suggest that the influence of pine martens is multifaceted. There are a limited number of opportunities to study both the movement of reintroduced martens as well as the interactions between martens and grey squirrels together. It is therefore likely that modelling the behaviour, survival and movement of these species will be key to enhancing our understanding of grey



squirrel and pine marten interactions, as well as predicting pine marten movement following translocation. Using the data presented in this thesis to populate landscape-scale models of movement could be integrated into feasibility studies for future marten reintroductions. To further elucidate the relationship between the two species in question, I suggest a number of avenues of additional investigation which should be addressed: 1) better understanding of variation in grey squirrel survival, followed by 2) the use of marten presence as a tool in grey squirrel management, and, over longer time scales, 3) how any change in grey squirrel populations affects red squirrels and bark stripping.

#### *Grey squirrel survival*

The most pertinent question remaining to be answered surrounds the effect of marten predation, documented in **Chapter 3**, and reduced squirrel foraging, documented in **Chapter 5**, on grey squirrel survival. Although I used trapping data in a capture-mark-recapture (CMR) structure to quantify squirrel survival (**Chapter 4**), it is likely that the time period employed was too short to reveal any true effect sizes. A longer-term capture-mark-recapture (CMR) study would be an effective approach to reveal changes in survival in squirrel populations recently exposed to a known density of pine martens. While this may still be possible in Wales, it would be more insightful if undertaken prior to, and immediately following marten releases. Such a study may be more revealing if carried out during the upcoming marten reintroduction in the Forest of Dean (Gloucestershire Wildlife Trust in 2019). A study which incorporates squirrel survival as well as assessing physiological impacts of martens on squirrels could contribute to our understanding of the impact of both predation (**Chapter 3**) and fear (**Chapter 5**). A CMR study would reveal any changes in population composition with regards to sex and age, as well as reproductive output by individuals. Trapping of squirrels could also be used as an opportunity to assess grey squirrel physiology through body condition assessment and stress level measurement. These studies would reveal short and long term patterns which may be tied in to predation, movement, resource acquisition or a reduction in foraging demonstrated by squirrels in **Chapter 3, 4 and 5**.

### *Integrated pest management*

While it is perhaps unlikely that marten recovery could cause the eradication of grey squirrels, my results, combined with those of previous studies suggest that martens could play a role in an integrated approach to grey squirrel management. If combined with trapping and killing, reintroduction of martens may contribute to a sustainable and widespread effort to control grey squirrel numbers. Grey squirrel culling is, in general, socially undesirable (Morgia et al. 2016; Hodgetts 2017, Dunn et al. 2018). The 'control' or killing of grey squirrels by humans is seen as intentional and 'un-natural', and killing for no purpose (e.g. not for consumption) is especially problematic (Crowley et al. 2018). Predation by the pine marten, conversely, is seen as a 'natural' process. By pairing the killing or reduction of grey squirrels with the recovery of a charismatic, native carnivore, the consequential eradication of grey squirrels is viewed in a more positive light (Hodgetts 2017; Crowley et al. 2018). Once the population-level impacts of pine marten lethal and non-lethal effects on grey squirrel populations can be quantified through survival studies, then trials of integrated management, which combine intensive trapping with low level marten predation, could be undertaken in experimental woodlands. This may facilitate greater social acceptability of grey squirrel eradication, allowing for more widespread management strategies and countrywide reduction in this invasive species.

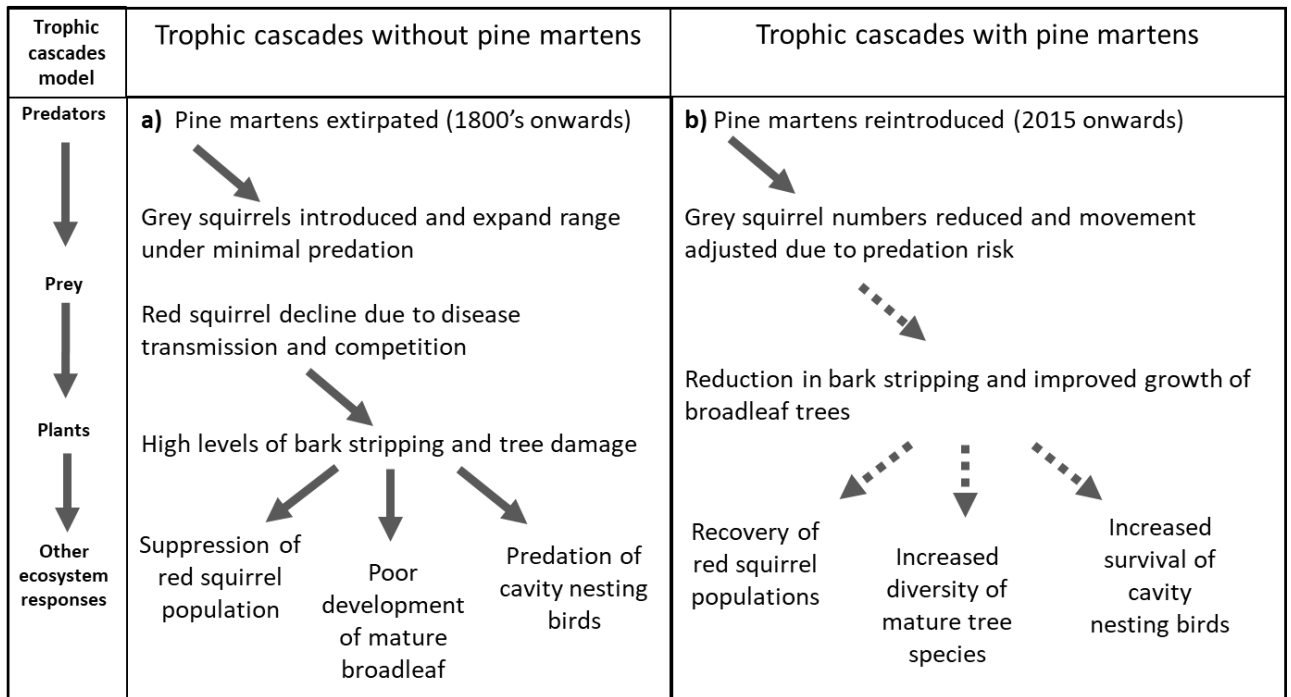
### *Long-term aims*

A second avenue of future investigation is driven by the over-arching aim of marten recovery in relation to grey squirrels. This is to i) facilitate red squirrel population recovery and ii) reduce tree damage. While the findings of this thesis do not directly address either of these aims, this work does represent the first step towards understanding the cascading effects of pine martens (Fig. 6.1).

#### *i) Red squirrel recovery*

Grey squirrel eradication is often discussed in the light of the conservation of the native red squirrel. With regards to the recovery of red squirrel populations, previous studies have suggested that reducing grey squirrels below a critical level may reduce disease transmission and competitive exclusion (Rushton et al. 2006), enabling the red squirrel to recover in the absence, or intense suppression, of this invasive species (Wauters et al. 2002; Gurnell et al. 2004).

Where grey squirrel populations have been much reduced or eradicated, such as on the island of Anglesey, red squirrel populations experienced reduced competition and disease exposure (Schuchert et al. 2014).



**Figure 6.1. Potential trophic interactions with and without pine martens in the UK** where a) shows the system when pine martens had been extirpated (1800's onwards) and b) shows the potential system after pine marten recovery (1995 onwards). Solid arrows indicate documented responses, dashed arrows indicate predicted or inferred responses. Based on figure from Ripple & Beschta (2004).

## ii) Bark-stripping reduction

Grey squirrels are also an important pest species for commercial forestry operations. The economic interest in grey squirrel eradication is therefore centred around a reduction in bark stripping and improvement of UK timber quality and production for commercial purposes (Kenward & Parish 1986; Crowley et al. 2018). As yet, there lacks a clear driving force behind bark stripping behaviour (Kenward & Parish 1986), however when populations are above a certain density, bark stripping behaviour is thought to be initiated (Mayle et al. 2007). If bark stripping is driven by a nutrient deficiency (Moller 1983; Nichols et al. 2016), aggression (Mayle et al. 2007) and/or juvenile dispersal (Kenward & Parish 1986), it is not clear how marten presence will affect this. If predation can reduce grey squirrel density but this in turn increases squirrel movement, reproduction in

the absence of competition, and/or dispersal into new territories (as suggested in **Chapter 4**), it is possible that conspecific aggression, a potential driver of bark-stripping, may in fact increase (Kenward & Parish 1986). Alternatively, if bark-stripping is driven by a lack of food, then the reduction in foraging demonstrated in **Chapter 5**, and potentially the resulting lack of cached nuts, may drive squirrels to increase bark stripping to access nutrient-rich tissues under tree bark in a time of food shortage (Gurnell 1996). There is great appeal in the potential role of pine martens in the reduction of tree damage via grey squirrel control (Crowley et al. 2018), with various organisations now funding projects to support the reintroduction of this species. There are however, many steps between pine marten recovery and reduction in tree damage (Fig. 6.1). Each of these steps occurs over very different spatial and temporal scales (Fig. 6.1). If the anticipated cascading effects do arise, a tangible difference in timber quality may not be manifest for a number of decades. Therefore, if the recovery of martens is to be utilised as a tool in grey squirrel control, marten populations must remain self-sustaining in the long-term.

### ***Concluding remarks***

The restoration of wolves to Yellowstone National Park is often referred to in studies investigating cascading effects and the landscape of fear. This is unsurprising given its encapsulation of the fundamental processes involved in ecosystem restoration. The Yellowstone study system demonstrates the progressive understanding of trophic cascades, from landscape scale patterns (Ripple et al. 2001), to predator-prey interactions (Ripple & Beschta 2003, 2004), to the consequences of such dynamics across entire food webs (Ripple & Beschta 2003, 2004, 2012; Halofsky & Ripple 2008; Ripple et al. 2014; Newsome & Ripple 2015). Cascading effects of predators are complex and can be expressed differently across ecosystems. The time scales required for the manifestation of predator impacts can vary substantially and, if the Yellowstone system represents a framework of investigation into trophic cascades, the exploration of the pine marten – grey squirrel dynamic is still in its early phases. Downstream consequences of predator restoration can only be predicted to a certain extent, but studies such as in this thesis can improve our knowledge of the ecological processes occurring at each step. My findings form a foundation

from which to advance our understanding of the cascading effects of pine marten recovery on grey squirrel population dynamics and consequently, red squirrel recovery and tree damage via interactions with grey squirrels. Without the knowledge of marten responses to translocation and reintroduction, and the resulting impacts they have on grey squirrels, it would not be possible to move forward in our investigation and understanding of this complex system. As plans for pine marten restoration across other parts of the UK continue, building on the information and interactions revealed in this work will help to construct a true understanding of the cascading effects instigated by the recovery of this charismatic small predator.

Restoration of ecosystem processes through predator reintroduction is an exciting field of research. The return of species such as the grey wolf and sea otter to North America stand as testimony to the success and wide-reaching positive impacts of such restoration attempts. We should therefore be encouraged and motivated that restoration of elements of ecosystems through predator reintroduction might be possible in the UK, but such projects should continue to be undertaken with caution, patience and most importantly, robust scientific evidence.



## Appendices

### ***Appendix 1: Methodological details of pine marten exposure calculation (Chapter 4)***

#### **Methods**

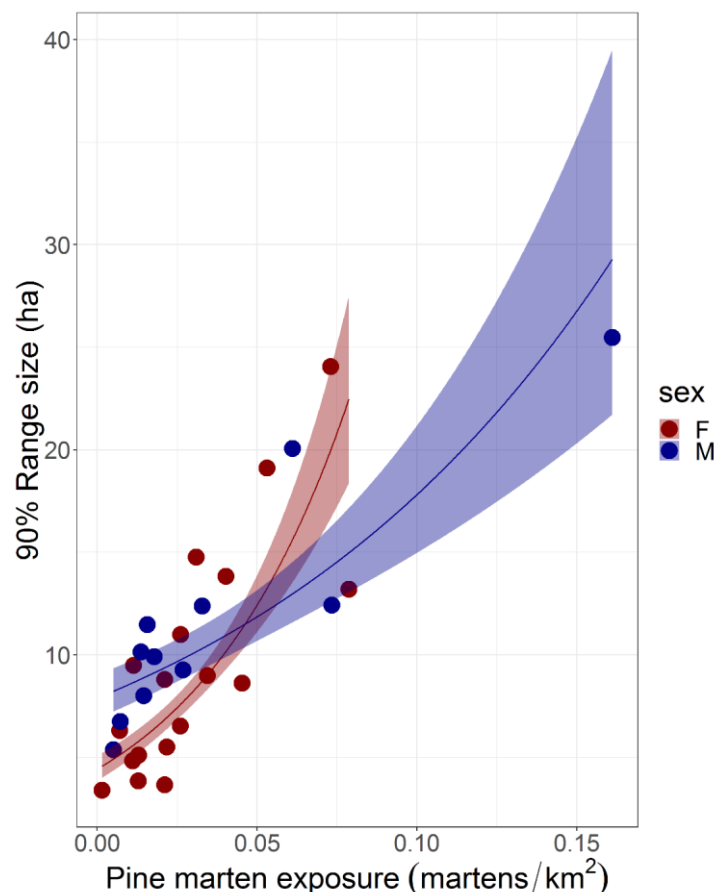
##### *Marten exposure calculation*

The influence of martens and their potential ranging extent was investigated over a range of spatial scales to understand how far-reaching their effects may be on prey (Levin 1992; Borger et al. 2006). Multiple smoothing parameters (500m, 1000m, 2000m & 3000m) were used to represent an increasing spatially-diffuse effect of martens. As the smoothing bandwidth (h) increases, we were 'allowing' the effect of the martens to extend further beyond the point at which they were located. By rasterising pine marten data across different spatial scales we were able to provide a range of estimates of pine marten exposure (density and distribution) when their precise locations generally remained unknown. Pine marten home ranges vary dramatically in size and have been shown to range from <1-8km<sup>2</sup> (Balharry 1993; Caryl 2008) subject to habitat quality and conspecific density, therefore these smoothing parameters represent a conservative estimate of ranging extent. The lowest parameter (500m) is thus close to the range extent of a grey squirrel and the upper parameter (3000m) is similar to that of many female martens. Absolute marten and squirrel locations could not be matched on a daily basis due to mismatch in the temporal and spatial resolution of location information from tracking each species (i.e. hourly locations from squirrels versus daily or weekly locations of martens). 'Marten exposure' therefore represents the potential marten density to which individual squirrels would be exposed over a period of approximately three weeks, the approximate duration of their tracking period

## Results

### *Analyses including outlier*

One individual had exceptionally high levels of marten exposure due to its residency adjacent to marten release pens, and was excluded from main text analyses due to its high leverage. Models were re-run including this individual (n=29). Results of analyses can be found in Table S1.1 & 1.2 and Fig. S1.1. The inclusion of this male squirrel did not change the overall significance of marten exposure on squirrel movement metrics at large spatial scales of marten extent (2000 and 3000m). However, an interaction between sex and marten exposure was found at 3000m, with male squirrels range sizes being larger than females at high levels of exposure (Table S1.1 & S1.2; Fig. S1.1).



**Figure S1.1. Effect of variation in exposure to translocated pine martens on home range size of grey squirrels.** Sexes respond differently to pine marten exposure, male squirrels are shown in blue and females in red. Pine marten exposure (martens per km<sup>2</sup>) is calculated using a bandwidth of 3000m. One male had exceptionally high levels of exposure and was not included in analyses in the main text.



**Table S1.1. Effects of variation in exposure of grey squirrels to translocated pine martens on grey squirrel ranging behaviours.** Calculated used the full dataset ( $n=29$ ), one male had exceptionally high levels of exposure and was not included in analyses in the main text. For each behavioural variable, four models were run; one for marten exposure (martens/km<sup>2</sup>) calculated at each pine marten kernel bandwidth (500, 1000, 2000 and 3000m). Effect sizes are from Generalised Linear Models. For each squirrel space use metric the averaged standardised effect size and relative importance (RI) of marten exposure in top models (lower and upper 95% confidence limits) is shown at each kernel bandwidth size. Light shading indicates a significant relationship between squirrel behaviour and marten exposure as the 95% confidence interval did not cross zero. NR indicates pine marten exposure was not retained in the top model set. Dark shading indicates marten exposure also had a significant interaction with sex. In this instance, the main effect of marten exposure is given first, followed by that of the interaction.

Kernel bandwidth	500m	1000m	2000m	3000m
Mean marten exposure (martens /km <sup>2</sup> )	0.009 ± 0.003	0.019 ± 0.006	0.031 ± 0.007	0.033 ± 0.006
Core (50%) range	0.08 (-0.29, 0.45) RI=0.27	0.50 (0.05, 0.95) RI=1	0.74 (0.17, 1.30) RI=1	1.06 (0.66, 1.47) RI=1 -0.94 (-1.64, -0.24) RI=1
Home (90%) range	0.122 (-0.28, 0.52) RI=0.4	0.50 (0.12, 0.88) RI=1	0.63 (0.28, 0.98) RI=1	1.03(0.69, 1.37) RI=1 -0.82 (-1.41, -0.23) RI=1
Daily distance travelled (km)	0.22 (-0.01, 0.44) RI=1	0.28 (0.08, 0.48) RI=1	00.31 (0.12, 0.50) RI=1	0.33 (0.15, 0.52) RI=1
Centroid shift (m)	-0.04 (-0.31, 0.40) RI=0.17	0.15 (-0.43, 0.73) RI=0.36	0.30 (-0.46, 1.05) RI=0.53	0.36 (-0.43, 1.15) RI=0.59

**Table S1.2. Summary of models of variation in grey squirrel ranging behaviours.** Results are from models including all individuals (n=29), one male had exceptionally high levels of exposure and was not included in analyses in the main text. Full averaged models included the effect of variation in local density of translocated pine martens within the squirrel home range (exposure), the number of martens that had been released into the landscape (martens), squirrel sex and an interaction exposure\*sex. For each squirrel behaviour variable, four models were run; one for each pine marten kernel bandwidth used to estimate marten density (500, 1000, 2000 and 3000m). Significant effects are where 95% confidence intervals do not cross zero and are shown in bold.  $R^2$  represents the likelihood-ratio based pseudo-R-squared value for the model.

Response Variable	Marten Bandwidth (m)	Full averaged model	$R^2$
50% Core range	500	sex + exposure + martens	0.210
	1000	sex + <b>exposure</b> + martens	0.262
	2000	Sex + <b>exposure</b> + martens + sex*exposure	0.440
	3000	sex + <b>exposure</b> + martens + <b>sex*exposure</b>	0.630
90% home range	500	sex + exposure + martens	0.185
	1000	sex + <b>exposure</b>	0.253
	2000	sex + <b>exposure</b>	0.368
	3000	sex + <b>exposure</b> + martens + <b>sex*exposure</b>	0.671
Daily Distance	500	sex* exposure	0.329
	1000	<b>exposure</b>	0.223
	2000	<b>exposure</b>	0.278
	3000	<b>exposure</b>	0.318
Centroid Shift	500	sex + exposure	0.084
	1000	sex + exposure	0.110
	2000	sex + exposure	0.147
	3000	sex + exposure	0.168

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