

Hazel dormouse ecology and conservation in woodlands

Submitted by Cecily E D Goodwin to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, Jan 2018.



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Abstract

The extent and quality of forested habitats have changed across Europe and as a result many forest species have suffered declines and range contractions. European legislation has been introduced to conserve those species that have been negatively impacted by widespread land-use changes. In order to assess the needs of declining species and the efficacy of these protective measures, the effects of habitat type, configuration and management on individuals and populations needs to be understood.

In this thesis, I have investigated patterns and drivers of variation in the status of populations of hazel dormouse *Muscardinus avellanarius* in the United Kingdom. I have assessed the effects of variation in habitat on hazel dormice at multiple spatial scales, and relate this to woodland management.

I first introduce the status of and threats to wooded ecosystems, globally, across Europe and the UK. I look at how conservation approaches have evolved to address the negative effects on woodland biodiversity from changes in landscape and habitat configuration. I discuss the existing evidence for evaluation of hazel dormouse habitat quality and preferences and current efforts to conserve the species.

I then assess the change in the UK hazel dormouse population between 1993 and 2014 using data from a citizen science scheme, the National Dormouse Monitoring Programme. I identify a decline in the national population of 72% (62 – 79% 95% Confidence Intervals) over this period. I also find no evidence for any biases arising from changes in surveying practices over the lifetime of the scheme, and conclude that this volunteer-based method is a robust way of monitoring the national dormouse population.

Next, I assess the environmental influences on variation in hazel dormouse population status and change. I demonstrate that dormouse abundances and breeding rates are positively affected by the extent of wooded habitat in the surroundings, favourable woodland species composition and active woodland management. Abundance and breeding are also higher on sites with warmer, sunnier climates though dormice are more abundant on sites with consistently

cold winters. Dormouse numbers are higher on sites with successional habitats while population trends are higher on larger woodland sites, those with more woodland in the surrounding landscape and with early successional habitat. Many changes in woodland habitats in the UK over the last century have reduced habitat features associated with high dormouse abundances, breeding rates or population trends, and are likely to have contributed to national population declines. Conservation of dormice would benefit from increasing the prevalence of particular woodland species, and active woodland management and the resultant structural and age diversity.

I then look at the effect of woodland habitat composition on the trophic ecology of dormouse individuals and populations. In one coppice-with-standards woodland, dormice were found to consume a high proportion of tree-derived foods in spring and autumn, and honeysuckle berries in autumn. Across woodland, dormice feed opportunistically on foods that are abundant in the habitat surrounding their resting site. Dormouse populations also display a larger niche breadth in summer than in spring, due to their consumption of a range of plant sources. Conservation of dormice in woodlands could be improved through evenly distributing food plants, and encouraging high invertebrate numbers.

At a finer scale, I use radio-tracking to examine the woodland vegetation species and structure preferences of dormice, and the effects of small-scale tree felling on their ranging and habitat use. I find that, for resting, dormice select areas with more vegetation of 5-10m and less high forest. While ranging, dormice use areas with higher proportions of edge habitat, vegetation of 5-10m, less high forest and denser canopies. I found that while tree removal prevents dormice from shifting their ranging area, such management activities are needed in the long-term to maintain the habitats dormice require.

Finally, I collate the findings of this thesis and discuss them within the context of wider woodland conservation and management. My work examines the habitat requirements of hazel dormice over multiple spatial scales and thus provides a range of conservation recommendations, from within individual woodland stands to landscapes. The results of this thesis have implications for the conservation of dormice and woodlands, and emphasise the importance of the appraisal of measures to protect threatened species.

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Author's declaration for co-authored manuscripts

Chapters 2,3,4 and 5 have been published or written for publication as co-authored academic papers. I developed the direction and research design for chapters 2,3,4 and 5 in conjunction with Robbie McDonald (RM) and Dave Hodgson (DH).

For chapters 2 and 3, all dormouse survey data was collected by licensed volunteers and collated by People's Trust for Endangered Species (PTES). I then organised and processed and analysed these data with advice from DH.

For chapter 3, climate data was gathered and processed by Andy Suggitt (AS). I designed the questionnaires in chapter 3 in conjunction with RM and PTES; PTES sent them out to volunteers and collected and collated the results. I then processed these data. I gathered and processed remote-sensing datasets with advice from James Duffy (JD) and Jon Bennie (JB). I analysed the data for chapter 3 with advice from Matthew Silk (MS) and DH.

I designed all the fieldwork for chapter 4 and conducted it with assistance from Matthew Rogers, Amy Campbell and Kelly Astley (KA). Stable isotope sample processing was done by myself and KA. I analysed the data.

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I wrote all 4 manuscripts, then amended and revised them in response to comments, suggestions and advice from RM and DH and other co-authors (JB, AS, JD, MS, Nida Al-Fulaij, George Swan, Steve Langton and Sallie Bailey).

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Chapter 1

Introduction

Chapter 1: Introduction

Forest and woodland ecosystems and their conservation

Forest and woodland ecosystems cover around 30% of the world's surface (FAO 2016) and provide many of the key regulating and supporting ecosystem services upon which humans depend. These include carbon storage, weather regulation, soil stability, erosion prevention and biodiversity (Rose & Chapman 2003, Brauman et al. 2007, Bonan 2008, Maes et al. 2012, Brockerhoff et al. 2017). They also deliver a wide range of cultural services and are highly valued by people (Brown & Reed 2000, Brockerhoff et al. 2017).

Globally, forests and woodlands are facing multiple, pressing threats including destruction, fragmentation, overexploitation of timber, climate change, tree diseases, change in community composition and inappropriate management (Wade et al. 2003, Bonan 2008, Meyfroidt & Lambin 2011). Forests are slow-growing ecosystems that can take hundreds of years to develop fully, and are often greatly altered by threats such as increasing frequency of fire, changing climatic conditions and increased herbivory (Bradshaw et al. 2009). The resulting loss of ecosystem function and habitat features is often irrevocable and can have devastating consequences for wildlife (Laurance 1997, Lindenmayer et al. 2014, Nordén et al. 2014).

Threats to forests often arise from conflicts between the conservation of these habitats and anthropogenic market, livelihood and consumption pressures (Brauman et al. 2007, Hauer et al. 2010, Phalan et al. 2011, Maes et al. 2012). Within the last century, rapid land use change and increasing intensification of agriculture and forestry have led to the loss of important wooded habitats, reductions in biodiversity and ecological community change (Wade et al. 2003, Young et al. 2005, Ferraz et al. 2009, Phalan et al. 2011).

These pressures have led to global changes in the pattern, habitat types and structure of woodland (Chazdon 2008, FAO 2016). Human activity affects forest ecosystems at a multitude of scales: from activities in single stands with impacts on structure and species composition (Paillet et al. 2010, Calladine et al. 2017, Kirby et al. 2017); to landscape-scale effects on the cover, configuration and type

of forest (Vellend et al. 2006, Chazdon 2008); to the global changes to nitrogen and carbon cycling with implications for climate and nutrient distribution (Waring & Running 2007).

In most regions of the world, forest loss and fragmentation is a concern, albeit one that plays out at different rates and at different scales. Currently, very high rates of primary forest loss are experienced in tropical and boreal regions, whereas in temperate regions much forest area has already been lost, with remaining piecemeal loss of forest patches to development and agricultural intensification in some places, while tree-planting, often of commercial tree species, is promoted in other areas (Hansen et al. 2013). Tropical forest area declined at a rate of 5.5 million hectares a year between 2010 to 2015, while temperate forest area expanded by 2.2 million hectares a year over the same timeframe due to afforestation (Keenan et al. 2015).

Widespread changes have also occurred in the composition of woodlands through the intensification of forestry, changes in management regimes and through exploitation of specific plants and animal species (Wulf 2003, Paillet et al. 2010, Miklín & Čížek 2014). The removal of many carnivore species for example has increased grazing pressure on forests through ecological release of herbivorous species (Fuller & Gill 2001). Climatic changes also affect forests globally, but do the most damage at greater latitudes, making conditions less suitable for certain tree species and increasing the frequency of disturbances such as storms and fire (Dong et al. 2003, Bradshaw et al. 2009).

Forest change and management in Europe and the UK

European ecosystems and landscapes were for the most part heavily modified during the early development of agriculture and settlement (Farrell et al. 2000, Rudel et al. 2005).

There have been significant shifts, however, in the habitat characteristics of European temperate forests over the last two centuries, with both intensification of timber production and abandonment of traditional broadleaf woodland management practices (Farrell et al. 2000, Young et al. 2005, Paillet et al. 2010). Historically, stages of 'forest transition' have involved the removal of older forests

followed by periods of replanting in response to inadequate supplies of forest products (Rudel et al. 2005). This has resulted in a large proportion of high, even-aged forest in Europe (Wulf 2003).

This trend is particularly apparent in the UK, where the simultaneous intensification of forestry and abandonment of traditional woodland management has led to a reduction in the abundance and distribution of structurally complex and spatially heterogeneous woodland (Hopkins & Kirby 2007, Quine et al. 2011). These processes have resulted in a predominance of two broad forest types, either intensively-managed commercial conifer plantations or mature, broadleaf high-forest (Hopkins & Kirby 2007, Kirby et al. 2017). Changes in agricultural and forestry practice and continuing urban development have also led to increased fragmentation of woodland habitats (Peterken 2002).

Forests cover 13% of the UK's land area, one of the lowest percentages in Europe (Forestry Commission 2011, Woodland Trust 2011). Even so, this has increased from a low of 4.7% following large-scale tree clearance in the industrial revolution (Woodland Trust 2011). In England and Wales, woodland area consists of 21% conifer and 56% broadleaf forest, with 33% consisting of other wooded habitats such as mixed forest, coppice, shrub and felled areas (Forestry Commission 2011). Individual areas of woodland in the UK are generally small. Woodland parcels in England have a mean area of 6ha, and in Wales, 9ha. A large number (around 200,000) of small woodlands of less than 2ha make up 11% of woodland cover in England and Wales. A smaller number (around 11,900) of larger woods of over 20ha make up 58% of woodland cover in England and 74% of woodland in Wales (Forestry Commission 2011). The area of coppice (including coppice with standards) in the UK has declined by 90% from 230,000ha to 23,000ha in the last 100 years (Harmer & Howe 2003). Shifts in the ecological communities of woodlands, notably increasing deer population densities, have further reduced structural complexity (Fuller & Gill 2001, Eichhorn et al. 2017).

Structural complexity and habitat heterogeneity within UK woodland has been shown to benefit biodiversity and provide important habitats for a range of key taxa (Wulf 2003, Paillet et al. 2010). Much of the research in the UK on the biodiversity consequences of forest habitat and management change has

focused on impacts on woodland birds (Fuller et al. 2007b, Quine et al. 2007), and butterflies and moths (Broome et al. 2011, Fartmann et al. 2013, Fox 2013). Many species of these groups, especially declining and threatened species, respond positively to increased structural complexity, the presence of an understorey and increased prevalence of glades, edges and open canopy (Fuller et al. 2007b, Quine et al. 2007, Broome et al. 2011, Calladine et al. 2017). Direct positive associations of these species have also been found with management practices which create these habitat conditions, such as rotation coppice and continuous cover forestry (Quine et al. 2007, Fartmann et al. 2013, Calladine et al. 2015). The decline in these habitats and management practices have been linked to declines in these species groups (Warren et al. 2001, Amar et al. 2006, Fuller et al. 2007b, Fox 2013).

While dramatic processes of change and transition in forest environments have occurred over the last 200 years, attitudes towards forest management and conservation have also changed over the last few decades (Farrell et al. 2000, Rudel et al. 2005, Schulz et al. 2014). The objectives of forest management have expanded beyond the delivery of timber products to consider wider recreational, cultural and biodiversity value and the provision of non-market ecosystem services (Lindenmayer 1999, Farrell et al. 2000). European-level policy has also influenced this transition to a wider definition of 'sustainable forest management', for example by introducing a variety of qualitative and quantitative measures for the pan-European assessment of sustainable management of forests (Wulf 2003).

There are many further considerations beyond legislative principles in the coordinated management of forests for both production and conservation, including corporate governance and social norms within the forest management community (Primmer & Karppinen 2010). This balance can be challenging, as many of the market forces exerting pressure on forest systems fluctuate over much shorter timeframes than forest ecological processes (Rudel et al. 2005). For instance, countries with a larger timber industry tend to have more centralised systems of forest governance, with more focus given to economic considerations and less emphasis placed on nature conservation (Schulz et al. 2014).

There has been a corresponding swell of research to guide the delivery of these new forest management objectives, including nature conservation (Spence 2001, Nalle et al. 2004, Hauer et al. 2010, Götmark 2013, Coll et al. 2018). While there are general conservation principles that can be applied, the conservation requirements of woodlands are variable and highly dependent on the landscape, climate and usage context (Lindenmayer 1999, Paillet et al. 2010, Götmark 2013). Forest conservation must also be implemented at different spatial scales, from the stand to the landscape (Lindenmayer et al. 2006). Landscapes that have been managed for hundreds of years in particular ways, for instance, will have particular suites of species that rely on these processes (Rudel et al. 2005, Grant & Edwards 2008). Rates of global environmental change present further challenges: climate change and the increasing spread of invasive species and of tree diseases means forest management must become more adaptable and responsive as ecosystems display less flexibility and greater instability (Lawrence 2017).

Conservation in UK forests

In the highly used and managed landscapes of the UK, there is inevitably a need for a certain level of intervention to mediate between different land-use pressures and nature conservation (Moilanen et al. 2005). This idea of regulated 'balance' through intervention has provided the framework within which nature conservation has developed in the UK (Adams 1997). The nature conservation movement originated in the industrial era, arising from fears surrounding the loss of species and the destruction of the beauty of the 'English Countryside'. With the onset of agricultural and forestry intensification in the 1950s, many ruderal and semi-natural habitats were lost, landscape character eroded and species began to decline (Benton et al. 2002). These threats led to the designation of national parks, where the vision of the countryside could be preserved, and the conservation of historical landscapes more easily regulated (Adams 1997). Outside these areas, however, conservation of wildlife and habitats became more challenging as farming and forestry practices in the wider countryside continued to intensify, habitats were lost and many species declined as a result (Benton et al. 2002, Gregory et al. 2005, Staley et al. 2012, Oliver et al. 2017).

Ever since the foundation of the Royal Society for the Protection of Birds (RSPB) and The National Trust in the Nineteenth Century, there has been a groundswell in conservation organisations and volunteer groups (Lorimer 2015, Kobori et al. 2016). These groups not only generate interest in conservation and wider environmental concerns and represent a strong conservation lobby, but also in some cases collect data for the monitoring of species and biodiversity (Lawrence & Turnhout 2010, Sutherland et al. 2010, Kobori et al. 2016). Today, there is a myriad of nature conservation organisations from habitat and land management based organisations such as The Woodland Trust and National Trust, to groups targeting wider habitat and species issues, such as the RSPB and Plantlife, to more species-specific groups, such as The People's Trust for Endangered Species and The Vincent Wildlife Trust.

In addition to the rising involvement of the third sector, species and habitat conservation approaches have, since the 1950s, become increasingly grounded in legislative measures. The Countryside Act (1968) introduced conservation measures for habitats and species, mainly focused on the creation of specific places for nature (Adams 1997). European Union institutions introduced further elements of species and habitat conservation legislation (Birds Directive 1979; Habitats Directive 1992) which were passed into UK law as part of The Wildlife and Countryside Act (1981) and the Conservation (Natural Habitats, &c.) Regulations (1994; consolidated in the Conservation of Habitats and Species Regulations 2010). European legislation also incorporated more environmental protections within agricultural policy (Common Agricultural Policy, 1962), in order to address the detrimental impacts of land management change on farmland wildlife. These measures include protections and provisions for wildlife habitats and species in farmed landscapes, termed Agri-Environment Schemes (AES). Species and species groups have also been used as indicators to monitor the progress of these conservation measures (Gregory et al. 2005, Sanderson et al. 2016).

Approaches to legislating for wildlife or habitat protection in forestry and woodland systems are not as integrated as in agriculture. Woodlands with specific species or habitat features of conservation value can be afforded protection through designation on the European level as Special Protection Areas for the Birds

Directive, or Special Areas of Conservation for the Habitats Directive. Sites of Special Scientific Interest or National Nature Reserves are also protected under national law (Wildlife and Countryside Act, 1981). Forestry systems are influenced by EU legislation on watercourse protection (Water Framework Directive, 2000), and there have been initiatives to increase the soil, air quality and fire-risk monitoring of forests (Young et al. 2005). While there are measures to protect small amounts of wooded habitat within farms and encourage tree planting within AES, there are no equivalent Environmental Stewardship programmes for forests to manage the environmental and biodiversity impacts of forestry practices, no 'Common Forestry Policy'. Conservation in forests and woodlands, that are not designated under other legislation, has therefore relied more on species-level protections, the self-regulation of industry and consumer pressure (Young et al. 2005, Schulz et al. 2014).

The Habitats Directive, and its transpositions into national law, also provides for the conservation of species under various Annexes, affording different levels of protection. Species are protected under EU law because they are threatened, supposedly rare or are of social or economic importance to the European Community. Under the Habitats Directive, habitat of around 900 Annex II species and the trade of about 90 Annex V species is strictly regulated and protected. Over 400 Annex IV species are given protection under the Directive at both the individual level, where it is an offence to kill or disturb individuals and destroy or disturb the resting and breeding places, and at the population level, as populations must be maintained in a 'Favourable Conservation Status'. Such a combination of individual- and population-level legislation assumes that the protection of individuals and individuals' habitats will multiply up to population-level benefits, increasing numbers and protecting threatened species (Ward et al. 2015). Research into the efficacy of this approach and the validity of this assumption has had mixed results (Schmeller et al. 2008, Santangeli et al. 2013, Koleček et al. 2014, Reid et al. 2014, Rossi et al. 2015, Sanderson et al. 2016). Furthermore, there has been additional ambiguity around the key concept of 'Favourable Conservation Status', leading to misinterpretation by EU member states in the past (Fenu et al. 2017).

The interaction between species and habitat legislative protections is not straightforward. Some research has found that habitat protections are harder to implement and enforce, in comparison to more defined species protections (Ostermann 1998, Wätzold & Schwerdtner 2005, Cantarello & Newton 2008). There is also dispute over the extent to which species protection has been able to provide for the conservation of habitats and wider biodiversity (Prendergast et al. 1993, Williams et al. 2017), and conversely whether habitat protections can provide sufficient safeguarding for threatened species (Davies et al. 2007).

Species conservation

Many nature conservation approaches focus on species-level protection, in order to target limited resources to species that are particularly at threat, are of evolutionary or ecological importance or particularly publicly appealing (Ando et al. 1998, Joseph et al. 2008, Drummond et al. 2010). This approach has received some criticism in favour of a more holistic approach to the conservation of biodiversity, habitats and ecosystems (Simberloff 1998, Wilson et al. 2006). In a real-world setting, however, a pragmatic approach often calls for the ease of assessment, application and auditing offered by a species focus in conservation (Mace et al. 2008, 2009, Lorimer 2015). Often, there is no choice but to rely on particular taxa for which data are available, to monitor biodiversity and to serve as surrogates for wider communities (Noss 1999, Rodrigues & Brooks 2007). Indeed, it has been argued that more diffuse ecosystem approaches are ill-defined and unappealing and will only dilute the conservation message, allowing further environmental destruction (Simberloff 1998). Well-chosen species conservation programmes can therefore be part of a range of approaches that form an effective conservation strategy (Mace et al. 2009).

Much debate has centred around the value of 'keystone', 'indicator', 'umbrella' and 'flagship' species approaches. (Caro & O'Doherty 1999, Andelman & Fagan 2000, Roberge & Angelstam 2004). All these concepts promote the idea that the conservation of a single species can also benefit other species, wider habitats and ecosystems, either through garnering conservation support (flagship); performing a valuable ecological role, with an impact that is greater than expected from its abundance (keystone); acting as an indicator of habitat or community status (indicator); or its habitats also being valued by many other species

(umbrella) (Simberloff 1998, Caro & O'Doherty 1999). These concepts are contentious, mostly because they are seen as an over-simplification, and are inconsistently defined and assessed, particularly in applied conservation practice (Simberloff 1998, Andelman & Fagan 2000, Lorimer 2015). Flagship species have come under particular scrutiny, as there is no assurance that a flagship species will also act as an indicator or umbrella species and may divert scarce resources away from other threatened species (Caro et al. 2004, Brambilla et al. 2013). On the other hand, if a flagship species is identifiable with particular threatened habitats, it can garner support and conservation attention for these habitats (Kontoleon & Swanson 2000, Leader-Williams & Dublin 2000). An argument for the use of flagship and umbrella species in woodlands, for instance, is the complexity of the environment and the fact that species are often cryptic (Roberge et al. 2008). Conservationists have argued therefore that each use of a flagship species should be assessed for its context-dependent individual merit (Leader-Williams & Dublin 2000). The perceived charisma of a species has consistently proved to be an important predictor of its public support (Colléony et al. 2017). Flagship species, once appraised for their simultaneous value as an indicator or umbrella species, can therefore be a valuable tool in gathering support and public backing for conservation efforts (Mace et al. 2009).

In order to conserve a species effectively, we need to understand the status and trajectory of its populations, its habitat requirements, the existence of other extrinsic threats such as disease and overexploitation, and how these pressures might interact (Rodrigues et al. 2006, Boyd et al. 2008, Reid et al. 2014, Oliver et al. 2017). Moreover, resource limits and the cost-effectiveness of conservation actions is increasingly seen as an important consideration (Joseph et al. 2008, Cook et al. 2017). The importance of developing such a fundamental understanding of a species' status and needs has received growing recognition (Sutherland et al. 2004). When these are understood it is possible to consider different species requirements concurrently and integrate their conservation into multi-functional land management (Görg et al. 2016). This allows more strategic conservation planning over large areas and over longer time spans (Fontaine et al. 2007, Bertolino et al. 2014).

Species monitoring

In order to gather the data that is required to assess species' distributions, status and habitat requirements, monitoring of populations is required (Nichols & Williams 2006). Monitoring is the repeated sampling of status (Gitzen & Millspaugh 2012) and when such information is collected over long periods, it can be used to determine population trends, conservation needs and responses to environmental change, and to indicate wider ecological health (Yoccoz et al. 2001, Buckland et al. 2005).

The high level of survey effort required to monitor populations effectively over wide areas and long timeframes can be achieved through the involvement of volunteer groups (Bonney et al. 2009). Wildlife monitoring by volunteers, or 'citizen science', has grown rapidly over recent years (Bonney et al. 2014). These programmes can allow people to become more engaged with the natural environment, and provide health, education and community cohesion benefits for participants (Newman et al. 2003, Silvertown 2009, Lawrence & Turnhout 2010, Tulloch et al. 2013).

Many wildlife monitoring programmes, however, do not explicitly define their objectives or address design issues that may affect the survey results (Yoccoz et al. 2001, Lindenmayer & Likens 2010, Gitzen & Millspaugh 2012). Securing the commitment and resources needed to ensure ongoing monitoring, especially with volunteer surveyors, is difficult (Hochachka et al. 2012, Reynolds 2012). Furthermore, providing for the maintenance of even sampling effort through time and across space is also challenging (Donald & Fuller 1998, Greenwood 2007, Dickinson et al. 2010). In schemes where selection and continued monitoring of sites is determined by volunteers and their availability, further uncertainty concerning the equivalence of monitoring over time is introduced (Fewster et al. 2000, Szabo et al. 2010, Reynolds 2012). It is therefore important to address these issues in the design of programmes and validate any resultant data and outcomes (Crall et al. 2011, Bonney et al. 2014, Burgess et al. 2017).

Monitoring mammals in the UK

There are now significant numbers of wildlife monitoring programmes in the UK, including large national programmes for bird, butterfly and bat populations (Freeman et al. 2007, Dennis et al. 2013, Barlow et al. 2015). Schemes for monitoring mammals have, in general, been less well-developed than those for other species groups (Battersby & Greenwood 2004, Wright et al. 2013). Progress has been made in mammal monitoring in the last two decades, however, and the use of volunteers in mammal monitoring procedures has been shown to yield reliable results (Newman et al. 2003). These advances have incorporated lessons from existing citizen science monitoring programmes, such as the value of using long-term population indices as opposed to total population sizes (Battersby & Greenwood 2004). The short-lived Tracking Mammals Partnership (TMP) was established by the Joint Nature Conservation Committee (JNCC) in 2003 to coordinate efforts towards monitoring mammals in the UK (Battersby 2005). The aims of the partnership were to facilitate better conservation and management of populations and fulfil international legislative obligations (Battersby & Greenwood 2004). While the TMP has not been active since 2009, the groups comprising the TMP continue to work together (JNCC 2015). The partnership comprised 23 organisations and specific programmes operate under the partnership, including the National Bat Monitoring Programme, monitoring 11 of Britain's 16 resident bat species since 1990; and the mammal monitoring arm of the British Trust for Ornithology's Breeding Bird Survey which has been running since 1995.

Other mammal monitoring schemes in the UK tend to be less deliberately structured, such as the National Gamebag Census run by Game and Wildlife Conservation Trust (GWCT), which is based on the number of game animals and their predators killed annually (Whitlock et al. 2003). Or they are relatively opportunistic, such as the Mammals on Roads scheme run by PTES, which uses the numbers of animals killed on roads from which to make inferences on population size and habitat associations (Battersby 2005). Both these schemes are subject to potential biases in spatial coverage and survey effort, and any extrapolation of the results to make population-level inferences must be validated. Moreover, schemes which generate more detailed population data

allow the UK to better fulfil its statutory monitoring and reporting requirements for Internationally protected species.

The Hazel Dormouse

Hazel dormouse *Muscardinus avellanarius* is a species of small, arboreal rodent of the family Gliridae, that lives across most of central Europe, the UK, Denmark and southern Sweden and parts of Russia (Hutterer et al. 2016). It is listed as Least Concern in the International Union for Conservation of Nature and Natural Resources (IUCN) global Red List, however the species account states that in areas towards the north of their range, such as the United Kingdom and Sweden, there is evidence of decline and range contraction (Hutterer et al. 2016). Within the UK, dormouse populations are distributed across Southern England and parts of Wales, the Midlands and Northern England (Mitchell-Jones & White 2009), though the species' range has contracted since the late 19th century (Fig. 1.1). The hazel dormouse is protected under Annex IV of the EC Habitats Directive (1992) and the UK Conservation Regulations (1994), Wildlife and Countryside act (1981) and Countryside and Rights of Way act (2000). Within forestry systems in the UK, best practice guidance is provided by the Forestry Commission to prevent foresters or woodland owners and managers falling foul of this legislation (Forest Research 2007). The dormouse has also been a UK Biodiversity Action Plan Priority Species since 1997 (JNCC 2007, 2010).

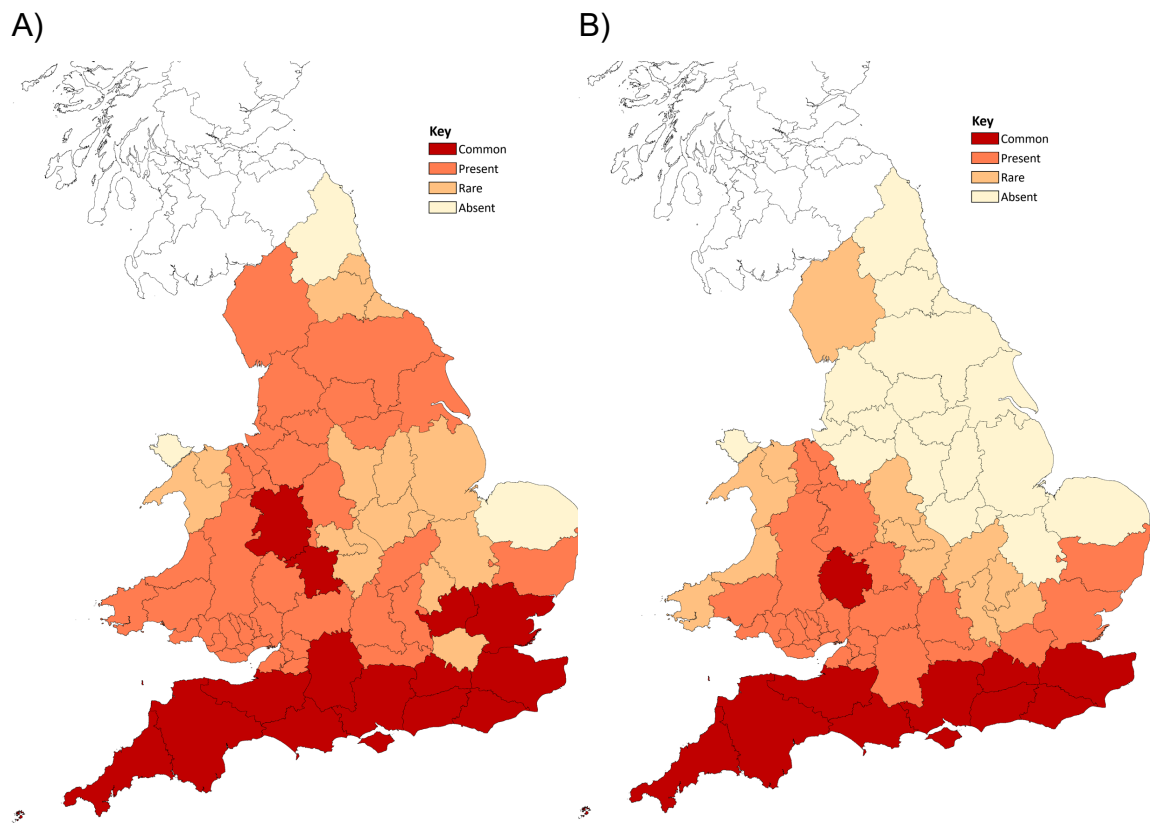


Figure 1.1. *The changing distribution of the hazel dormouse in Britain across counties of England and Wales. A) Prevalence classifications of the abundance of dormice in the Victorian Era. Data from Rope (1885) and Victorian County histories. B) Prevalence classification of the abundance of dormice across counties of England and Wales 2011-2015. Data from the National Dormouse Database. Source: People’s Trust for Endangered Species, 2017.*

Dormice are relatively long-lived for a small mammal, with lifespans of up to four years (Juškaitis 1999a, b). They hibernate in winter months in response to shortening photoperiod, but may come out of hibernation in response to higher temperatures, which can increase winter mortality with detrimental effects on populations (Juškaitis 1999c, Csorba 2003, Bieber et al. 2012, Reiners et al. 2012). However, in very mild climates, some populations have been found not to hibernate at all. During the active season (late spring, summer and early autumn), individuals can also enter facultative torpor during the day (and occasionally at night), the likelihood of which is determined by ambient temperature, photoperiod, food availability and animal weight (Juškaitis 2005a). Dormice spend daytime periods in woven nests in tree cavities, old birds’ nests or squirrel dreys, or in scrub such as bracken bramble (Bright & Morris 1991, Verbeylen 2012). Female

dormice produce between one and two litters a year of between three and six young. Young generally breed for the first time the year following their birth, but there is evidence that some breed within the same year they are born (Juškaitis 2003). Dormouse populations have shown evidence of density dependence in that breeding rates and population growth are reduced in higher density populations (Juškaitis, 2013, 2003). However, density dependence has not been found in all populations (Sanderson 2004).

Dormice require a variety of invertebrate and plant food, and therefore rely on a succession of flowers and fruits becoming available over time (Richards et al. 1984). This has meant they have been traditionally associated with highly species rich woodland (Bright & Morris 1990, 1993, Reiners et al. 2012), and areas with higher amounts of light and warmth such as hedgerows, edge habitats and glades within woodlands (Bright & Morris 1990, Berg & Berg 1999, Juškaitis & Šiožinytė 2008). They have also been associated with dense vegetation and shrub, similarly reflecting the requirement for a range of food sources, but also with plenty of branch connections to allow movement and provide nesting habitats (Bright & Morris 1990, Juškaitis et al. 2013, Mortelliti 2013).

In the UK, dormice have increasingly been found in a wider range of habitats such as certain ages of conifer plantation and coastal scrub (Chanin & Woods 2003, Juškaitis 2007a, Trout et al. 2012a, Wuttke et al. 2012), although it is thought dormice exist in lower densities in these habitats and their value for dormouse populations as a whole is not clear (Juškaitis 2007a). In the landscape scale, dormice are more likely to occur in larger woodlands with greater amounts of wooded habitat in the surroundings, with more woodland corridors and hedgerow connections between them (Bright et al. 1994, Bailey et al. 2002, Mortelliti et al. 2011, Reiners et al. 2012, Encarnação & Becker 2015).

A major threat to hazel dormice is the loss of woodland habitats, particularly semi-natural woodlands. The loss of woodland corridors and hedgerows (Mortelliti 2013, Encarnação & Becker 2015) leaves dormice populations more isolated and vulnerable to inbreeding depression and extinction (Bani et al. 2017a, b, Iannarilli et al. 2017). The transition to less structurally and compositionally diverse forest types, and decline of traditional woodland management practices such as

coppicing, is likely to have reduced the amount and quality of dormouse habitat (Bright et al. 1994, Bright & Morris 1996), while the impact of deer populations on coppicing regrowth and woodland shrub structure has further reduced the amount of this habitat (Eichhorn et al. 2017).

It has also been suggested that changing climatic conditions have had additional detrimental effects on dormice, especially in the UK, where the species is at the edge of its range (Bright & Morris 1996). These include effects on the timing of breeding and hibernation and in changing activity patterns (Bright et al. 1996, Juškaitis 1997a). The likelihood of dormouse presence in a woodland site is increased in areas with dry, warm springs and summers and cold winters (Bright & Morris 1996, Reiners et al. 2012). Studies of the species in captivity have additionally found dormice arouse from hibernation more frequently and lose fat resources at a faster rate in response to high temperatures (Mills 2012). Consequently, recent changes in climate, with warmer winter temperatures, larger fluctuations in temperature and increasing precipitation could have had detrimental population impacts (Horton et al. 2010, The Met Office 2015).

The conservation of the hazel dormouse in the UK has been based principally on raising awareness of the species and its habitats, and producing guidance on how best to conserve and manage those habitats (Bright et al. 2006). Because of this, and their popular appeal, they have been used as an indicator and flagship species for coppice and structurally diverse woodland (Morris 2003). A statutory Species Recovery Programme was introduced for the hazel dormouse in Britain in 1992, part of which involved a search for dormouse feeding signs in The Great Nut Hunt in 1993 (Mitchell-Jones & White 2009). A reintroduction project, based on a captive breeding programme, was also implemented in 1993 in order to reclaim areas of lost range or where dormice had become locally extinct (Mitchell-Jones & White 2009).

The National Dormouse Monitoring Programme (NDMP), now co-ordinated by the PTES, was established in 1988 in order, originally, to monitor the status of populations at a few 'key sites' for dormice in England (Bright & Morris 1995). The scheme started on only five sites in two counties and has expanded over 27

years to cover around 400 sites in 52 counties annually in England and Wales (Jones et al. 2009). See Fig 2.1 for the distribution of NDMP sites in 2014.

In order to monitor sites, a gridded network of specially-designed nest boxes, which allow easy access to dormice during their diurnal resting period, are positioned at head height and spaced at around 20m in woodland (Morris et al. 1990, White 2012). Due to the gridded sampling design of the survey, sites are not established in linear features such as hedgerows (PTES 2016). The sites are checked at least twice a year before and after breeding but can be checked up to once a month (White 2012). Biometric data on the sex, weight and age of dormouse individuals are also recorded (Jones et al. 2009). The scheme involves at least 1200 licensed volunteers and unlicensed trainees and observers, who receive materials and reports on the findings and progress of the programme (White 2012). The programme thereby gives people the opportunity to interact with a charismatic and otherwise elusive woodland mammal, provides training opportunities and increases awareness of dormice and wider woodland conservation (Jones et al. 2009).

The original aims of the NDMP were to i) track the status of national dormouse populations; ii) enable comparisons between sites with different habitats or management; iii) enable changes in populations to be monitored as habitats changed; iv) involve people in dormouse conservation and woodland ecology; v) highlight the need for a comprehensive system of monitoring Britain's mammals. While there have been reports published by PTES from the scheme, there has been only one unpublished piece of academic work on data from the NDMP to date. Sanderson's (2004) PhD thesis on the information in the first nine years of data from the NDMP, provided an insightful first assessment of the initial trends and the power of the scheme to predict population change. Even at that early stage the programme was able to detect a 50% decline over 25 years, although a full appraisal of the data and the effect of potential survey differences was not conducted.

The UK is the only country with a national dormouse monitoring programme, although other countries have smaller-scale regimes (Juškaitis 1995, Verbeylen 2003). Variation in the status of dormouse populations is, therefore, more

thoroughly understood in the UK than across most of central Europe. Sanderson (2004) used data from the NDMP to illustrate a decline in dormouse populations in the UK of 23% from 1993 to 2002, and informal assessments and reports from PTES suggest declines are ongoing.

The Thesis

The main focus of this thesis is to assess population change in hazel dormice in the UK and to understand how these might relate to woodland and forestry management. In so doing, I aim to establish how environmental changes could have contributed to variation in dormouse population status, and guide recommendations within the context of wider woodland conservation.

Specifically, I aim to:

- I. Assess dormouse population change in Britain over 22 years.
- II. Understand the drivers of hazel dormouse population status in UK woodlands, and habitat and management effects on hazel dormouse populations.
- III. Evaluate the trophic ecology of dormice in relation to woodland habitat composition.
- IV. Investigate the habitat preferences of dormice in relation to woodland habitat composition and structure.

I will approach these using a mixture of national monitoring data collected by volunteers, large-scale, high-resolution habitat and climatic data and empirical fieldwork data. Following this introduction, the thesis is structured into four chapters relating to the four objectives above, and concludes with a general discussion. In each case, I have sought to produce practical recommendations for dormouse conservation and woodland management.

In **Chapter 2**, I focus on a critical appraisal and validation of 21 years of nest box data collected by volunteers as part of the National Dormouse Monitoring Programme. I investigate if there is any evidence of survey bias arising from changes in practice or scope during the progression of the scheme. I then conduct population trend analysis to understand dormouse population change in the UK.

In **Chapter 3**, I use data from the NDMP to assess the relative importance of environmental influences on the abundance, breeding rate and trend of dormouse populations in woodland sites with differing climate, landscape, habitat and management characteristics. I do this by analysing population data validated in Chapter 1 alongside a variety of remotely-sensed, questionnaire-derived and weather data.

In **Chapter 4**, I investigate the trophic ecology of dormouse populations and individuals in different woodlands through an assessment of the stable isotopes of dormice and their putative food items. I examine dietary variation between locations and seasons and test the effects of woodland habitat composition and resource abundance on the trophic niches of dormice.

In **Chapter 5**, I assess dormouse use of woodland species and habitat structure by using radio-tracking and remote-sensing to examine ranging and nesting behaviour in two woodlands. I also investigate the proximate effects of tree felling on the ranging and nesting behaviour of dormice.

In **Chapter 6**, my general discussion provides a synthesis of my findings, the themes arising from across the work, and contributions to knowledge of dormouse ecology and conservation. The chapter also discusses the wider implications for woodland conservation.

Chapter 2

Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse *Muscardinus avellanarius* population.

Chapter 2: Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse *Muscardinus avellanarius* population.

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Abstract

In order to conserve threatened species, knowledge of the status, trends and trajectories of populations is required. Co-ordinating collection of these data is challenging, especially for inconspicuous species such as the hazel dormouse *Muscardinus avellanarius*.

The UK National Dormouse Monitoring Programme (NDMP) is comprised of nest box recording schemes organised by volunteers. The number, size, and coverage of these schemes has varied over time. Such changes risk conflation of genuine population trends with covarying artefacts, including survey effort and expansion into sites of variable quality.

I provide a robust analysis of count data from 400 NDMP sites from 1993 to 2014 and demonstrate that changes in counts are not an artefact of survey characteristics. In relation to the International Union for Conservation of Nature (IUCN) Red List criteria, I conclude that dormouse counts in nest boxes are an index of abundance appropriate to the taxon and allow the inference of population reduction of 72% (95% confidence intervals 62 – 79%) over the 22 years from 1993 to 2014, equivalent to a mean annual rate of decline of 5.8% (4.5 – 7.1%). This decline is ongoing.

I highlight difficulties in assigning an IUCN Red List conservation category to a population, given variation in apparent trends over consecutive time-periods. In eight out of 13 sliding window intervals of 10 years from 1993 to 2014, the 95% confidence intervals overlap a decline of 50%. While average population decline over 10-year periods suggests that the hazel dormouse should be classified as Vulnerable, a precautionary approach would not rule out the category of Endangered in the United Kingdom, given the lower bounds of population change estimates, the mean annual rate of decline and ongoing decline.

Ongoing decline in the hazel dormouse population is despite a high level of species protection and widespread conservation measures. The hazel dormouse is a UK Biodiversity Action Plan Priority Species and a European Protected Species, and the causes of population reduction are not well understood and may not have ceased. An urgent appraisal of dormouse conservation is required to ensure the species' favourable conservation status.

Chapter 3

Effects of climate, landscape, habitat and woodland management on hazel dormouse *Muscardinus avellanarius* population status

Chapter 3: Effects of climate, landscape, habitat and woodland management on hazel dormouse *Muscardinus avellanarius* population status

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Abstract

Although strictly protected, British populations of the hazel dormouse *Muscardinus avellanarius* declined by 72% from 1993 to 2014. Using National Dormouse Monitoring Programme data from 300 sites across England and Wales, I investigated variation in hazel dormouse population status in relation to climate, landscape, habitat and woodland management.

Dormice were more abundant and produced more litters on sites with warmer, sunnier springs, summers and autumns. Dormouse abundance was also higher on sites with consistently cold local climate in winter. Habitat connectivity, woodland species composition and active site management were all correlated with greater dormouse abundance and breeding. Abundances were also higher on sites with successional habitats, while the abundance of early successional bramble habitat, woodland area and landscape connectivity were important for population stability.

Diversity in the structure of woodlands in Britain has decreased over the last 100 years, and the habitats I found to be associated with more favourable dormouse status have also been in decline. The conservation status of hazel dormouse, and that of woodland birds and butterflies, would benefit from reinstatement or increased frequency of management practices, such as coppicing and glade management, that maintain successional and diverse habitats within woodland.

Introduction

Critical appraisal of the environmental variables that affect the status of threatened species can help determine the relative influence of factors that might more easily be modified, such as habitat and management, alongside those that cannot, such as climate (Pressey et al. 2007, Groves et al. 2012). Furthermore, understanding the drivers of variation in status at different spatial scales can allow the identification of regions that offer the best conservation opportunities as well as the distinguishing characteristics of sites that offer high habitat quality, even when favourable location is accounted for (Erasmus et al. 1999, Chalfoun & Martin 2007). Such assessments are especially pressing for vulnerable or protected species facing multiple threats, and where legislation makes action to conserve them a legal imperative (Koleček et al. 2014, Sanderson et al. 2016).

The hazel dormouse *Muscardinus avellanarius* is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992), and the UK Habitats Regulations (1994 and 2010). The species is categorised on the International Union for Conservation of Nature (IUCN) Red List as Least Concern. Towards the north of its range, such as in the United Kingdom, the species is in decline (Hutterer et al. 2016) and a recent, robust analysis of dormouse counts from 400 sites across England and Wales revealed a 72% (95% confidence intervals 62 - 79%) decline in the UK dormouse population from 1993 to 2014 (Goodwin et al. 2017). This decline, together with evidence of range contraction (Bright & Morris 1996) substantiates a Red List categorization of dormice as “Vulnerable” or possibly “Endangered” in the UK (Goodwin et al. 2017). Dormouse declines are particularly concerning given their strict protection and the significant monitoring and conservation attention this species has received over recent decades (White 2012). Understanding the needs of threatened species and whether legislative instruments are serving as effective tools in their conservation are therefore both vital in developing effective policy and practice (Pärtel et al. 2005, Ramirez et al. 2017).

The proposed causes of decline in dormouse populations include habitat loss and fragmentation and declining habitat quality (Bright & Morris 1996, Mortelliti et al. 2011, Amici et al. 2015). Recent climate change may also have contributed to dormouse declines. Milder, more variable winter conditions have been linked to

higher over-winter mortality, and wetter spring and summer weather may have negatively impacted populations through reductions in activity and the availability of food (Bright & Morris 1996, Juškaitis 1999c, Juškaitis et al. 2016). At a larger scale, changes in landscape structure, primarily via agricultural intensification, have led to increased fragmentation of woodland habitats and the loss of semi-natural vegetation (Peterken 2002, Hopkins & Kirby 2007), reducing habitat availability for dormice and compromising their ability to disperse among woodlands (Bright & Morris 1996, Mortelliti et al. 2011).

There have been significant shifts in the habitat characteristics of European temperate forests, with both intensification of timber production and abandonment of traditional broadleaf management practices, such as coppicing and creation of glades and rides (Young et al. 2005, Miklín & Čížek 2014, Kirby et al. 2017). This has resulted in a predominance of two woodland types: intensively managed conifer plantations and broadleaf high-forest (Paillet et al. 2010). This trend is particularly apparent in the UK, where the simultaneous intensification of forestry and abandonment of more traditional management regimes has led to a reduction in the amount of spatially heterogeneous and structurally complex woodland (Hopkins & Kirby 2007, Quine et al. 2011). Shifts in the ecological communities of woodlands, notably increasing deer population densities, have further reduced structural complexity, with negative consequences for biodiversity (Eichhorn et al. 2017). Heterogeneous, multi-layered woodland brings biodiversity benefits (Lindenmayer et al. 2006, Kirby et al. 2017) by providing important habitats for a range of key taxa such as butterflies and moths (Broome et al. 2011, Fartmann et al. 2013, Fox 2013), woodland birds (Fuller & Gill 2001, Fuller et al. 2007a, Quine et al. 2007) and mammals (Ramírez & Simonetti 2011).

Dormice have been associated with early- to mid-successional wooded habitats that often arise from traditional management regimes, such as coppicing and ride and glade maintenance (Capizzi et al. 2002, Sozio et al. 2016). However, studies of the effects of habitat variation and management interventions on dormice have focused on few sites or for limited periods, due to the logistical difficulties of examining multiple sites over appropriate timescales (Juškaitis 2008, Trout et al. 2012b, Sozio et al. 2016). The National Dormouse Monitoring Programme (NDMP) consists of nest box recording undertaken by volunteers on a large

sample of sites across England and Wales. It has been running since 1988 and by 2017 had encompassed over 600 sites. The spatial and temporal scale of the Programme therefore allows for assessment of populations across different habitat, landscape and climate contexts. Sampling effort (the number of nest boxes) is known and NDMP count data have been shown to provide reliable indices of relative abundance that are robust to the variation in survey implementation that is intrinsic to such Citizen Science schemes, including changes in effort over time and on sites surveyed in different months or for different numbers of years (Goodwin et al. 2017). In this study, I have used NDMP data to assess the climatic, landscape, habitat and management correlates of dormouse abundance, breeding and population trends, with a view to understanding and countering dormouse decline in the UK.

Methods

Dormouse population data

Grids of dormouse nest boxes are established on NDMP sites across England and Wales and dormice are counted by licensed volunteers up to once a month from May to September, with at least one pre-breeding survey in May/June and one post-breeding survey in September/October. Detailed survey methodology is provided in the NDMP guidelines (PTES 2016) and details of the validation of NDMP data for population monitoring are provided by Goodwin et al. (2017). Sites have been monitored for 1-27 years and contain up to 500 boxes. Data from the first five years of the programme (1988 - 1992) were excluded to prevent year effects being confounded with site effects arising from small numbers of survey sites ($n < 30$). Population indices were calculated using data from 300 sites that had been surveyed for at least five years during the period from 1993 to 2014, and on which more than one adult dormouse had been found. Sites surveyed for five years or more will have some detectable trend and using only sites where dormice had been found means indices represent relative population measures that can be compared among sites. In order to examine the effect of seasonal climatic variables, dormouse counts from all months of the survey season were used.

Weather and climate data

Monthly climate data were obtained from the UK Met Office, gridded at 5 x 5 km horizontal resolution. Location-specific climate estimates were derived from the grids via Inverse Distance Weighting, using the centre-points of the nearest nine grid squares. As temperature (minimum, mean and maximum) and rainfall (total monthly rainfall and number of days > 10mm rainfall) variables were closely related, one temperature and one rainfall variable, which best explained variation in dormouse indices (models with lowest AICs), were selected for each season (Appendix 2: Table S2.1). Each weather variable was centred (mean-subtracted) and scaled (divided by the standard deviation) across all sites and averaged for each site across all years, giving an average value describing the climate of each site relative to other sites. Sun, rain and temperature site averages often remained closely correlated and so I conducted Principal Component Analyses (PCA) to capture variance in climate on sites (Appendix 3: Table S3.1). In analysing climate effects on dormice, I wanted to examine both the major axes of climatic variation, using the first Principal Components (PCs), as well as more unusual or distinctive combinations of conditions, using PCs that explained > 2% of variation. I excluded all those that explained < 2% of variation in the data.

Landscape and habitat data

Five datasets gathered from remote-sensing were used to assess habitat, landscape and habitat change (Appendix 2: Table S2.1): 1) the National Forest Inventory (NFI) for 2011-2014 from Forestry Commission England (Forestry Commission 2016) was used to classify wooded habitat areas; 2) Natural England (Spencer & Kirby 1992) provided ancient woodland cover; 3) the Countryside Survey 2007 from the Centre for Ecology and Hydrology (Brown et al. 2016) provided hedgerow length; 4) the Joint Research Centre European Commission Forest Data (Pekkarinen et al. 2009, Soille & Vogt 2009, Kempeneers et al. 2011) from 2006 provided forest type (broadleaf or conifer) and spatial type (edge, isolated and interior); and 5) Environment Agency composite LiDAR (Light Detection and Ranging) data provided vegetation height at 1m resolution for a subset of NDMP sites (Environment Agency 2016).

The total area covered by Ancient Woodland and each EC Forest and NFI habitat type was summed at three scales: the area covered by the nest box scheme, the

whole woodland site and the surrounding landscape within a 1km perimeter, and transformed into proportions to control for variation in site size. Change in the proportions of wooded habitats in different years was used as a measure of habitat turnover at sites. As the NFI classifies habitat broadly and detects habitat patches of 0.2ha and larger, I used a binary measure of whether there was any change from 2011 to 2014. For EC Forest spatial habitat type, I quantified the amount of change in habitat types between 2000 and 2006. Habitat variables were centred (by subtracting the mean) and scaled (by dividing by the standard deviation) prior to analyses due to their very different measurement scales.

Using LiDAR data, I calculated metrics based on the canopy density and proportion of different vegetation heights for a subset of sites. Canopy density was defined as the density of vegetation height points over 4m (Mihók et al. 2009, Scheffer et al. 2014). A sliding window average (5m window) for canopy density was calculated across sites and the standard deviation of this value used to quantify variation in canopy density. As these variables were all correlated, they were converted into Principal Components describing different vegetation structure types on sites (Appendix 3: Table S3.2). PCs explaining > 2% of the variation in the data were used.

Management and site vegetation data

Questionnaires were sent to NDMP site monitors in 2014 and 2015 to gather data on species composition and the management regimes of sites. Monitors were asked to record the abundance of trees and shrubs on a DAFOR (Dominant >75%, Abundant 51-75%, Frequent 26-50%, Occasional 11-25%, Rare 1-10%, plus Absent) scale. The tree and shrub species that were found on at least 50% of sites ($n = 11$ species) were then used in analysis. Simpson's diversity index was calculated for vegetation composition on each site. Site monitors were also asked about the area covered, timing and frequency of coppicing, thinning, clearfell, ride and glade management. Management data were converted into variables quantifying broad management differences in order to standardise reporting; sites were classified into those that reported management and those that did not and the total extent of management was calculated by summing the areas subject to different management practices in each year. Information on the species composition and habitat types of sites can be found in Appendix 4.

Statistical analysis

All analyses were conducted within the R platform (version 3.3.2).

Dormouse population metrics

In order to compare site characteristics to dormouse population metrics and control for between-year variation in dormouse counts, time-independent, site-level indices of dormouse abundance, breeding and population trend were derived, using the approach applied by Goodwin et al. (2017). Indices were derived through models fitted to counts of dormice or breeding events with explanatory terms for year and site, and an offset for number of boxes used, to control for survey effort (Appendix 2B). Correlation between Trend and log-transformed Abundance indices was investigated using Pearson's product-moment correlation (ρ).

Effects of environmental and management factors on dormouse populations

Two forms of analysis were conducted on the effects of climate, habitat, landscape and management characteristics of sites on each of the three dormouse population indices: Abundance, Breeding and Trend. See Fig S2.1 in Appendix 2 for a schematic of the analytical pathway. First, I ran a Generalised Least Squares (GLS) model, using the R package nlme (Pinheiro et al. 2017), including a rational-quadratics spatial correlation function to control for the fact that some sites were closer and more likely to be similar, but not to explicitly control for the location of sites (Dormann et al. 2007). This was termed the 'proximity model', which accounts for correlations in the similarity of nearby sites, but not explicit differences in the dormouse population status of sites in different areas. Second, I ran a 'location model', a generalised additive model (GAM) fitted using the R package mgcv (Wood 2011), and including an easting and northing smoothed interaction term within the model to account for all variation caused by the spatial location of that site relative to other sites.

I performed these two analyses, the GLS proximity and GAM location model, on the effects of the same climate, landscape, habitat and management variables on dormouse population metrics as I did not want to dictate *a priori* whether spatial differences in dormouse population traits were determined by the similarity of nearby populations or by their geographic location. The GLS proximity model would therefore show which environmental characteristics operated over broader

spatial scales, up to the regional and national level, whereas the GAM location model would show which environmental characteristics operated on a smaller spatial scale, at the local level, as differences in dormouse populations arising from site location are controlled for, i.e. this analysis would show what made a site particularly good or bad for dormice given its location.

Dormouse Abundance and Breeding Indices were log-transformed to normalize their distribution and all models contained a Gaussian error structure. All models included a weighting term that weighted the Abundance, Breeding and Trend Indices by their standard error, and thus by the accuracy with which they were estimated; In GAM models this was a direct weight and so was entered as $1/\text{standard error}$, whereas in GLS models it was expressed as a fixed variance function and so was entered as $\sim\text{standard error}$.

Model selection was conducted using information theoretic approaches based on comparison of Akaike's Information Criterion (AIC) among candidate models (Appendix 1). For both the national-level proximity analysis and local-level location analysis, a two-stage selection was conducted: First, initial exploratory analysis for four separate suites of environmental variables (climate, landscape, habitat and management) was performed separately for Abundance, Breeding and Trend Indices of sites. All variables that were included in initial analyses are shown in Appendix 2: Table S2.1. Initial variables were selected using biological rationale, but a two-stage process was deemed necessary in order not to limit the research to a set of a pre-determined hypotheses regarding dormouse habitat preferences (van de Pol et al. 2016). Potentially important variables were identified if they had a significance of $p < 0.15$ when conditional model averaging was performed following model selection (Davies et al. 2011). Each set of potentially important variables was then combined into a second stage comparative model for each national (proximity) and local (location) analysis of each population index, and model selection was performed. Interactions between explanatory variables were not explored due to uneven representation of variable combinations (Zuur et al. 2010). Full model averaging was then performed across the top model set to calculate parameter estimates and confidence intervals.

Effects of vegetation structure on dormouse populations

The effects of vegetation structure Principal Components derived from LiDAR (Appendix 3: Table S3.2) on indices of dormouse abundance ($n = 48$ sites), breeding ($n = 35$ sites) and trend ($n = 46$ sites) were modelled using a linear regression model with a Gaussian error structure. The sites selected for LiDAR analysis were stratified by region, so spatial terms were not included in this model. The effects of the original LiDAR-derived variables (Appendix 3: Table S3.2) were also modelled using linear regression as validation. Model selection was undertaken using the same approach as above and full model averaging was used to determine the effect sizes and confidence intervals.

Results

The mean dormouse Abundance Index was $5.2 (\pm 0.3 \text{ SE})$ dormice per 100 nest boxes, mean Breeding Index was $0.6 (\pm 0.04)$ litters per 100 nest boxes and mean population Trend Index was $0.946 (\pm 0.016)$, which is equivalent to a 5.4% population decrease each year. The average size of the woodland area of the sites was $1.4 \text{ km}^2 (\pm 0.1 \text{ km}^2)$, of which an average of $0.09 \text{ km}^2 (\pm 0.004 \text{ km}^2)$, approximately 6.4%, was monitored with nest boxes. Dormice were most abundant in the South-East area (Fig. 3.1). There was no significant correlation between the dormouse Abundance and Trend Indices of sites ($\rho = 0.1$, $t_{213} = 1.5$, $p = 0.14$).

Woodland management was reported to have been conducted on 88% of sites and information on the management practices themselves was reported for 63% of sites. At these sites, an average of $0.03 \text{ km}^2 (\pm 0.004 \text{ km}^2)$, this equates to 12% ($\pm 2\%$) of the woodland area under the control of the site managers, was subject to yearly management activities. There had been habitat turnover, detected by NFI datasets (2011 - 2014), on 22% of sites over 4 years, however, the finer-scale EC Forest datasets reported change on 98% of sites over 6 years (2000 - 2006), with an average change in habitat of 13% ($\pm 1\%$).

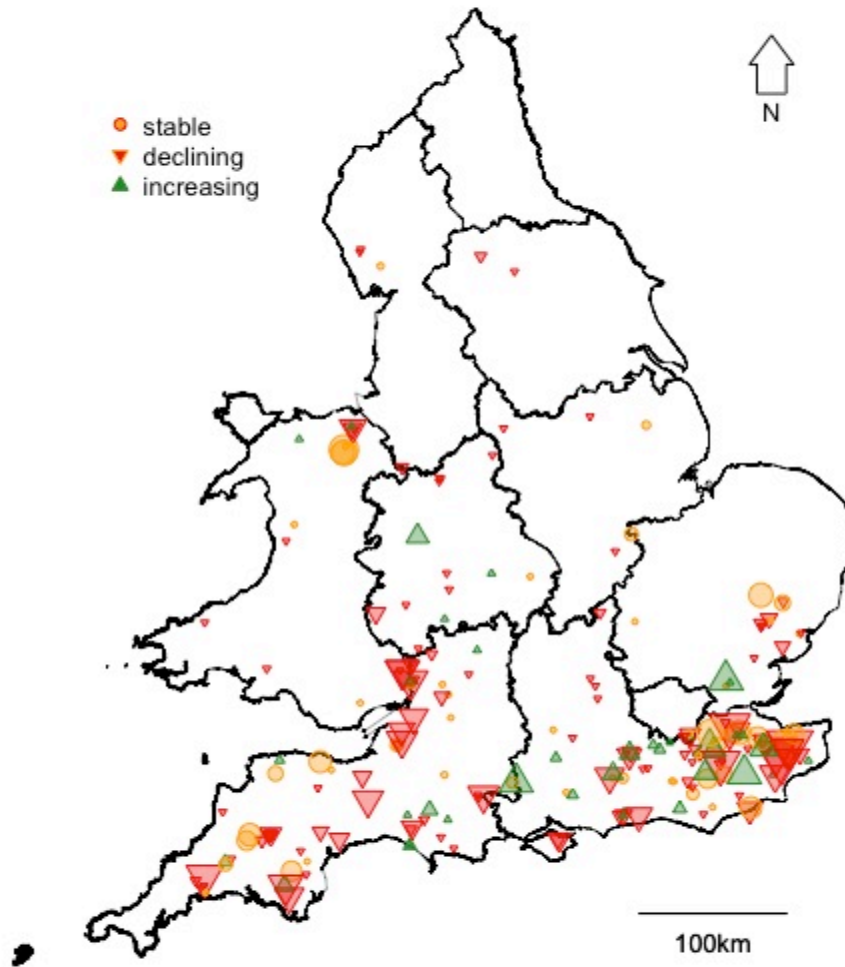


Figure 3.1. The location of 215 National Dormouse Monitoring Programme sites in England and Wales and their dormouse Abundance and Trend Indices, 1993 - 2014. Shape and colour indicate whether the site population is increasing (Trend Index > 0.05), stable (Trend Index of between -0.05 and 0.05), or declining (Trend Index < -0.05). The size of points is scaled by the log-transformed dormouse abundance indices and thus is a relative indicator of population size; small populations (< 3 individuals per 100 boxes) are all represented by the smallest size point to aid visual interpretation.

The effects of environmental and management factors on dormouse populations

At a national-scale, in the proximity-based analysis, variation in dormouse Abundance Indices was negatively related to the first climate Principal Component (PC1) (Fig. 3.2), indicating that dormice were more abundant on sites characterised by a climate of warmer and sunnier springs, summers and

autumns. Location-based, local-scale analysis identified that site location was important in determining the Abundance Index of a site; 38% of variance in abundance could be explained by location alone, while 27% could be attributed to habitat and management factors. Site-level climatic variation explained 7% of variance in Abundance Indices and, when controlling for the location of sites, colder, less variable winter temperatures (PC3) were related to higher Abundance. Dormouse Abundance Indices in national and local analyses were greater on sites that conducted woodland management (Figs. 3.2 and 3.5A). Greater dormouse Abundance was associated with greater reported abundances of honeysuckle and yew in national analysis and of birch and of shrub habitats in local analysis. Greater abundance of conifer was associated with lower dormouse Abundance in both national and local analyses. In national analyses, more woodland in the surrounding area was associated with higher dormouse Abundance while in local analysis, sites with more woodland edges (> 25m from other woodland) had lower dormouse Abundance Indices.

At a national-scale, variation in dormouse Breeding Indices was also negatively related to climate PC1 (Fig. 3.3), indicating that dormice had more litters on warmer, sunnier sites. Location explained 19% of variance in dormouse Breeding Indices, while a similarly large proportion of variance at 27% could be attributed to habitat and management factors. Site-level climatic variation explained only 1% of variance in Breeding Indices and, when controlling for the location of sites, local climatic factors did not significantly affect dormouse Breeding. Dormouse Breeding Indices in national, but not local, analysis were greater on sites that conducted more woodland management (Figs. 3.3 and 3.5B). Greater dormouse Breeding Indices were associated with greater reported abundance of hazel in national analysis and of willow in local analysis. Greater abundances of conifer and sycamore were associated with lower dormouse Breeding Indices in both national and local analyses, though the presence of mixed broadleaf/conifer habitat was positively associated with dormouse Breeding (Fig. 3.3). In local analyses, sites with lower vegetation diversity and more woodland in the surrounding area were associated with higher Breeding Indices (Fig. 3.3).

Climate variables had no significant impact on dormouse population Trend Indices at either a national or local scale (Fig. 3.4). Location was less influential

in population trends, explaining only 3% of variance in Trend, while local climate explained 1% of variance and habitat and management factors a further 9%. Dormouse population Trend Indices in national and local analyses were higher (more positive) on larger sites and lower (more negative) on sites with greater abundance of mixed broadleaf/conifer habitat (Fig. 3.4). Higher Trend Indices were associated with greater reported abundance of bramble and with more woodland habitat in the surrounding area in national analyses (Fig. 3.4).

Effects of vegetation structure on dormouse populations

Abundance and Breeding Indices were significantly and negatively related to LiDAR Principal Component 4 (Fig. 3.6). Dormice were therefore more abundant and had more litters on sites characterized by a high proportion of vegetation that was 5 to 10m tall, less high forest, less vegetation of 1 to 2m tall, and less variation in canopy density. Dormouse population Trend Indices were not associated with any LiDAR PCs. Analysis of single LiDAR variables supported these results, but did not capture combinations of correlated woodland structure. Abundance Indices were significantly negatively related to the proportion of vegetation over 10m tall (-6.48; -10.00, -2.95 95% CIs), Breeding Indices were significantly negatively related to the proportion of 2-5m vegetation (-6.25; -10.92, -1.59 95% CIs) and Trend Indices were not related to LiDAR variables.

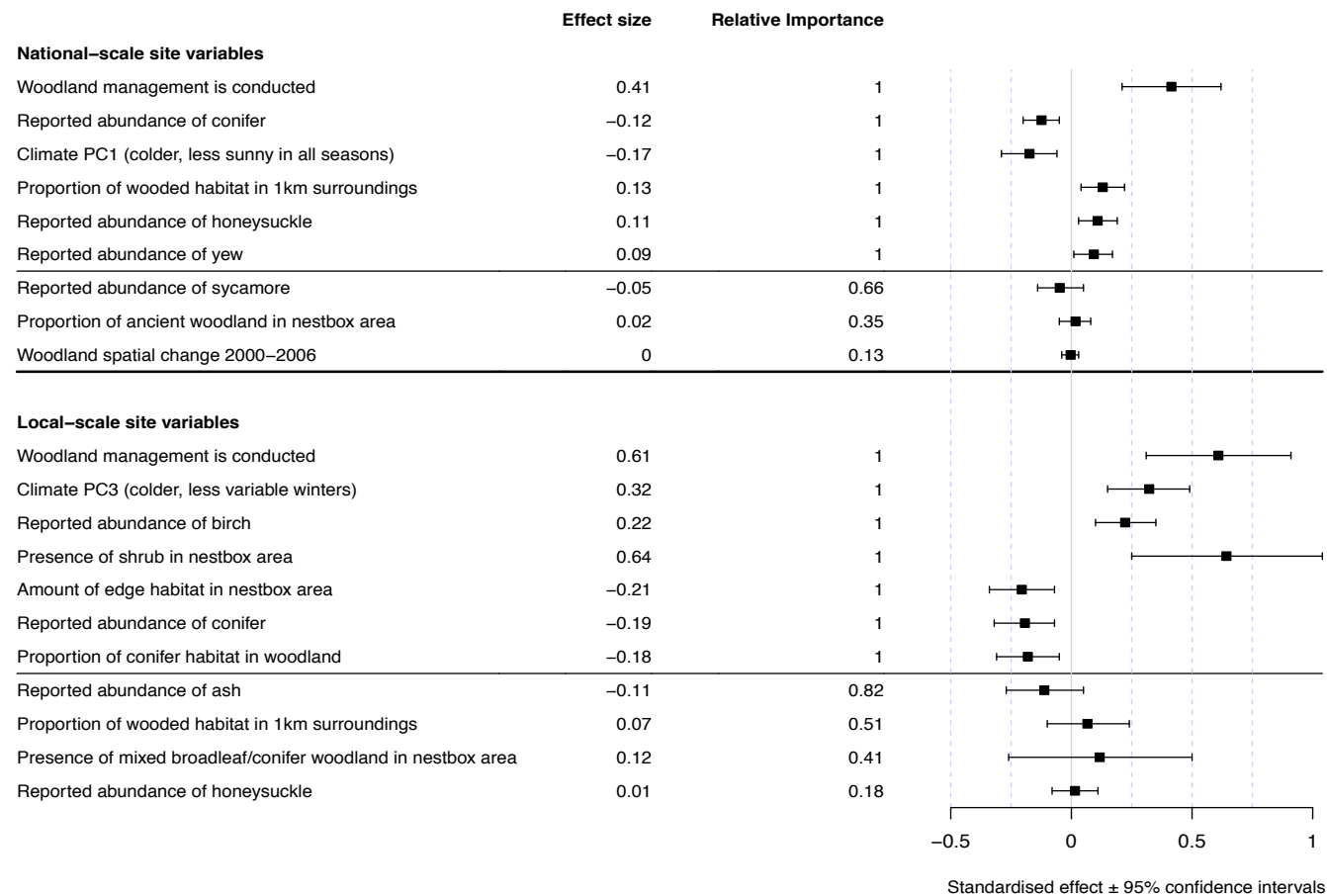


Figure 3.2. The effects of climate, landscape, habitat and management variables on dormouse **Abundance Indices** on 180 sites in the National Dormouse Monitoring Programme, 1993-2014. National-scale effects are from Generalised Least Squares proximity analyses and local-scale effects are from Generalised Additive Modelling, controlling for spatial location. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance in the top model set are shown. ‘Reported abundance’ of plant species is derived from questionnaire data.

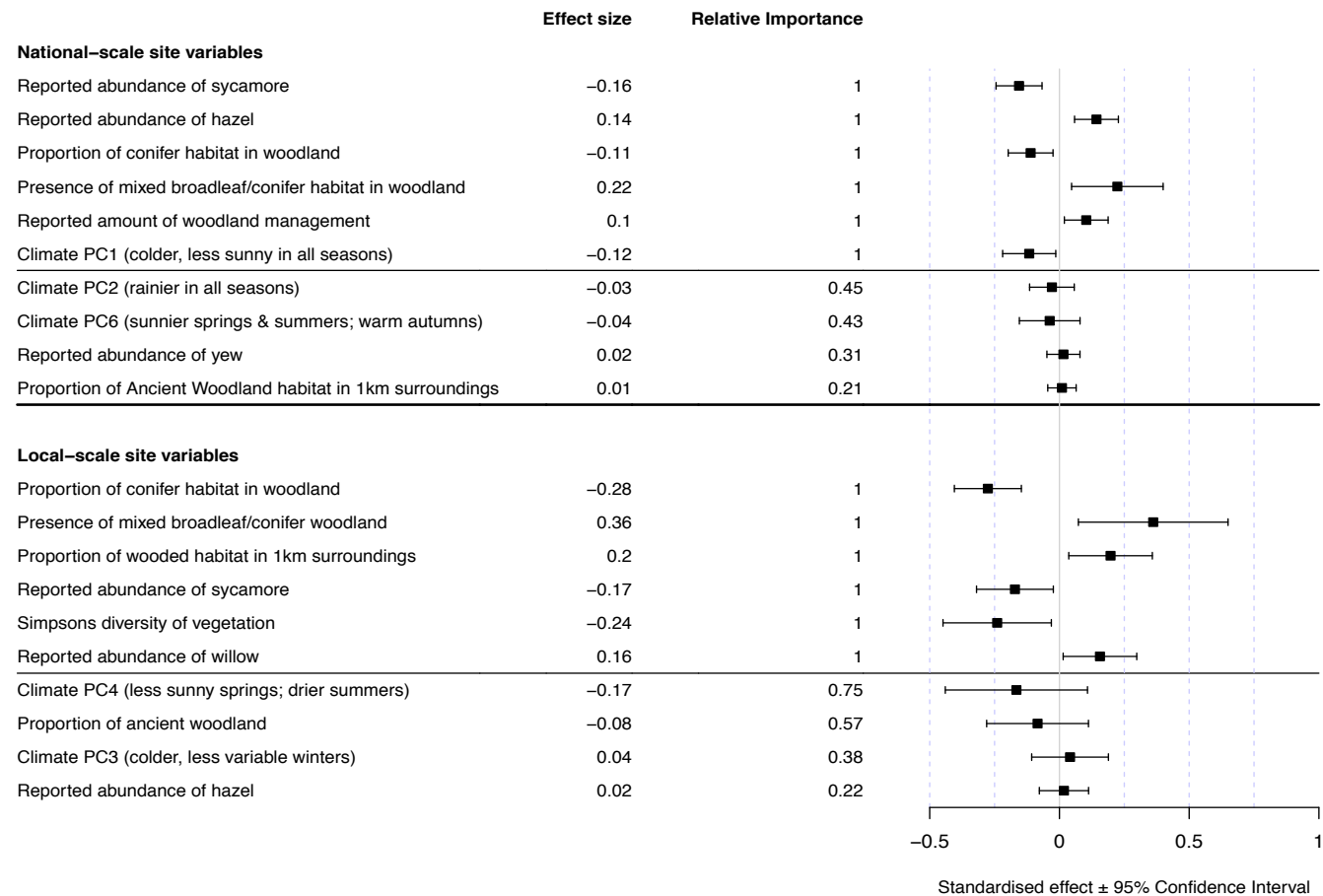


Figure 3.3. The effects of climate, landscape, habitat and management variables on dormouse **Breeding Indices** on 140 sites in the UK National Dormouse Monitoring Programme, 1993 - 2014. National-scale effects derived from Generalised Least Squares proximity analyses and Local-scale effects from Generalised Additive Modelling, controlling for spatial location. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance (RI) in the top model set are shown. 'Reported abundance' of plant species is derived from questionnaire data.

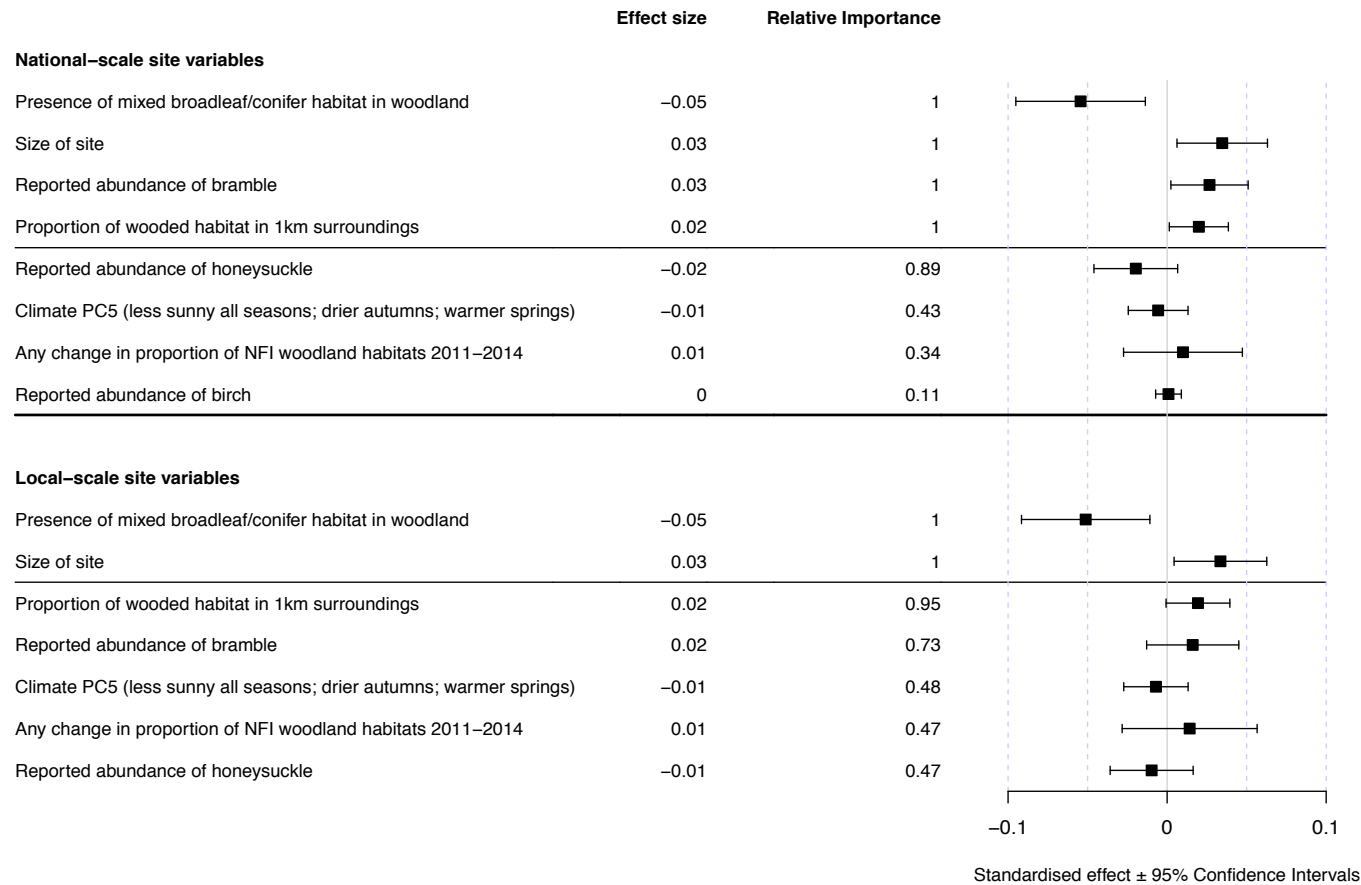


Figure 3.4. The effects of climate, landscape, habitat and management variables on dormouse population **Trend Indices** on 182 sites in the UK National Dormouse Monitoring Programme, 1993 - 2014. National-scale effects derived from Generalised Least Squares proximity analyses and local-scale effects from Generalised Additive Modelling, controlling for spatial location. Averaged standardised effect sizes (error bars indicate 95% Confidence Intervals) across the top model set and relative importance in the top model set are shown. 'Reported abundance' of plant species is derived from questionnaire data.

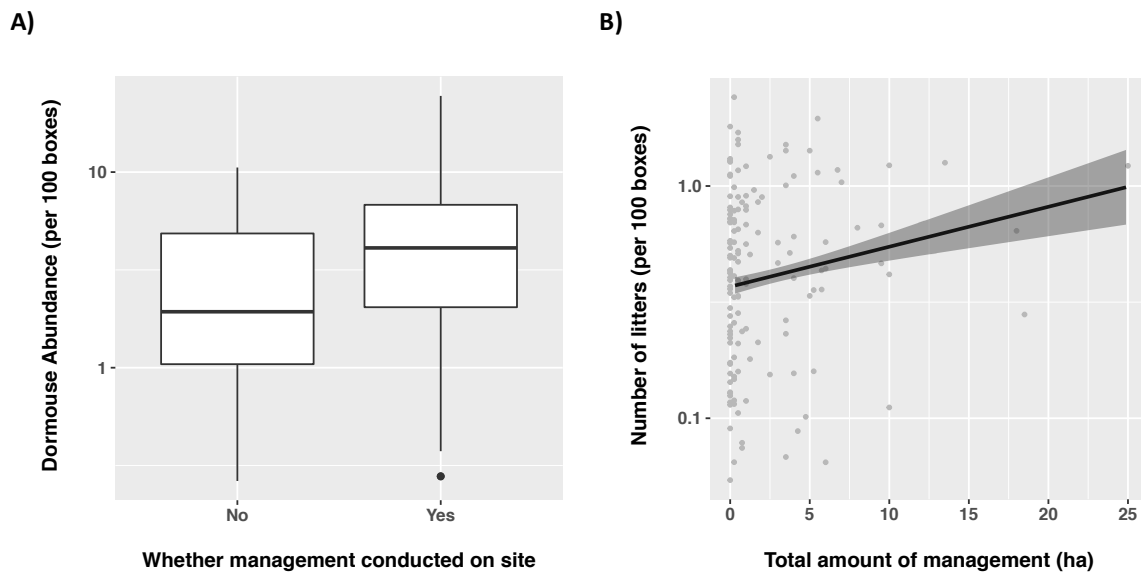


Figure 3.5. The effects of significant management variables on A) dormouse Abundance Indices B) Breeding Indices. A) the dormouse Abundance Indices of sites where management is and is not conducted; B) the effect of the total amount of management on the dormouse Breeding indices of sites (from national scale Generalised Least Squares analyses). Plots A and B are on a logarithmic scale.

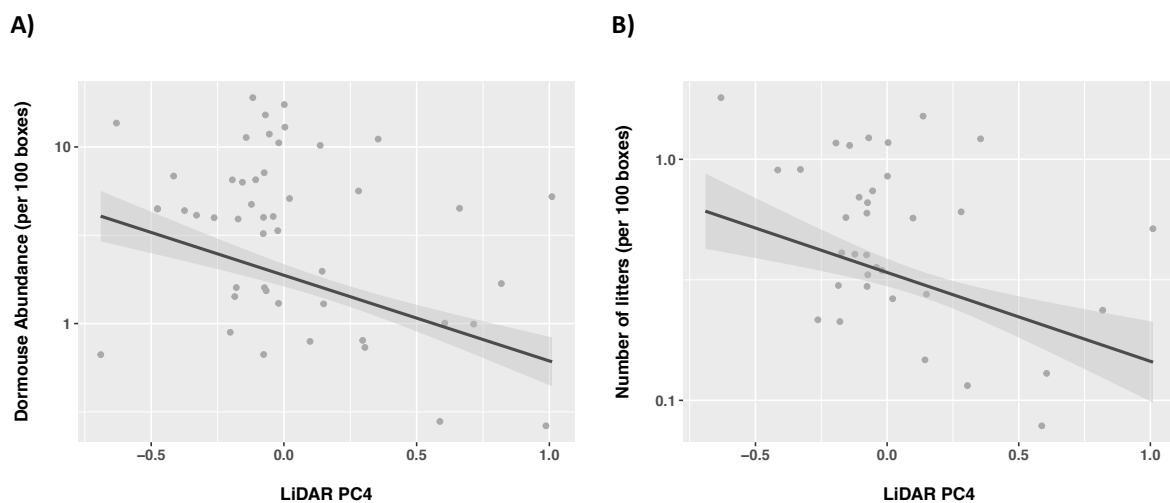


Figure 3.6. The effects of vegetation structure PC4 on A) dormouse Abundance Indices and B) Breeding Indices (from linear regression analyses). Vegetation structure is described by Principal Component Analysis of LiDAR data.

Discussion

My analysis of the records of a large sample of dormouse monitoring sites indicates that some of the explained variance in dormouse abundance and breeding was attributed to factors that, from a site management point of view, are intractable, i.e. location and regional and local climate. However, the influence of habitat and woodland management together outweighed the influence of climatic variation and, across the board, greater dormouse abundance and more breeding were associated with active woodland management. Thus, habitat and woodland improvement at a site level hold substantial potential for improving the prospects of dormouse populations in the UK. To this end, there were site features that were associated with both greater abundance and breeding of dormice, while other site attributes favoured one and not the other and so improved management might target varying requirements at different stages of the dormouse life cycle.

In relation to climate, dormice were more abundant and had more litters on sites characterised by warm and sunny springs, summers and autumns. Locally, sites with consistently cold winters also had greater dormouse abundance, highlighting the importance of consistency in cold conditions for over winter survival of dormice (Bright & Morris 1996).

In terms of habitat and the importance of specific plants, dormouse abundance was greater on sites with more honeysuckle, yew and birch. Whilst breeding was not affected by the abundance of these three species, sites with more litters, but no greater abundance, had more hazel, more willow and less sycamore. High abundance of conifers was a negative attribute for both abundance and breeding, though where conifers were mixed with broadleaf trees, this was a positive for breeding, but not abundance. In relation to landscape, dormice were more abundant and bred more on sites with more woodland in the surrounding area and more positive trends in dormouse populations were apparent in larger woodlands.

To be explicit, this study suggests that the status of dormice in the UK could best be enhanced 1) at a landscape scale by measures to increase woodland size and reduce fragmentation and 2) at a site scale by implementing active management that fostered

areas of shrub and successional habitats (Bonnet et al. 2016) trees and shrub habitats in the range of 5-10m, and favoured honeysuckle, yew, birch, hazel, willow and bramble but removed conifer and sycamore.

Dormice have been adopted as a flagship species for woodland conservation over several decades (Morris 2003). The fact that decline in dormouse populations in the U.K. is ongoing indicates that their conservation status is far from favourable and that pressures on populations continue to be significant (Goodwin et al. 2017). A better understanding, as provided here, of the large-scale effects of habitat composition and management on dormouse populations might also be used to substantiate and refine their role as an indicator species, highlighting the various pressures on woodland environments. While many species have been shown to thrive in more mature woodland, as opposed to the mid-successional stages preferred by dormice (Honnay et al. 1999, Russo et al. 2004), mature woodland in Europe has suffered from a general reduction in structural and species diversity and is often even-aged and lacking in understorey and edge vegetation (Honnay et al. 1999, Müllerová et al. 2015). This reduction in complexity, often as a result of declining frequency or intensity of management, has affected many taxa, including woodland birds (Fuller & Gill 2001, Quine et al. 2007, Calladine et al. 2017), butterflies (Davies et al. 2007, Broome et al. 2011, Fartmann et al. 2013), and other mammals (Ramírez & Simonetti 2011). Furthermore, the variation in age and structure that I have shown to be positive for dormice can also be highly valued by people (Filyushkina et al. 2017). Thus, creating better woodland habitat for dormice has the potential to increase its recreational and aesthetic value to people.

The habitats I found to be associated with favourable indices of dormouse populations have declined markedly in the UK over the last century (Hopkins & Kirby 2007, Kirby et al. 2017). At the same time, habitats associated with reduced dormouse abundance and breeding, including fragmented woodland, conifer plantation, sycamore and high broadleaf forest have markedly increased (Young et al. 2005, Hopkins & Kirby 2007). These changes in habitat and landscape character are attributable in large part to the loss of wooded habitats and declines in certain woodland management practices, notably coppice and ride and glade creation (Hopkins & Kirby 2007). Localised studies have found that woodland becomes favourable for dormice one to five years following

management (Capizzi et al. 2002, Juškaitis 2008), and within these mid-successional habitats, dormouse survival is higher and condition is better (Mortelliti et al. 2014, Sozio et al. 2016).

While changes in woodland management in Britain can be attributed to many factors, such as changes in wood markets and technological change (Quine et al. 2011), individual-level protective legislation for the hazel dormouse may also have created impediments to more favourable woodland management. The EC Habitats Directive (1992) and the UK Habitats Regulations (1994 and 2010) create a legal requirement to consider the risk to dormice, including individual animals, posed by habitat alteration. This could discourage landowners from managing their woodland, in order to mitigate the short-term risk of accidentally killing individuals or destroying breeding and resting places, and may contribute to a perception that habitats must be 'preserved' (Hull et al. 2002). Over time, this concern for individual dormice might, perhaps ironically, amount to degradation of habitat quality, leading to a general failure to comply with other legal obligations, and the overall intent, of the Habitats Directive to maintain the species' 'Favourable Conservation Status' (Epstein et al. 2016). Other European Protected Species, such as the Siberian Flying squirrel *Pteromys volans* have similarly been shown to have been ill-served by individual level-protection when conservation threats relate mainly to changes in habitat quality (Santangeli et al. 2013, Jokinen et al. 2015). A substantial majority of NDMP site monitors stated that conservation was the primary objective of their site. Counter-intuitively, the perception, if any, of the need for habitat 'preservation' might therefore be most marked on sites where dormouse conservation is a key aim.

Forest management takes many forms and the more commercial practices of larger-scale thinning and clearfell were not well represented in the sample of sites in this study. Larger-scale commercial clearfell could result in habitat loss, fragmentation and population constriction and isolation (Trout et al. 2012b, Bogdziewicz & Zwolak 2014). Caution should therefore be applied when generalizing the positive effects of management to sites with different objectives. General principles, however, can be applied to different site types (Hartley 2002, Paillet et al. 2010) including the importance of a mosaic of age-classes and favoured species.

All of these sites were in woodland and my findings in relation to habitat should therefore be interpreted in this specific context, i.e. particular features might be beneficial only when located within woodland. Dormice and many other species can thrive in mature woodland where they benefit from features such as increased numbers of tree cavities for nesting (Bright & Morris 1992). The demonstration of the importance of successional and actively managed habitat to dormice nevertheless is valid in widening the focus from ancient woodland habitat, which has been considered in some studies to be the principal habitat for dormice (Harris et al. 1995, Newman et al. 2003, Bailey 2007).

Greater abundance of specific plants was associated with greater dormouse abundance (honeysuckle, yew and birch) and more breeding (hazel and willow). These have all been shown to be important sources of food and, in some cases, nesting material for dormice (Richards et al. 1984, Juškaitis et al. 2016). Hazel and willow may be associated with increased breeding as they provide willow inflorescences and hazel buds, flowers and catkins in spring and hazel nuts in autumn (Juškaitis & Baltrūnaitė 2013). Simpson's diversity index of vegetation on sites was negatively related to breeding indices on the local level. This is a rather counter-intuitive result as dormice rely on a variety of food plants through the season, however high species diversity could represent reduced cover of preferred plants.

A key habitat feature for dormice that I was not able to measure is the understorey layer (Bright & Morris 1990, Juškaitis et al. 2013). LiDAR is usually used to detect only the canopy layer and there is currently a paucity of publicly available data on horizontal woodland structure. There are promising developments in this field however, with the introduction of new technologies such as terrestrial radar scanning (Eichhorn et al. 2017) and waveform LiDAR (Anderson et al. 2016). Further studies on the influence of understorey layers will be beneficial as the data and technology become more available.

The effect of climatic features was more pronounced in this study, relative to other work on dormouse site occupancy in continental Europe (Mortelliti et al. 2014, Becker & Encarnação 2015). This is most likely due to the greater significance of climatic variation at the latitudinal range edge of any species, which has previously been linked

to the restricted distribution of the species in Britain (Bright & Morris 1996). The main axis of climatic variation among these dormouse sites (PC1) varied regionally and comprised differences in temperature and sunshine hours, which markedly influenced dormouse abundance and breeding. The influence of temperature on dormouse distribution has similarly been reported by Bright et al. (1994). Warmer, sunnier weather aids the flowering and ripening of fruits, and extends the activity period of dormice, allowing for greater foraging opportunities (Bright 1996, Bright & Morris 1996). When controlling for regional climatic effects, I found that dormice were less abundant on sites with local climates characterized by warmer, more variable winter temperatures (PC3). This accords with such weather patterns reducing hibernation survival, and ultimately population abundance (Bright & Morris 1996). Climate projections of milder, wetter winters therefore highlight the possibility of detrimental impacts on dormouse populations in England and Wales in future (Jenkins et al. 2009)

In my previous appraisal of the volunteer-collected data from the NDMP, I found no major sampling errors intrinsic to the survey methodology (Goodwin et al. 2017). That is not to say that such citizen science surveys are without their shortcomings; data can be somewhat sporadic and tend not to be collected under rigid sampling regimes. In this analysis, I aimed to increase the reliability of my findings by only including sites surveyed for at least 5 years, which have been shown to give a reliable index of population size (Juškaitis 2006, Mills et al. 2016), and by weighting the site indices in statistical analyses, in order to take into account their accuracy. Some potential survey biases nevertheless remain, as sites might consistently be surveyed in different months or at different times of day, though it is highly unlikely that survey approaches will vary systematically between habitats. Another source of reported survey variation, and one which does vary highly within the NDMP, is the density with which nest boxes are used (Juškaitis 2005b). Although nest box density was included in models and found that it did not explain any more variation than the number of nest boxes (Appendix 2B). As plant and management data were provided by volunteers there may be some element of inaccuracy in reporting, though I used broad plant species abundance categories and very broad management classification in order to reduce any effects of inconsistency. A potential problem might persist if dormouse detection probability varied between habitats. It has been suggested that box use by dormice decreases in summer as shrubs, particularly brambles, grow to densities that provide

good nesting habitat for dormice (Verbeylen 2012). This potential detection bias, which would decrease apparent abundance relative to actual abundance, was in fact associated with higher dormouse abundance, breeding and more positive trends in models. Shrub, honeysuckle and bramble, which are all preferred dormouse nesting habitats (Hurrell & McIntosh 1984, Bright & Morris 1992, Berg & Berg 1998), had positive effects on abundance, breeding or trend. Dormouse use of boxes may also be lower in woodland with a high abundance of natural tree cavities (Bright & Morris 1991, 1992). However, plantation conifers tend to have very few natural cavities (Bunnell 2013) and thus the lower dormouse Abundance Indices observed in this habitat are unlikely to be arise from this bias. The association between reduced breeding and higher abundance of sycamore, however, might indeed be confounded by this detection bias. Higher temperatures have also been found to reduce the probability of nest box use (Mortelliti et al. 2014) but again I found higher abundances associated with higher temperatures. Consequently, rather than producing spurious habitat effects, any detection biases might mean estimates of the effects of climate and habitat factors may be underestimates.

Despite the high profile of the dormouse in Britain and its adoption as a flagship species for woodland conservation, populations have continued to decline over the last 25 years (Goodwin et al. 2017). The attributes of sites exhibiting favourable population status coincide with woodland habitats that have been in decline in Britain over the last century. Changes in management practices have been integral to this decline and I have illustrated that management is an important determinant of dormouse status. Further, large-scale evaluation of the effects in practice of variation in the timing, frequency and intensity of management would be beneficial in refining conservation recommendations and optimizing these alongside the wider objectives of woodland management. Further studies on the demographic drivers, such as the movement and survival of individuals between habitats, would also help to build a more comprehensive picture of effective management (Harris et al. 2015). A long-term effort to foster woodland protection at a landscape scale with immediate implementation of more active woodland management at a site scale is required to counter dormouse population declines and to aid their recovery as an important feature of woodland biodiversity.

Chapter 4

The effects of woodland composition and food availability on the trophic niche of the hazel dormouse *Muscardinus avellanarius*

Chapter 4: The effects of woodland composition and food availability on the trophic niche of the hazel dormouse *Muscardinus avellanarius*

Abstract

The scale at which variations in food availability affect the foraging habits of individual animals can determine how spatial variability in habitat might in turn affect populations. The trophic ecology of a species, in relation to spatial and temporal variation in resource availability, can therefore have important implications for the management of its habitats and its conservation.

I compared the effects of dormouse intrinsic traits (e.g. sex and weight) and extrinsic resource availabilities on the trophic characteristics of dormice individuals and populations. These were determined by stable isotope analysis of dormouse hair tissue and of their putative food items in different woodland habitats in spring and summer/autumn.

The trophic level of individual dormice was related to the abundance of invertebrates in the surrounding habitat and in the woodland as a whole. Dormice therefore appear to exploit invertebrates in proportion to their availability. A detailed assessment of dietary composition, however, suggests that the proportions of invertebrates and tree seeds and flowers in the diet are also affected by the abundance of food plants in the local habitat. Dormouse populations exhibit a larger trophic niche in summer than in spring, which is driven mostly by the consumption of foods derived from a wider variety of tree and shrub species. I did not find any consequences of isotope signatures or food availability for the physiological condition of individuals or the status of populations. This may be because, on the sites I studied, dormice can adapt to different food availabilities without detrimental individual and population effects. Dormice are opportunistic feeders, making use of abundant food resources at a local scale. Habitat conservation for dormice, therefore, should ensure an even supply of food plants across the wood and abundant invertebrate populations.

Introduction

A significant component of a species' habitat requirements is a supply of adequate food resources in a spatial and temporal distribution amenable to its foraging strategy (Polis et al. 1997). An understanding of diet and habitat use can therefore enable more effective conservation measures to be implemented through improved provision of these resources (Newsome et al. 2010, 2015, Lyngdoh et al. 2014). Clearly, however, diet composition is dynamic and depends on the intrinsic characteristics of the animal and extrinsic variation in environment, such as habitat and food availability (Newsome et al. 2010, Ben-David & Flaherty 2012).

Diet composition of individuals, both within and between populations, can vary spatially – e.g. between habitat types or microclimates (Anderson et al. 2009, Mustamäki et al. 2013), demographically – e.g. between age classes or sexes (Inger et al. 2006, Blanco-Fontao et al. 2013), and temporally – e.g. between seasons (Jaeger et al. 2010, Codron et al. 2011, 2013).

For instance, seasonal shifts in resource use are relatively common in temperate environments that experience seasonal variation in the abundance of plants, including their buds, flowers and seeds, and invertebrates (Inger & Bearhop 2008). The consistency of a population's trophic niche through time and across space can determine the seasonal adaptability of animals to the availability of resources (Inger et al. 2006, Phillips & Eldridge 2006). Similarly, an understanding of the effects of habitat on diet composition can allow predictions of the likely effects of differences or changes in resource availability (van der Putten et al. 2004, Cucherousset et al. 2011). The scale at which variation in the availability of food impacts the diet of a species might also provide an indication of its requirements for the spatial distribution of resources (Vander Zanden et al. 2000).

The availability of food sources and the feeding habits of individuals can have ramifications for their condition, breeding and survival (Anderson et al. 2009, Cucherousset et al. 2011, Vander Zanden et al. 2014). If these differences in resource availability or feeding strategy affect many individuals in a population, they can, in turn, impact population rates of recruitment, dispersal and abundance (Ben-David &

Flaherty 2012). Therefore, an understanding of the trophic habits of individuals and populations can provide insight into interactions with its habitats and thus the relative value of habitat conservation measures.

Stable Isotope Analysis (SIA) has been widely employed in the characterisation of animal diets, movement and foraging ecology and provides a means of quantifying and comparing the trophic characteristics of individuals and populations (Kelly 2000, Crawford et al. 2008). SIA methods exploit the fact that ratios of heavy to light stable isotopes in a consumer's tissues reflect those in their diet and provide a powerful means of characterising diet composition and variation (De Niro & Epstein 1978, Inger & Bearhop 2008). SIA can additionally capture an animal's general trophic characteristics – such as the trophic level at which it feeds – by quantifying the differences between nitrogen isotopic signatures and those of the surrounding habitat (Post 2002, McCutchan et al. 2003).

Niche characterisation through stable isotopes can be less susceptible to the biases present in some, more conventional, dietary analysis, such as the differences in digestibility of food sources in faecal analysis (Hobson & Clark 1992). It also tends to reflect longer timeframes than the 'snapshots' provided by stomach or faecal analysis and so can provide a more robust representation of general feeding behaviour (Araújo et al. 2007). This ability of stable isotope signatures to generalise over longer timeframes enables quantification of the trophic niches of populations (Fink et al. 2012, Newsome et al. 2012). Various methods to accurately characterise trophic features of populations have emerged. Metrics developed by Layman et al. (2007, 2011) define a population's isotopic position, niche size, and the distribution of individual stable isotope signatures within a population. These metrics can then be compared between populations in different seasons and between habitat and resource settings, in order to determine the relationships between populations and their habitats across time (Crawford et al. 2008, Inger & Bearhop 2008).

The hazel dormouse *Muscardinus avellanarius* is a small arboreal rodent that is protected under Annex IV of the EU Habitats Directive (1992). It is widespread across Europe, but in areas to the north of its range it is in decline (Hutterer et al. 2016). In the UK, recent analysis of a national citizen science monitoring scheme has revealed

population declines of 72% (95% confidence intervals 62 - 79%) from 1993 to 2014 (Goodwin et al. 2017). Population declines merit a IUCN Red List categorisation of dormice in the UK as 'Vulnerable', and possibly 'Endangered' (Goodwin et al. 2017). It is important, therefore, to gain a further understanding of the species' ecology in areas where populations are in decline.

The status of hazel dormouse populations is partly determined by quality and configuration of their habitat (Chapter 3, Mortelliti et al. 2014, Sozio et al. 2016). While some elements of habitat, such as the proportion of conifer, are related to differences in both abundance and breeding, other habitat variables affect abundance and breeding differently. Such variation will be partly attributable to the requirements for, and value of, different food resources at different points of the season (Inger et al. 2006, Anderson et al. 2009). Hazel dormice require a succession of plant and invertebrate food resources throughout the period in which they are active (Richards et al. 1984, Juškaitis 2007b). The identity of tree and invertebrate species selected by dormice has been shown to vary between different habitats (Richards et al. 1984, Sara & Sara 2007, Juškaitis & Baltrūnaitė 2013), suggesting that, far from being specialist feeders, dormice are reasonably adaptable in their selection of food items (Juškaitis 2007b). It has also been suggested that dormice feed at different trophic levels depending on seasonal phenological change and the abundance of alternate resources (Eden & Eden 2001, Juškaitis 2007b). Of different invertebrate guilds, there is the most evidence that dormice consume adult and larval Lepidoptera, and aphids (Richards et al. 1984, Juškaitis & Baltrūnaitė 2013, Chanin et al. 2015). Invertebrate consumption may be highest in spring when plant food is less abundant (Chanin et al. 2015), after which dormice may progress to eating soft and then hard mast as it becomes available (Richards et al. 1984, Juškaitis & Baltrūnaitė 2013).

In this study, I examined the effect of dormouse traits (sex, weight, state of torpor and age class) and of habitat variation (the abundance of different food-types in the surrounding habitat), on the diet of hazel dormouse individuals and populations. In doing so, I wanted to investigate whether dietary variation could be attributed more to intrinsic or extrinsic factors, or a combination of both. I investigated the effects of seasonal local resource availability on the trophic signature of individuals within woodlands, and the effect of site-level food availability on trophic characteristics of

populations. I then assessed whether habitat or trophic signature had any ramifications for individual condition or population status. I also conducted a comprehensive dietary assessment for the dormouse population of one high-quality woodland habitat across two seasons. Through this assessment of the trophic responses of dormice to their habitat, I aim to gain a better understanding of the effects of food resource configuration within woodlands. This knowledge can in turn inform the conservation of dormice through habitat improvement.

Methods

Sample collection and processing

I sampled dormice at 20 study sites located across the South and Midlands of England, and Wales, in a range of habitat types from hazel coppice to mixed conifer and broadleaf forest. Of these, 12 sites, where adequate sampling was conducted, were included in analyses (Fig. 4.1; Table 4.1). Dormice were surveyed using dormouse nest boxes on these 12 sites in the late spring and early summer (May or June; referred to throughout as spring sampling for simplicity), and on 6 sites in the autumn (September or October) of 2015. Late spring and autumn sampling were chosen as I used dormouse hair to sample stable isotope signatures of dormice, and most studies of the moult of hazel dormice identify a moulting period in spring and a second in late summer (Lozan 1970, Homolka 1978, Juškaitis & Büchner 2013). Samples collected in autumn will therefore comprise hair grown in the summer and reflect summer diet, whereas hair sampled in May or June will have grown over spring and reflect spring diet.

Hair samples were plucked using tweezers from the upper left hind leg of each animal that weighed over 10g, as all juvenile dormice over this weight would be feeding independently from their mother. Each animal's sex, age class (adult or juvenile), weight, and state of torpor (active or torpid) were recorded and animals were then returned to nest boxes. All work was conducted under license from Natural England and with the approval of the University of Exeter Animal Welfare and Ethical Review Board.

In order to assess the relationship of the trophic characteristics of a population to its status, time-independent, site-level indices of dormouse abundance, breeding and trend on sites were calculated over a period of monitoring of at least 5 years from 1993 to 2017. Following Goodwin et al. (2017), indices were derived through models fitted to counts of dormice or breeding events, with explanatory terms for year and site, and an offset for number of boxes used, to control for survey effort (Appendix 2B).

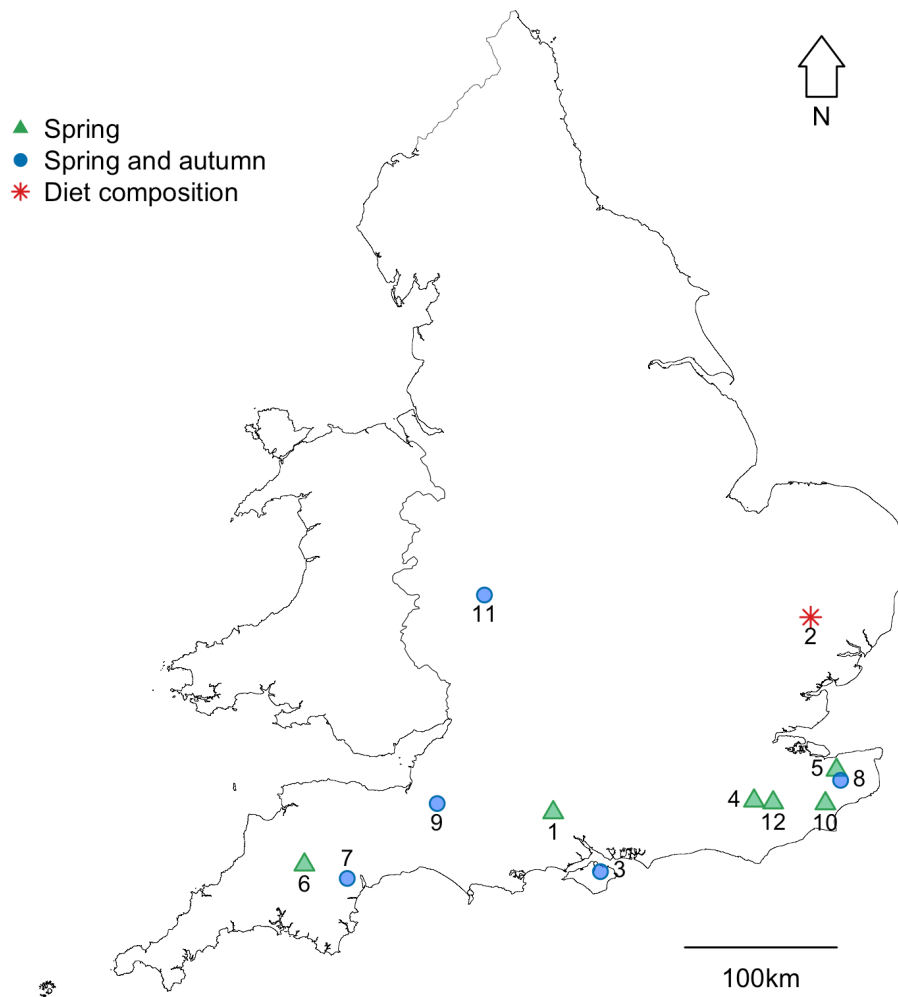


Figure 4.1. Locations of the 12 sites in the UK where dormice were sampled for stable isotope analysis of their diets, and site baseline isotope signatures established. Sites are labeled with their numbered ID (see Table 4.1). Sites sampled in spring 2015 are shown as green triangles and sites sampled in both spring and autumn 2015 are blue circles. Bradfield Woods, for which dormice were sampled in spring and autumn 2015, and for which diet composition was assessed in detail, is marked as a red star. National boundaries are also shown.

Table 4.1. The number of dormice sampled and used in population and individual analyses in spring and autumn on each site. The three sites shown in red are used in the within-site comparative analysis of population trophic niche in spring and autumn using SIBER Bayesian ellipse estimation.

Site ID	UK region	Grid ref	County	No. dormouse samples in spring		No. dormouse samples in autumn	
				<i>Ind. analysis</i>	<i>Pop. analysis</i>	<i>Ind. analysis</i>	<i>Pop. analysis</i>
1	South-West	SU23	Wiltshire	5	-	-	-
2	East	TL96	Suffolk	10	10	18	24
3	South-East	SZ59	Isle of Wight	7	14	4	14
4	South-East	TQ64	Kent	10	12	-	-
5	South-East	TR16	Kent	5	-	-	-
6	South-West	SX69	Devon	12	12	-	-
7	South-West	SX99	Devon	16	17	11	12
8	South-East	TR15	Kent	10	10	-	-
9	South-West	ST53	Somerset	6	11	-	-
10	South-East	TR03	Kent	7	-	-	-
11	West-Midlands	SO87	Worcestershire	4	-	10	12
12	South-East	TQ74	Kent	8	-	-	-

Food availability

In order to ascertain the local availability of plant and invertebrate food, surveys were undertaken along four 50m transects of 2m width at North, South, East and West directions from each nest box in which a dormouse had been sampled. A distance of 50m approximates the average maximum nightly distances travelled from a nest site by hazel dormice (Bright & Morris 1992, Juškaitis 1997, Chapter 5). All individual trees and plants over 1m in height found within the transect strip were recorded. A sample of all potential food sources encountered on each transect was gathered. Samples were collected from all plant species that had been identified from the literature as being potentially important in dormouse diet (Richards et al. 1984, Bright & Morris 1993, Juškaitis 2007b, Sara & Sara 2007, Juškaitis & Baltrūnaitė 2013, Juškaitis et al. 2016).

As spring hair samples represent early spring diet and autumn hair samples represent summer diet, there is a potential mismatch between the availability of foods when hair is grown and when food samples were collected. Within a single woodland, however, there are variations in light and warmth which means that plants of the same species come into flower and fruit at different times in different areas (Chazdon & Pearcy 1991, Chen et al. 1999). This means that flowers and fruits that were available at the time of hair growth are likely to be available in some areas of the woodland when samples were collected.

The proportion of the plants recorded that were also dormouse food plants was used as a measure of the availability of plant food in the surrounding area. This proportional measure is more representative of the spatial coverage of food plants in the surrounding area, and therefore somewhat reduces the confounding influence of plant density. For instance, large stems will be under-recorded compared to extent of spatial coverage in the canopy, and small stems will be much more highly recorded compared to spatial coverage. However, the proportion of food plants correlates strongly with their total number (Spearman's Rank correlation test $R_s = 0.82$, $p < 0.001$), and is therefore still related to absolute abundance of food resources. The Simpsons diversity index of vegetation in the area surrounding the nest box was also calculated.

Invertebrate samples were taken via standardised tree beating at five points around each occupied nest box: one sample adjacent to the nest box and one at the end of each transect. Samples were frozen at -80°C before invertebrates were identified to Order and counted. Invertebrate counts used in analysis were the numbers of herbivorous and omnivorous invertebrates (at the Order level) found in the habitat surrounding each dormouse's nest box. The Simpson's diversity index of invertebrate Orders in the area surrounding the nest box was also calculated (Simpson 1949).

An index of total food availability was also calculated as the sum of the centred (by subtracting the mean of the sample) and scaled (by dividing by the sample standard deviation) proportion of food plants and invertebrate abundance.

Stable isotope analysis

To facilitate comparison of dormouse stable isotope signatures among sites, I established a common baseline for each site of isotope signatures of plants. Baseline isotope values were needed for each site so that the offset of dormice isotopes and thus their local trophic level could be estimated (Post 2002). Flowers were used as baseline samples for sites, as these have been found to be the main dormouse food source in Spring (Juškaitis & Baltrūnaitė 2013), and were present on all sites. Flowers included were: blackberry *Rubus fruticosus*, black bryony *Tamus communis*, dogwood *Cornus sanguinea*, gorse *Ulex europaeus*, hawthorn *Crataegus monogyna*, honeysuckle *Lonicera periclymenum*, rowan *Sorbus aucuparia* and wayfaring tree *Viburnum lantana*. At all sites, 5 - 15 flower samples (mean 7.7 ± 0.7 SE) were analysed. In total 104 flower baseline samples were analysed: 12 samples were outside the expected range of plant isotopic values or further than 2.5 standard deviations away from the sample mean and so considered to be the result of experimental error and excluded (Kohn 2010). The mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for baseline samples for each site were calculated in order to form one baseline value for each element for each site.

In order to test for consistency between individuals, duplicate hair samples (2 separate plucked samples from the same area) were analysed where possible (there were 75 occasions when two samples were taken from dormice in the same sampling event).

The repeatability of these duplicate samples was also investigated using linear mixed effects models in the R package rptR (Stoffel et al., 2017). These analyse the proportion of variation in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ which is attributable to the identity of the individual from which the sample was taken. 95% Confidence Intervals are generated through bootstrapping the data and running the model 1000 times.

In addition to comparison among sites, I constructed a detailed assessment of the diet composition of dormice at one site (Bradfield Woods) in Suffolk (Parnell et al. 2010, Codron et al. 2012). For this site, stable isotope analysis of all potential food sources collected from the area around an occupied nest box was conducted to reliably quantify the variation between sources (Phillips 2012). For parts of flowers (anthers, stems, petals) and fruits (stones, seeds, outer flesh), each constituent part was analysed separately and, when shown to be similar, were subsequently grouped. I then grouped species-level food sources into six food groups (Appendix 5) to capture isotopically and biologically-meaningful variation (Phillips & Gregg 2001). The six food groups were: Hazel, Honeysuckle (Juškaitis et al. 2016, Juškaitis & Baltrūnaitė 2013, Richards et al. 1984); Lepidoptera (the main invertebrate food source proposed by other studies; Chanin et al. (2015), Juškaitis et al. (2016)); Omnivorous Invertebrate Orders (representing other potential invertebrate food sources; Juškaitis (2007), Richards et al. (1984)); Shrubs (flowers, vegetative parts and early berries and catkins in spring and seeds, nuts, berries and late flowers in autumn) and Trees (oak and willow flowers in spring and acorns and ash seeds in autumn). These were broad groupings as there were large overlaps between species within food groups; and my hypotheses were focused on the general foraging niche of dormice in different seasons (Appendix 5; Phillips & Gregg 2001, 2003, Phillips et al. 2005).

Processing of all plant and invertebrate samples prior to analysis involved drying the samples for 24 hours in a freeze-drier and homogenising with a mortar and pestle. Between 0.4 and 0.8mg of dormouse hair or around 1mg of dried and homogenised plant or invertebrate sample was weighed into tin capsules. The masses of the stable isotopes of carbon and nitrogen were then quantified using elemental analysis-isotope ratio mass spectrometry. Stable isotope ratios were expressed as δ values in ‰ (parts per mil), the ratio of heavy to light isotope relative to the isotopic ratios of an international standard for each element: the Vienna Pee Dee Belemnite (VPDB) for

$\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$. Estimated precision was $\pm 0.1\text{‰}$ based on standards run within sample batches.

Statistical analysis

R version 3.4.2 (R Core Team 2017) was used for all analyses.

Before any statistical analysis, dormouse $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were adjusted in relation to the isotopic baseline for each site in order to allow comparison of values between sites. This was done by first subtracting the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic baselines for each site from the mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic baselines for all sites. For each element, this generated the distance of the isotopic baseline of each site from the mean of all sites. This distance was then subtracted from the value for each dormouse on that site to give adjusted $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values, scaling dormouse isotopic signatures by their relative position from the isotopic baseline of their woodland site (Post 2002).

Individual analysis

Only sites with samples from more than five dormice were used in isotopic analysis of individuals, in order to ensure robust characterisation of the isotopic values of dormice on particular sites.

To analyse between-individual variation in the adjusted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of dormice, linear mixed effect models with a Gaussian error structure and a random effect for site were used. Explanatory demographic variables were state of torpor, weight, age class and sex, and food availability variables were the proportion of food plants in the surrounding woodland and Simpson's diversity index of vegetation, the invertebrate abundance count and the Simpson's diversity index of invertebrate Orders.

All model selection was done via an information theoretic approach using ranked comparison of AICc values and model averaging over the top model set (Whittingham et al. 2006, Lindberg et al. 2015) using the MuMIn package (Bartoń 2017). All models included in the top model set were within 2 ΔAICc of the top model (Burnham &

Anderson 2002). Conditional model averaging was performed as there were a limited number of specific explanatory variables regarding resource availability (Grueber et al. 2011). For population analysis, where models had a small number of explanatory variables, backwards stepwise selection was also performed for validation. Correlations between explanatory variables were investigated using Spearman's Rank correlation tests prior to individual level analyses. If explanatory variables were correlated above 0.5 R_s , they were precluded from appearing together in models, and the best predictor would appear in higher ranked models (Appendix 1).

A generalised linear mixed model with a binomial error structure and a logit link function was used to look at the effect of dormouse traits (sex, weight and age class) and environmental variables (availability and diversity of plant and invertebrate food and total food availability) on the probability that adult animals were in torpor. A linear mixed effect model with a Gaussian error structure was then used to examine the effect of the same explanatory variables (replacing weight with torpor) on the weight of adult animals. Weights were log-transformed to normalise their distribution.

Dormouse diet composition

Bayesian stable isotope mixing models (SIMMs) were used to assess the probability of contributions of the six food groups to dormouse diet, using the R package SIMMR at a population level and the package SIMMR-solo for individual dormice (Parnell et al. 2010). The enrichment of heavy isotopes arising from the ingestion and transfer of carbon and nitrogen to consumer (dormouse) hair was accounted for by calculating Trophic Discrimination Factors (TDFs). This was done through the R package SIDER (Healy et al. 2017) which uses phylogenetic methods to estimate TDFs and has been shown to improve the fit of Bayesian stable isotope mixing models (Swan et al. In review).

The estimated proportions of food sources for each individual were then compared to food availability (proportion of food plants and invertebrate abundance) using Spearman's Rank correlation test (R_s). The relationship between the likelihood of torpor and estimated mean dietary proportions for each dormouse was investigated using a generalised linear model with a binomial error structure and a logit link

function. The effect of the same dietary proportions on the weight of dormice was investigated using a linear regression model with Gaussian error structure.

Population analysis

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and five ellipse-based metrics (Layman et al. 2007, 2011) were used to characterise the isospace occupied by dormouse populations sampled in spring and autumn. This was done using R package SIBER (Jackson et al. 2011) for all site visits that had at least 10 individual dormouse isotope signatures. At least 10 dormice were sampled on 7 site visits in spring, and 4 site visits in autumn, resulting in a total of 11 site visits with adequate sample sizes to conduct population-level analyses (Table 4.1). Population isotopic ellipse-based metrics used were: Standard Ellipse Area corrected for small sample sizes (SEAc); Range of carbon values (C range); Range of nitrogen values (N range); Nearest-neighbor distance (NND); and mean distance to centroid (CD) (Layman et al. 2007, 2011). The effect of site and season on the isospace metrics ($n = 11$) was investigated with linear regression models. For Spring samples, the effects of the mean proportion of food plants and mean invertebrate abundance around nest boxes on the isospace metrics of dormouse populations ($n = 7$) was investigated in separate linear regression models with Gaussian error structures. Bonferroni correction was used to correct for multiple hypothesis testing, as the effects of the availability of plants and invertebrates were investigated in separate models. Some isospace metrics (SEAc, C range, N range) were log-transformed to normalise their distribution.

For sites that were visited in both spring and autumn and on which more than ten dormice were sampled in each visit, comparisons could be made between the niche space occupied across seasons within sites (Table 4.1). Means and credible intervals of Standard Ellipse Areas were calculated via Bayesian methods (Jackson et al. 2011). Differences between Bayesian estimates of SEAc for the two different seasons on each site was calculated via the mean (\pm 95% CIs) difference between 1000 draws from posterior estimates of SEAc in each season (Jackson et al. 2011). Overlaps between the ellipses in each season on each site was calculated in a similar way, by estimating the overlap between the 2 ellipses in 1000 draws from posterior estimates.

This was then converted to the mean (\pm 95% CIs) percentage overlap of 1000 draws from posterior estimates of ellipses in each season (Jackson et al. 2011).

The relationship between dormouse population status (Abundance, Breeding and Trend Indices) and each measure of that populations' isotopic niche (mean N, mean C, SEAc, C range, N range, CD and NND) was investigated in single explanatory variable analysis. These tests were then corrected for multiple hypothesis testing via Bonferroni correction.

Results

Individual trophic characteristics

Duplicate samples taken from individual dormice at the same time showed more consistency compared to samples taken from different dormice on the same site. The mean difference between $\delta^{15}\text{N}$ of duplicate samples from the same individual was 0.35‰ (± 0.04 SE), compared to a difference of 1.11‰ (± 0.10 SE) between individuals on the same site. The mean difference between $\delta^{13}\text{C}$ of duplicate samples from the same individual was 0.21‰ (± 0.05 SE), compared to a difference of 0.64‰ (± 0.05 SE) between individuals on the same site. Measures taken at the same time from the same dormouse showed high repeatability as assessed through linear mixed effects models: baseline-adjusted $\delta^{15}\text{N}$ values had a repeatability of 0.91 (0.84, 0.94 95% CIs), and $\delta^{13}\text{C}$ values had a repeatability of 0.87 (0.78, 0.92 95% CIs).

150 dormouse isotopic signatures from 12 sites were analysed (99 signatures from spring and 51 from autumn). There were no significant differences between the $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values of dormice with respect to sex or age class, weight, state of torpor or season. There were significant effects of invertebrate abundance on dormouse isotope signatures; dormice with more invertebrates in the area surrounding their nest box had higher $\delta^{15}\text{N}$ signatures (an increase of $2.23 \delta^{15}\text{N}$ for every 100 invertebrates (0.44, 4.01 95% CIs); RI = 1; Fig. 4.2) and lower $\delta^{13}\text{C}$ values (a decrease of $-1.55 \delta^{13}\text{C}$ for every 100 invertebrates (-2.73, -0.36 95% CIs); RI = 1). Dormice with a higher Simpson's diversity of vegetation in the surrounding areas also had higher $\delta^{15}\text{N}$ signatures (Effect size = 2.54 (0.34, 4.73 95% CIs); RI = 1). The proportion of food plants and the diversity of invertebrate Orders in the habitat surrounding the nest box, however, had no significant effects on the isotopic signatures of dormice.

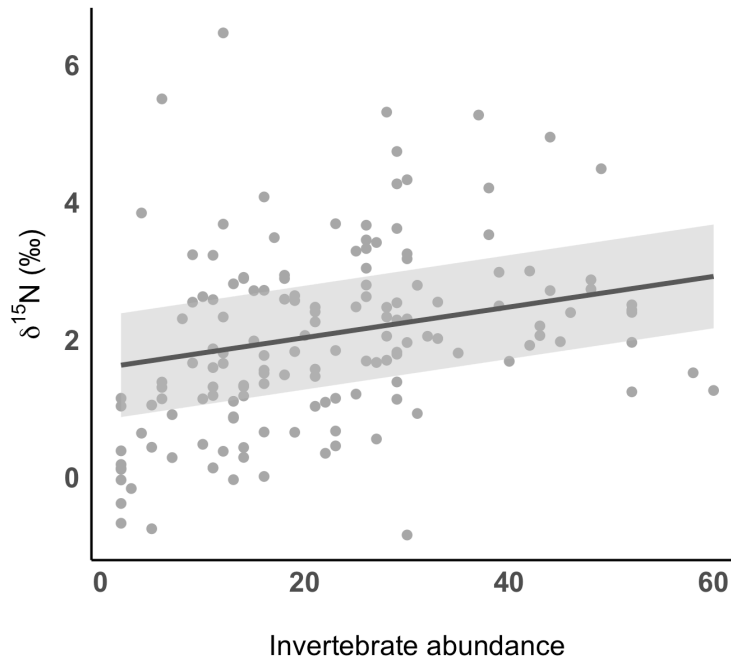


Figure 4.2. Relationship between $\delta^{15}\text{N}$ of dormouse hair samples and the abundance of invertebrates. Invertebrates were sampled at 5 points surrounding the nest box (one point 5m from the nest box; 4 points 50m from nest box), and the invertebrates collected from all these points were summed for each nest box. $\delta^{15}\text{N}$ signatures were standardized by adjusting by the isotopic baselines of sites.

Adult dormice were more likely to be in torpor in spring ($n = 132$, Effect size = 3.76 (-1.42, -6.11 95% CIs); RI = 1) and when they weighed more ($n = 132$, Effect size = 0.26 (-0.03, -0.49 95% CIs); RI = 1). There were no significant effects of sex or food availability on the state of torpor. Adult dormice were significantly heavier in autumn ($n = 132$, Effect size = 0.16 (0.11, 0.21 95% CIs); RI = 1) and males were significantly heavier than females ($n = 132$, Effect size = 0.09 (0.05, 0.13 95% CIs); RI = 1). There were no significant effects of food availability on weight.

Diet composition

For Bradfield Woods in Suffolk in spring, 104 plant and 57 invertebrate samples were analysed and 158 plant and 59 invertebrate samples for autumn. This represented an average of 6.4 (± 0.6 SE) plant and 14.6 (± 1.6 SE) invertebrate samples for each nest box in which dormice were captured and sampled.

Tree flowers contributed more to spring diet than other food groups, making up an estimated 35% of dormouse diets (10 - 56% 95% CIs; Fig. 4.3). Tree seeds were also important in summer diet, contributing 27% of the diet (13 - 41% 95% CIs) of dormice sampled in autumn, as were honeysuckle flowers and berries, which formed 26% of the diet (11 - 41% 95% CIs; Fig. 4.3). The differences in these two groups between the two seasons were the most pronounced: 73% of the distribution of estimates of tree consumption in spring were larger than those for summer diet; and 74% of the distribution of estimates of honeysuckle consumption in summer were larger than those in spring.

The estimated contributions of each food group to the diets of dormice across both seasons were related to food availability in the area around the nest box occupied by the individual. The mean estimated proportion of honeysuckle in the diet was positively related to the proportional availability of food-plants in the surrounding habitat ($R_s = 0.44$, $p = 0.010$). The contributions of Lepidoptera and of omnivorous invertebrates to dormouse diets were both significantly negatively related to the proportion of food-plants in the surrounding area ($R_s = -0.41$, $p = 0.017$; $R_s = -0.44$, $p = 0.009$, respectively).

The weight and probability of torpor of individual dormice were not significantly related to their diet composition.

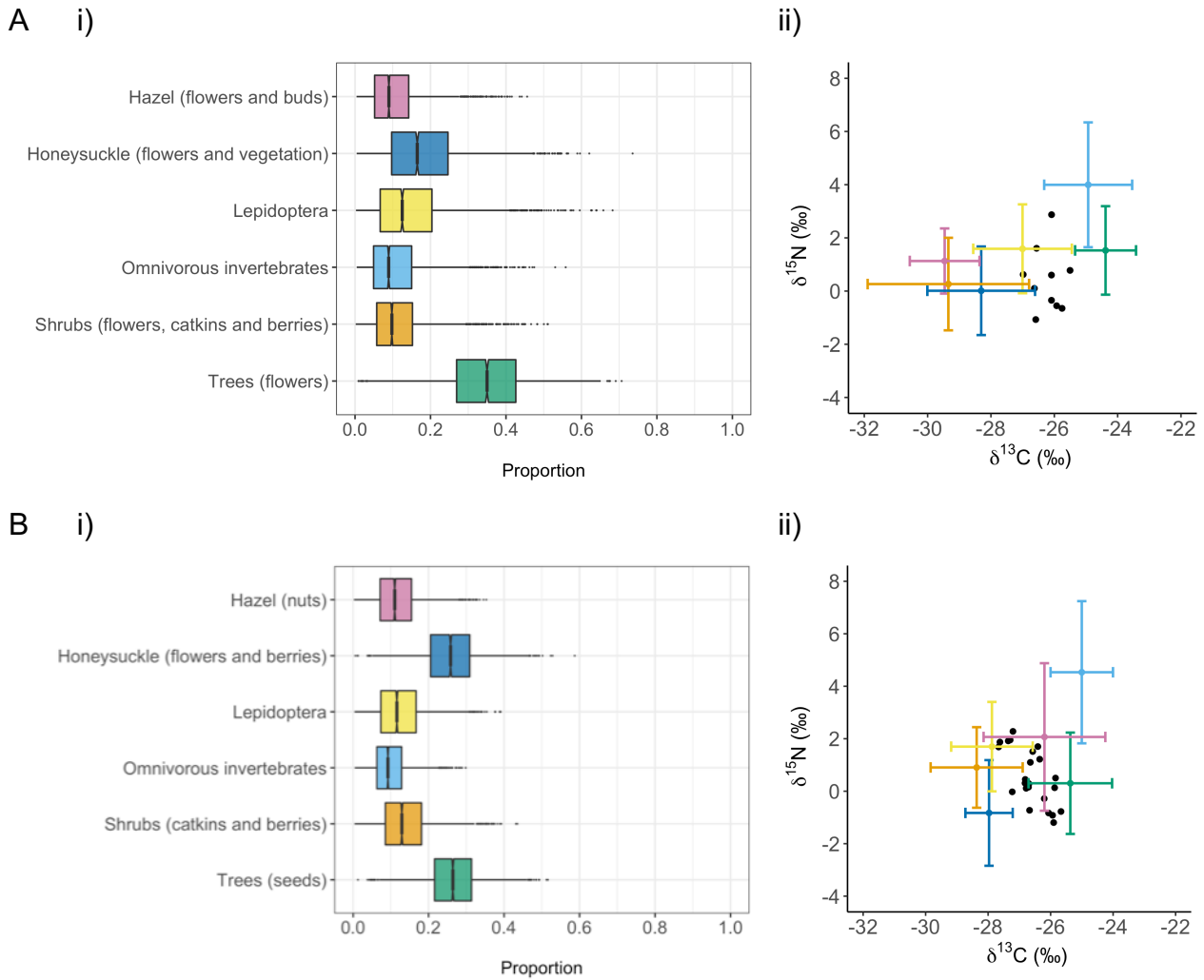


Figure 4.3. Isotopic signatures and estimated dietary contributions of putative food sources to dormouse diet from samples taken in spring and autumn. (i) Estimates of the proportional contribution of each food group to the diets of sampled dormice, as calculated by Bayesian mixing models in SIMMR for samples from Bradfield Woods taken in A) spring and B) autumn. (ii) The mean \pm standard deviation error bars of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for the food groups and the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for the sampled dormice (black points) for Bradfield Woods and taken in A) spring and B) autumn. In (ii), trophic discrimination factors have been applied to adjust dormice isotopic position downwards for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Population trophic characteristics

When corrected for multiple hypothesis testing, the mean $\delta^{15}\text{N}$ values of dormice in spring were higher on sites with greater abundances of invertebrates (Effect size = 0.05 (0.01, 0.09 95% CIs); RI = 0.54). The mean $\delta^{13}\text{C}$ values of dormice populations in spring were not related to measures of food availability.

The extent of dormouse trophic niches (SEAcS), was significantly greater for populations sampled in autumn than in spring (Effect size = 0.94 (0.19, 1.69 95% CIs); RI = 1; Fig. 4.4A). This difference appeared to be most attributable to the increased ranges in $\delta^{13}\text{C}$ values, which were also greater for dormice sampled in autumn (Effect size = 0.61 (0.22, 1.00 95% CIs); RI = 1; Fig. 4.4B). There were no differences in any of the other Layman's metrics (SEAc, C range, N range, NND and CD) between sites, or in relation to mean proportion of food plants or mean numbers of invertebrates sampled in spring.

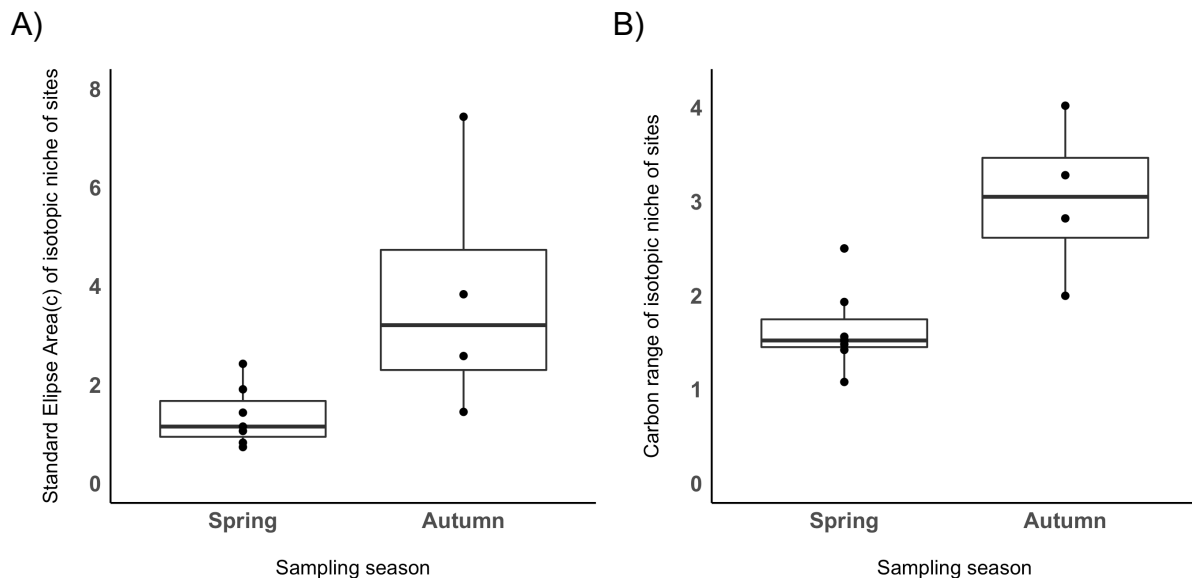


Figure 4.4. A) The trophic niche area (Standard Ellipse Area (c)) and B) Carbon ranges of dormouse populations of sites sampled in spring and autumn. Boxplots show the median (central line) and the 25th and 75th percentiles (box). Points showing the values for single sites are included.

For the three sites that were visited in both spring and autumn and on which over 10 dormice were sampled in each visit, Bayesian estimates of SEAcS were larger for populations sampled in autumn than in spring (Fig. 4.5). SEAcS in spring and autumn were different in over 95% of the comparisons between probability distributions on 2 of 3 sites. Mean differences in the estimates of SEAcS in spring and autumn of 4.99 (1.33 - 10.33 95% CIs) and 1.58 (0.33 - 3.59 95% CIs); the third site had a non-significant size difference of 0.69 (-0.31 - 1.65 95% CIs) (Fig. 4.5B).

Before Bonferroni correction, the isotopic range of Carbon values was related to reduced breeding in dormouse populations (Effect size = -0.60 (-1.10, -0.11 95% CIs); RI = 1). When corrected for multiple hypothesis testing, no measures of population status (Abundance, Breeding and Trend Indices) on sites were related to any measures of isotopic niche (mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ or LMs).

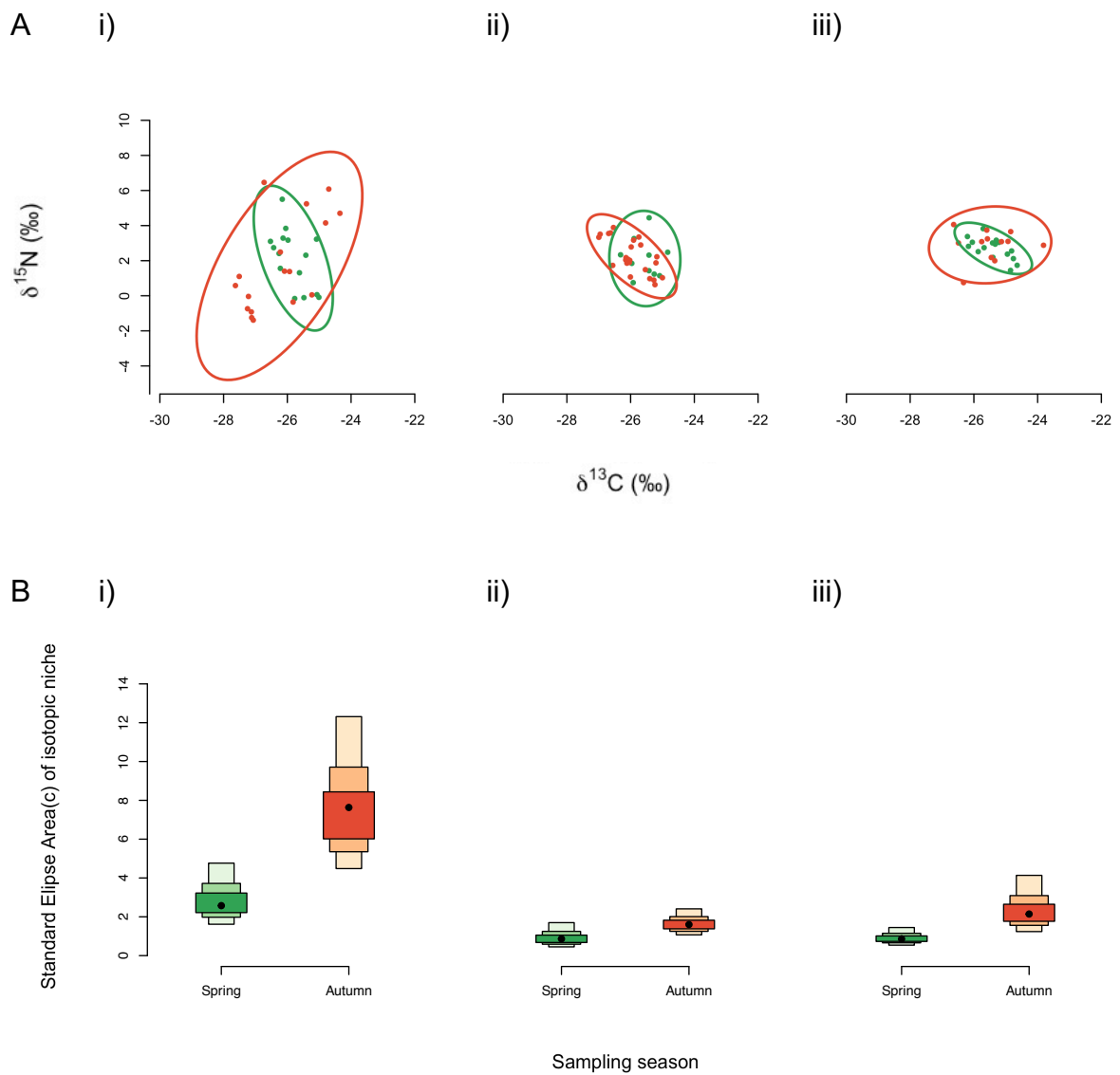


Figure 4.5. The niche space occupied by dormouse populations sampled in spring (green) and autumn (orange), as calculated by Standard Ellipse Area corrected for sample size (SEAc), for the three sites (i, ii, iii) sampled in both seasons. A) The isotopic values of dormice sampled in spring and autumn and ellipses (SEAc) describing the isospace these occupy for the 3 sites. Isotope values are adjusted by site isotopic baselines. B) The Bayesian posterior estimates of the ellipse sizes (SEAc) of dormice populations sampled in spring and autumn on the 3 sites.

Discussion

Stable isotope analysis of dormouse tissue and of putative food sources reveals that foods from trees were important in dormouse diets in both spring and summer. This emphasises the importance of large trees that produce a significant number of flowers in spring and mast in summer and autumn. It also suggests that tree seeds (particularly from ash and oak) may play a larger role in dormouse diet than has been previously assumed (Juškaitis 2007b, Ancillotto et al. 2014). Honeysuckle was an important food source, reflecting its abundance in the woodland. The lack of representation of hazel in samples taken in autumn, despite its reported preference and dominance in the woodland, may represent the fact that hair was grown over the summer period before hazelnuts had fully ripened.

All three analyses (individual, mixing model and population level) provide evidence that dormice are opportunistic feeders, feeding on foods that are more readily available within their local habitat. Invertebrate abundance at different spatial scales was important in determining trophic level ($\delta^{15}\text{N}$) of dormice and invertebrates may play a more important part in dormouse diet than other studies have claimed (Likhachev 1971, Juškaitis 2007b). Slightly more counterintuitively, the $\delta^{13}\text{C}$ values of dormice were negatively related to the abundance of invertebrates. This could be because dormice rely more heavily on food sources from trees, which have higher $\delta^{13}\text{C}$ values (Fig. 4.3), when there are fewer invertebrates available in spring. The availability of food plants was also related to the estimated proportions of honeysuckle, omnivorous invertebrates and Lepidoptera in the diet for the single-site mixing model. Similarly, the relationship between higher $\delta^{15}\text{N}$ values and increased diversity of vegetation is counterintuitive, as one might expect higher proportions of vegetation to be eaten when more plant species are available. On the other hand, diverse vegetation communities are inevitably composed of some species which do not bear large quantities of flowers or fruit. Dormice might therefore require a reasonable dominance of fruiting and flowering species in woodland habitat.

These findings illustrate that dormice are adaptable feeders, specialising on food resources that are locally abundant (Juškaitis 2007b, Juškaitis et al. 2016). This counters previous suggestions that dormice have very specific feeding habits

(Richards et al. 1984, Morris 2003). Even within generalist species, local adaptations to resource availability are important for determining trophic ecology (Ben-David et al. 1997, Layman & Allgeier 2012, Camus & Arancibia 2013). Understanding that this response can occur at such a small scale, in this case within a 50m radius of the occupied nest box, suggests that dormice adapt to their local resource conditions and do not travel further from the nest site to acquire specific resources (Vander Zanden et al. 2000).

While I found relationships between food availability and dormouse isotopic signatures, I found no consequences of differences in food availability or isotopic signature on the condition of individuals. This could be due to the fact that the dormouse's flexible feeding strategy means they acquire adequate nutrition from whatever food is available with no ramifications for individual's condition (Juškaitis 2007b, Juškaitis et al. 2016). On the other hand, physiological consequences of diet may be subtle and act over longer timeframes, especially compared to demographic and seasonal parameters.

The size of a population's trophic niche was greater when sampled in autumn, corresponding with findings at single sites that dormice have a varied diet of both invertebrate and plant foods over the summer and early autumn (Richards et al. 1984, Bright & Morris 1993). The higher range of $\delta^{13}\text{C}$ values in summer diet indicates this larger niche is driven by consumption of a greater diversity of plant foods. This effect may be particularly pronounced on the sites I studied, as greater seasonal diet variability in better quality habitat has been found with other species (Blanco-Fontao et al. 2013). This is in accordance with other findings that dormice tend to eat a great proportion and range of plant matter in summer and early autumn (Richards et al. 1984, Bright & Morris 1993, Juškaitis et al. 2016).

Despite some relationships between food availability and population trophic niche, I did not find any population-level consequences of differences in population isotopic characteristics. This may be due to the small number of sites I looked at, resulting in limited power to detect subtle habitat effects. Alternatively, it could be that food resources are not a limiting factor on the sampled sites, which have relatively high-density dormouse populations and a high number of food plants. Other environmental

factors, such as climate or landscape, might therefore affect population dynamics on these sites to a greater extent (Chapter 3). More detailed studies to identify physiological mechanisms by which diet can have population-level consequences would be valuable (Lobo & Millar 2011, Shaner et al. 2013).

The connections I found between food availability and trophic position, and the consistency of this finding in individual and population level analyses and mixing models, highlights that stable isotope analysis can provide some broad insights into dormouse feeding ecology (Araújo et al. 2007). In woodland settings, where putative food groups overlap in their isotopic signatures, and where dormice appear to have broad, generalist diets, the degree of taxonomic resolution provided by isotopic methods is not as great as might be provided by other methods, such as molecular analysis of faeces (Inger & Bearhop 2008). The strength of the isotopic approach is that it can represent diet composition over longer timeframes and is thus less sensitive to short-term dietary changes (Richards et al. 1984). I found that for a surprisingly generalist species, however, isotopes cannot disentangle fine-scale variation within shrub, tree and invertebrate groups used in mixing models, and cannot build a detailed picture of the likelihood of specific plant and invertebrate foods being consumed (Araújo et al. 2007). Further work on the extent to which dormice consume specific food sources would be beneficial (McEachern et al. 2006).

There are some important caveats to the results of this study, particularly to do with the sampling of sources for the mixing model. Principally, there is uncertainty about exactly when the tissue sampled, i.e. hair, was grown. I aimed to control for the influence of moulting by always sampling from the same region and choosing sampling times following two broad timeframes during which hair growth is documented, by specific studies of moulting (Lozan 1970, Homolka 1978, Juškaitis & Büchner 2013). There is still some disagreement, however, in the timing of moult in dormice, which may differ in different climates and habitats. The consistency between samples from the same individual, indicates that hair is growing in the same area at the same time, even if it is not known exactly when it was grown, and rely on broad periods of hair growth. The broad timeframes covered by these periods mean conclusions about feeding cannot be more temporally specific, and some more detailed temporal differences in trophic ecology may be masked. The food sampling was subject to

several, likely minor, practical constraints: I was only able to collect plant and invertebrate samples in the daytime and up to human head height; I was unable to include aphids, an invertebrate group reportedly consumed by dormice (Juškaitis 2007b), as they were generally <3mm and so were not effectively sampled through the tree-beating method; and finally I was unable to sample bird's eggs, which have been found to be consumed by dormice (however only <4% of diet in early summer; Sara & Sara 2007, Juškaitis & Baltrūnaitė 2013, Juškaitis et al. 2016). Given the grouping of food species into broad groups and the small size and low biomass of aphids, I consider these sampling omissions to be unlikely to have substantially altered my conclusions.

By analysing landscape-scale count data, the status of dormouse populations has been shown to be more favourable, in terms of abundance, breeding and population trends, in woodlands that contain particular food species, (namely hazel, willow, honeysuckle, bramble, birch and yew), and which are subject to management that fosters these species (Chapter 3). Here I have again highlighted the importance of specific food sources to dormice, honeysuckle in particular, but have also provided additional evidence of the importance of trees such as oak throughout the year, arising from their extensive flowering in spring and seed production in summer/autumn. I have further shown that dormice readily exploit invertebrates where these are available in quantity. My dietary analyses, therefore demonstrate the means by which dormice might benefit from woodland management plans that take into account that they consume a variety of plant foods in the autumn, readily exploit invertebrate foods, and are affected by small-scale differences in food availability.

Chapter 5

Habitat preferences of hazel dormice *Muscardinus avellanarius* and the effects of tree-felling on their movement

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Abstract

Modern management of multifunctional woodlands must address many and various demands, including for recreation, timber production and the conservation of biodiversity. The responses of individuals and populations of protected species to woodland management and habitat change are often not well understood.

Using radio-tracking and LiDAR, I investigated the short-term habitat preferences of hazel dormice *Muscardinus avellanarius*, and their ranging and resting behaviours before and after small-scale tree felling, following a before-after control-impact design. Mean dormouse home range size was 0.51ha (\pm 0.07 SE, $n = 16$) and did not vary between sexes or among sites, though heavier animals had smaller ranges.

Dormice preferred mid-height woodland habitat (5-10m tall), with low proportions of high forest (over 10m tall), for both ranging and resting sites. Ranging habitats were often on woodland edges and in relatively dense vegetation. Dormice preferentially used yew, rowan and hazel during ranging. There was no difference in the distances travelled by dormice before and after felling, but in areas where trees had been felled dormice showed less evidence of a shift in ranging area than those in unfelled areas.

Although the limited response of dormice to tree felling activities has the potential to be associated with increased mortality and/or limited dispersal, the requirements of dormice for mid-successional and edge habitats that arise after tree removal means that a dynamic optimum of felling and regeneration is essential for conservation of dormouse populations.

Introduction

Woodlands are increasingly required to fulfil multiple functions including recreation, conservation and the production of timber and other forest products (Pimental et al. 1992, Schulz et al. 2014). Realising these multiple objectives often involves woodland management activities such as harvesting, thinning, coppicing or ride and glade maintenance (Quine et al. 2011). However, woodlands are often home to protected and threatened species that may be adversely affected, whether individually or collectively, directly or indirectly, by management activities (Lindenmayer 1999). These species are often protected by national and international legislation, making it a legal imperative for private and public woodland owners, and in some cases statutory authorities, to reduce or mitigate actual or potential harm caused by forestry activities (Young et al. 2005). This can have major consequences for forestry and woodland management, and substantial resources are dedicated to addressing protective legislation in developing forest management practice (Nalle et al. 2004). The responses of protected species to tree removal are frequently not as well understood as might be desired, both in relation to short-term effects on individuals and longer-term, or larger-scale, effects on population dynamics (Blumstein 2010). Likely effects are therefore often assumed and general mitigation measures are applied (Reinert et al. 2011). Understanding how protected species use their woodland habitats and react to silvicultural and other habitat management activities is therefore key to designing management plans and employing resources most efficiently (Cook et al. 2017).

The hazel dormouse *Muscardinus avellanarius* is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992), and the UK Habitats Regulations (1994 and 2010). Dormouse populations in the United Kingdom have undergone declines of 72% (62 - 79%, 95% confidence intervals) from 1993 to 2014 (Goodwin et al., 2017). This decline has been attributed to changes in climate, and woodland habitat configuration and quality (Chapter 3). The hazel dormouse is an arboreal species, inhabiting woodland, forest and scrub areas and has often been associated with successional wooded habitats (Bright & Morris 1990, Juškaitis 2007a, Becker & Encarnação 2015). It therefore exemplifies the problems posed by being obliged to conserve a species by using protection at the level of the individual, in a system that is subject to frequent management and alteration of habitats. This problem

is especially pertinent to dormice, as they are also likely to require active management to maintain their favoured habitats and thereby facilitate population persistence (Sozio et al. 2016; Chapter 3). Studies have shown that the management of woodland habitats increases the survival and body condition of dormice within those habitats (Sozio et al., 2016), and populations across whole woodlands are resilient when management has taken place in parts of the woodland (Juškaitis, 2008; Trout et al., 2012). Studies of many woodlands across the UK have shown that populations respond positively to woodland management (Goodwin et al., 2018). Knowledge of the response of individual dormice to silvicultural activities, best exemplified by tree felling, is therefore needed in order to be able to start balancing any potential short-term effect on individuals with the longer-term conservation requirements of dormouse populations.

Most studies of the effect of forest management on small mammals have compared communities of small mammals in managed stands of forest to those in old growth forest (Lindenmayer 1999, Carey & Harrington 2001, Zwolak 2009, Fauteux et al. 2012). However, this approach does not separate the proximate effects of forestry on populations (survival, emigration, changes in range use) from longer term habitat changes (Escobar et al. 2015). It is therefore important to examine the immediate behavioural and ecological responses of individuals to woodland management.

Dormice have been shown to occur in greater numbers, with increased survival and breeding success, in woodland vegetation of medium heights or with a developed understorey, and successional and scrubby habitats (Capizzi et al. 2002, Juškaitis & Šiožinytė 2008, Sozio et al. 2016). Survey methods used in these studies capture broad habitat associations, often of resting sites (Chapter 3), whereas telemetry can fine-tune conservation recommendations for the provision of habitats required for different activities, such as resting and ranging (Bright & Morris 1992), as well as investigation of behavioural responses to changes in their environment (Doerr & Doerr 2005). Remote sensing data now also make it possible to look at the selection of different vegetation structures (Garabedian et al. 2017), which are important for a variety of arboreal mammals (van der Ree & Bennett 2003, Wilson et al. 2007, Falconi et al. 2015, Berry et al. 2016, Linnell et al. 2017). Understanding the preferences of

animals can aid in predicting the likely effect of changes in vegetation structures, e.g. through tree removal and woodland management (Eyre et al. 2010).

I explored the ranging behaviour and preferences for tree species and vegetation structure shown by hazel dormice in two woodlands in England. I investigated the effects of tree felling within the ranges of dormice on both these sites. I tracked dormice before, during and after tree felling occurred, as well as in control areas of the sites, where no tree felling was carried out.

Methods

Study sites

The study was conducted in two mixed broadleaf and conifer sites, in south Devon (SX813892) and central Kent (TQ530374) in England (Fig. 5.1). The sites were selected as they had established and well-known dormouse populations, varied woodland habitat and had planned ongoing tree felling activities.

Birch *Betula* spp. was ubiquitous while various conifers, oak *Quercus* spp. and honeysuckle *Lonicera periclymenum* were the most common and widespread species. Sweet chestnut *Castanea sativa*, alder *Alnus glutinosa* and bracken *Pteridium aquilinum* were found across more than half of the sites, while beech *Fagus sylvatica*, ash *Fraxinus excelsior*, willow *Salix* spp., sycamore *Acer pseudoplatanus*, lime *Tilia* spp., hazel *Corylus avellana*, holly *Ilex aquifolium*, cherry *Prunus* spp., buckthorn *Rhamnus cathartica* and *Rhododendron* spp. were in fewer than half but more than 20% of the sites. The two sites have similar ecological histories and management regimes and are both being converted from commercial conifer plantation to a mix of semi-natural broadleaved woodland, shrub and heath (Fig. 5.1). Both sites have watercourses running through them and areas of wet woodland. The vegetation structures were similar between sites, with the major difference being that vegetation heights were slightly higher and there was a higher proportion of open ground on the South Devon site (Table 5.1). The vegetation species composition was slightly different between sites, however two of the three most abundant species groups on both sites were birch *Betula* spp., occurring in all of the dormouse ranges studied, and various conifer species, occurring in 96% of ranges. Sweet chestnut *Castanea sativa*,

oak *Quercus* spp. and honeysuckle *Lonicera periclymenum* were also one of the 10 most abundant species at both sites. The identity of the other most abundant species in the areas differed. In Kent, buckthorn *Rhamnus cathartica*, *Rhododendron* spp., bramble *Rubus fruticosus* and yew *Taxus baccata* were found within between 30 - 50% of all the dormouse ranges, whereas they were absent in Devon. Whereas hazel *Corylus avellana* and cherry *Prunus* spp. were reasonably abundant within the areas studied in Devon but not recorded in Kent.

Table 5.1. Summary of vegetation structure at study sites in South Devon and Central Kent. Measures are means taken from all sampling points, i.e. those used by and available to dormice. Mean SD of vegetation height is the mean standard deviation in a 3m x 3m sliding window (see Methods).

Site	Mean vegetation height (m)	Mean SD of vegetation height (m)	Mean canopy density	% under 1m	% 1-2m	% 2-5m	% 5-10m	% over 10m
South Devon	8.34	2.32	0.62	4.56	3.48	17.54	37.58	36.84
Central Kent	9.71	3.16	0.60	10.10	3.82	10.51	32.27	43.31

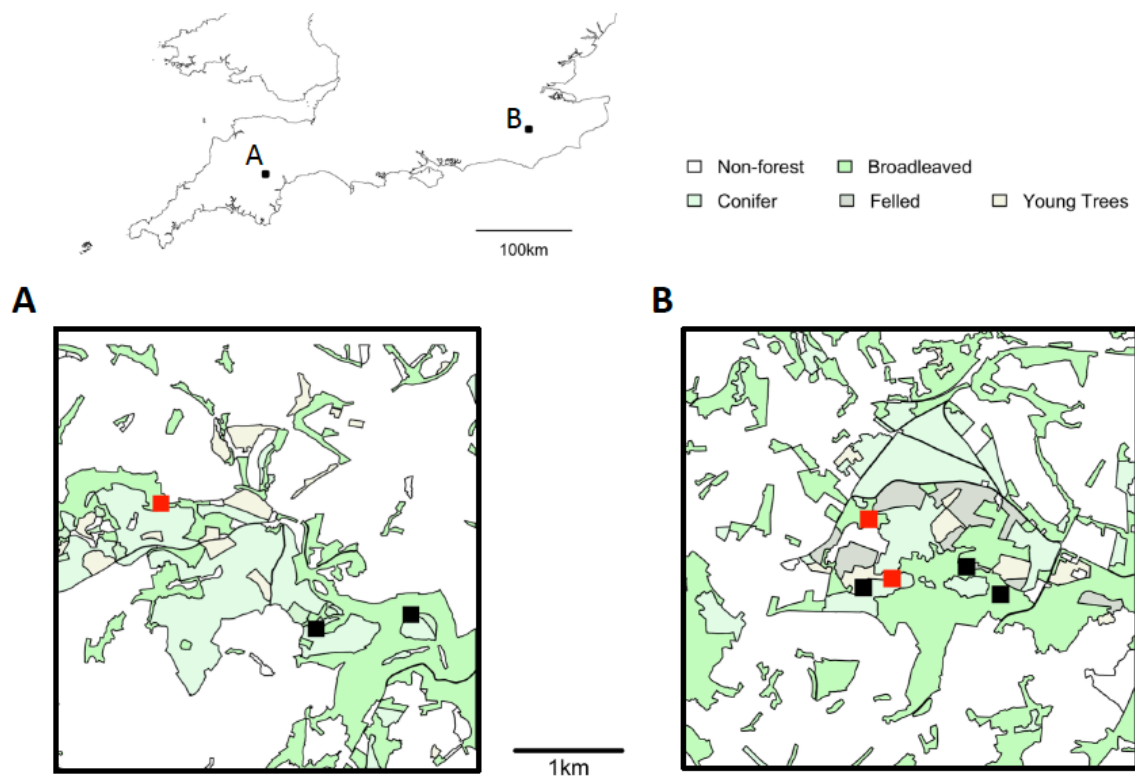


Figure 5.1. Locations of the two sites at which dormice were radio-tracked and details of the distribution and composition of woodland habitats in the surrounding landscapes. Site A is in south Devon and B is in central Kent. Woodland habitat categories are from the National Forest Inventory 2015. The areas in which dormice were tracked and where felling was conducted are shown as red squares and the control areas in which dormice were tracked are shown as black squares.

Tracking methodology and felling protocol

Dormice were captured during surveys of nest boxes that had previously been deployed for dormice. VHF radiocollars of between 0.8 and 1.1g (3 - 6% of dormouse weight) were fitted to 20 dormice. 9 dormice were in areas of the sites in which trees would be felled, and 11 in control areas where no trees would be felled. The sex and weights of dormice were noted during collar fitting. The study was undertaken under licence from Natural England and the Home Office and with approval from the University of Exeter Animal Welfare and Ethical Review Board. Prior to deployment in the field, a video assessment was made of the night-time activity of two captive zoo dormice wearing dummy collars and no changes to movements were observed; other

studies have similarly reported no discernible impediment to dormice from radiocollars (Bright & Morris 1990).

Radiotracking was conducted between 29th September and 21st October 2015, as felling or woodland management activities are usually carried out at this time of year and dormice are not often torpid during the day. Most location fixes were made by directly locating the animal to a specific tree or canopy area and recording the location with a handheld GPS device. Due to inaccessibility (steep slope, river) some location fixes were obtained via triangulation, from a mean distance of 28m from bearings taken at two fixed points marked with a handheld GPS. A daytime fix was taken for each dormouse to record resting locations. Due to different numbers and locations of dormice on the two sites, nighttime sampling rates varied; an average of 3.8 - 5.3 fixes per 24-hour period were taken for each dormouse in Devon, and 2.4 - 3.0 fixes in Kent. Fixes were not taken within one hour of each other to reduce spatial autocorrelation of recordings. The time at which individuals were located was rotated to ensure comprehensive coverage of each animal over the active period (Fieberg 2007, Fieberg & Börger 2012).

Dormice were tracked for a period of days before and after tree felling was conducted following a Before-After-Control-Impact (BACI) design. Tree felling took place 5 - 7 days after tracking had begun and dormice were tracked for 8 - 11 days following felling. Trees were removed from 3 areas on the Devon site and 2 on the Kent site. The mean size of felled areas was 0.1ha (0.06ha SE). All dormice in felling areas were located in nest boxes situated from 0m to 100m from felling operations when trees were being felled. The mean distance was 38.6m (10.7m SE) and 6 dormice were in areas where trees adjacent to the nest box were felled. On these days in felling areas, the daytime locations of dormice were recorded on two additional occasions: once prior to the start of felling operations and once after operations had ended. Felling measures were similar on both sites, in that they consisted of clearing small areas of conifer, or mixed conifer and broadleaf trees, to create glades. The main difference was that a larger area of mostly conifer was removed on the South Devon site, compared to the site in Kent (Fig. 5.2).

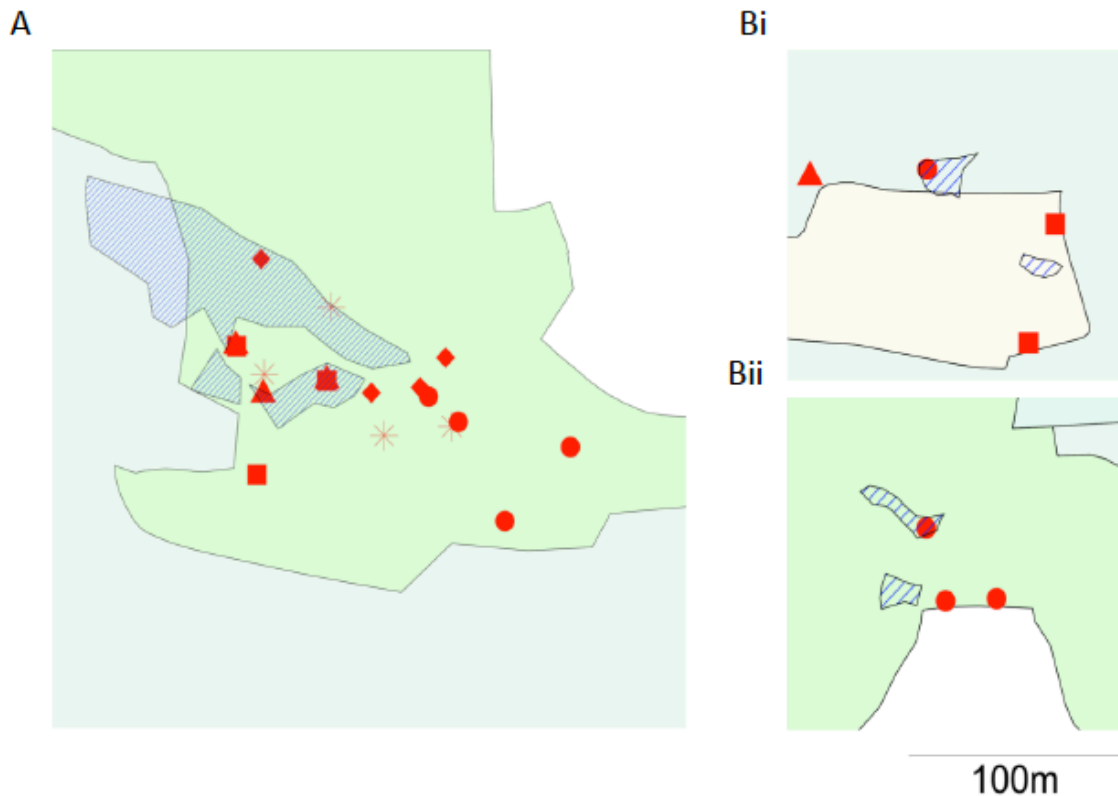


Figure 5.2. Locations of daytime resting sites of dormice (red points) in areas where tree felling was carried out in A) South Devon and B) Central Kent. Areas where trees were completely removed are shown as hashed blue areas. Individual dormice in the different areas are shown with different symbols (circle, triangle, square and star).

Habitat data collection

The species of tree or shrub in which each dormouse was located was recorded. Conifer species were grouped, as were willow species, to ensure consistency in species classification. Data on the availability of tree species in the range of each dormouse were collected around a central point of its range, identified from radio-tracking; four 50m transects were walked on North, South, East and West compass directions and all trees or shrubs >1m high within 1m either side of the transect were recorded.

Light Detection and Ranging (LiDAR) data were used to assess vegetation structures. LiDAR measures canopy height from above at a fine scale, and is used here to derive measures of canopy height and density, as well as spatial heterogeneity in structure.

These canopy metrics will also reflect, to some extent, variation in the amount of light penetrating the canopy and so might act as a proxy for productivity and vegetation density below the canopy. Such remotely sensed data are powerful in that they are available at fine scale across large areas of woodland and can be more consistent than terrestrial surveys. However, measures of height at the canopy clearly cannot capture all understorey characteristics, the implications of which may vary among tree species. The implications of using LiDAR data are discussed further below. Digital Surface Models (DSMs) and Digital Terrain Models (DTMs) were acquired from BlueSky International for 2014 for the Kent site, and from the Tellus project for 2013 for the Devon site. DTMs were subtracted from DSMs to obtain vegetation heights. Data was resampled to 1m resolution for BlueSky data (original resolution of 50cm), using average values, making the datasets comparable. See Figure 5.3 for examples.

Space-use analysis

To describe the dormouse ranges, I calculated Kernel Density Estimates (KDEs) from radio-tracking locations (Fieberg 2007, Laver & Kelly 2008). Ranges based on a standard time period of 13 days were used to enable equivalent comparisons of space use. Asymptotic distributions were investigated to look at estimated range size and 95% Confidence Intervals (calculated from 1000 bootstrap samples), with increasing sample size (Laver & Kelly 2008, Calabrese et al. 2016). Asymptotes in range sizes were reached over the 13-day period by individual dormice (Appendix 6) and ranges estimated over a standardised number of days have been shown to be robust (Börger et al. 2006, Kochanny et al. 2009, Fieberg & Börger 2012). Temporal autocorrelation was investigated using the R package *ctmm* (Calabrese et al. 2016). KDEs were calculated using H-plugin smoothing bandwidth selection, as this did not over-smooth the data and is suitable for small sample sizes and animals with partially clumped space use (Gitzen et al. 2006, Walter et al. 2011, 2015, Fieberg & Börger 2012). Bivariate normal smoothing and a default grid resolution of 151 x 151 cells were used in kernel density estimation. The 95% contour level and 50% contour level of the KDEs were extracted as measures of the areas of total range and core range. 95% CIs were calculated for each 95% and 50% KDE with 1000 bootstrap samples with replacement.

Range size estimates had high 95% CIs, so distances travelled and centroids of ranges were also used to investigate space use and the effect of felling (Fieberg and Börger, 2012). The night-time extent of ranging was calculated as the distance between each night-time fix and the resting site the dormouse had used the previous day (Fieberg & Kochanny 2005). The distance between centroids of KDEs calculated before and after felling were used to assess the extent to which dormice ranges had shifted (Fieberg & Kochanny 2005). 95% CIs around centroid distances were calculated using bootstrapping with replacement to generate 1000 samples of centroids before and after felling and calculating the difference between them.

Habitat preference

The preferences of dormice for aspects of vegetation structure were investigated for night-time ranging and resting site selection in the day. I used a use-availability design (Aebischer et al. 1993, Boyce & McDonald 1999, Warton & Aarts 2013), comparing habitat characteristics of used locations from radio-tracking to those of available locations, determined at a set of randomly sampled locations (Aarts et al. 2013). For assessing night-time habitat preference, a set of random points was generated around each day-time resting site. Differences between the coordinates of day-time resting sites and of night-time active fixes for all dormice were calculated, and locations at these distances were randomly sampled to reflect biologically meaningful accessibility (Matthiopoulos, 2003). For every day spent at each resting site, 50 random locations were sampled. This generated an average of 204 (± 30 SE) random locations in the habitat surrounding each nesting site.

For assessing preferences for day-time resting site habitat, 100 random locations in a 100m radius around each resting site were sampled. These were not weighted by distance, as dormice could shift their resting location up to this distance in a night. This gave an average of 886 (± 175 SE) randomly sampled locations of possible resting habitat for each dormouse.

To account for a margin of error in locating animals arising from VHF and GPS accuracy (GPS mode accuracy was 3m), canopy variables in a 5m radius around each randomly generated location and each location used by dormice. For the random

locations, those that fell within open areas were excluded. The eight canopy variables calculated in each 5m buffer were: variation (standard deviation) in canopy height; canopy density (proportion of vegetation heights >4m); local variation in canopy density (the standard deviation in canopy height of a 3 x 3m sliding window around each pixel averaged within the 5m radius around each location); and proportion of vegetation 0-1m; 1-2m; 2-5m; 5-10m; and >10m. Spearman's rank correlation tests were used to investigate co-linearity between these canopy variables (Zuur et al. 2010), many of which were correlated. A Principal Component Analysis (PCA) was therefore conducted for canopy variables giving a set of principal components (PCs) for each analysis (Appendix 7). All PCs explaining more than 5% of variation in the data were used in analyses of vegetation structure.

Preferences of dormice for particular tree species were assessed using a similar use-availability design. Estimates of availability were calculated through bootstrapping (with replacement) the available trees 1000 times. Each sample was the same size as the number of records of trees used by each dormouse. 95% CIs for the availability of tree species was calculated for each dormouse range and aggregated across dormice (Appendix 8).

Statistical analyses

R version 3.4.2 (R Core Team 2017) was used for all analyses.

All model selection (excluding tree species preference models – see below) was performed using an information-theoretic approach and the effects of explanatory variables were derived through multi-model inference via model averaging. This approach involves assessing candidate models of all possible combinations of explanatory variables and ranking these by Akaike's Information Criterion (AIC), adjusted for sample size (AICc) (Whittingham et al. 2006, Lindberg et al. 2015). These models were fitted by Maximum Likelihood for mixed effects models. The top set of models most likely to explain variation in dormouse behaviour measures were all those within 2 Δ AIC of the top model (Burnham & Anderson 2002). Full model averaging was performed across this top model set, weighted by their relative AICc values, to calculate effect sizes of explanatory variables. Full model averaging sets effect sizes

at zero when variables are not present in a model and is thus more conservative (Grueber et al. 2011). 95% Confidence intervals were calculated for effect sizes and significance was determined by whether or not these confidence intervals overlapped zero. The relative importance (RI) of each variable is defined as the proportion of models within the top model set that included that term. For models with small numbers of explanatory variables, stepwise selection was also performed and all results proved robust. In analyses where the response variable was at the level of individual dormice (e.g. dormouse ranges), site was included as an explanatory variable to account for differences between sites. In analyses where the response variable was single instances of habitat use (e.g. habitat preference), dormouse identity was included as a random or fixed factor to control for variation arising from the identity of the dormouse.

To investigate whether 95% and 50% range areas and mean distances travelled varied between dormice, a linear model with a Gaussian error structure was used with site, weight and sex as explanatory variables. Range sizes were square-root transformed and mean distances travelled were logged to normalise their distribution. The relationship between distances travelled from the daytime resting site and the hour of night and the implementation of tree felling was analysed in a generalised linear mixed model framework with dormouse identity as a random effect (Bolker et al. 2009). Distances were square root transformed to normalise their distribution. A linear model with a Gaussian error structure was used to test for a difference between range shifts of dormice in felling treatments and non-felling controls. This model included site as a fixed term to control for site identity. Distances between range centroids before and after felling were logged to normalise their distribution.

To assess tree species preferences, generalised linear modelling with a negative binomial error structure was used to model counts of use and availability for each tree species for each dormouse. A saturated model with a three-way-interaction between used/available, tree species and dormouse ID was simplified via backwards step selection (Crawley, 2013). Whether terms explained a significant proportion of variance was determined by likelihood-ratio tests. For each dormouse, the difference between recorded use and each of 1000 bootstrap samples of tree species availability was used to calculate 95% CIs for each tree species available to each dormouse.

These were then averaged across dormice for each tree species that was used by at least two dormice, and importance denoted by whether 95% CIs overlapped zero.

To analyse vegetation structure preference for day-time resting and night-time ranging, mixed effect logistic regression modelling, with a binomial error structure, logit link and random effect for dormouse identity was used (Aarts et al. 2008, Beyer et al. 2010). This was done in two ways: first, models were run with the explanatory variables as original individual scaled LiDAR variables and then second with explanatory variables as continuous, scaled principal components derived from LiDAR canopy measures. In the first method, many of these variables were correlated so model selection precluded any variable pair with correlations of $> 0.5 R_s$ from being included together in models. This method, however, understates the importance of variables with correlations to many others, and cannot capture the combination of intercorrelated aspects of vegetation structure that characterise woodland habitats. The explanatory variables used in the main analyses were therefore the continuous, scaled principal components derived from LiDAR canopy measures (Aarts et al. 2008, Matthiopoulos et al. 2011).

The fit of logistic regression models was evaluated using repeated k-fold cross-validation procedures (Boyce et al. 2002) using code modified from the R package *hab* (Basille 2015). The final model was fitted to a portion of the data (a 'training set') and used to predict values for the remaining data (a 'test' set). Huberty's (1994) heuristic was used to calculate the division of training and test data (Fielding & Bell 1997). The equal-area binned distribution of the test data and predictions from the model was compared via a Spearman's Rank Correlation test (R_s ; Wiens et al. 2008). This was conducted separately for used and available habitat, and repeated 100 times. The fit of the model was assessed through R_s correlations for used habitat, and t-tests on the differences between the correlation values of used and available habitat.

Results

Ranging behaviour and resting sites

The number of fixes taken for each dormouse ranged from 14 to 96; those tracked for over 13 days had at least 34 fixes. After collar failure and loss, 16 dormice were tracked for 13 days or more: eight in felling areas and eight in control areas, with four males and females in each.

The mean range area used by dormice (95% KDE) over a thirteen-day period was 0.51ha (± 0.07 ha SE) and the mean core area (50% KDE) was 0.09ha (± 0.02 ha SE) (Fig. 5.3). The mean number of resting sites for each dormouse was 2.7 (± 0.3 SE, Range 1-5). The mean night-time distance ranged from the preceding resting sites was 46.3m (± 1.3 m SE). For individual dormice, the mean distance travelled ranged from 9.5m (± 0.4 m SE) to 61.3m (± 3.6 m SE). 43% of resting sites were in dormouse nest boxes (25 out of 58 resting sites). The other 33 resting sites were in abandoned squirrel dreys, birds' nests, or tree hollows ($n = 21$), low shrub, e.g. bramble *Rubus fruticosus*, or bracken ($n = 10$), a tree guard ($n = 1$) and a tree stump ($n = 1$).

Sex and site did not significantly affect the overall (95% KDE) or core (50% KDE) ranges of dormice or the mean distances they travelled from resting sites. However, heavier dormice used smaller ranges (Effect size = -3.03, (-5.74, -0.31 95% CIs), Relative Importance (RI) = 1) but not smaller core ranges (RI = 0.64) and travelled less far from resting sites (Effect size = -0.07, (-0.11, -0.02 95% CIs); RI = 1).

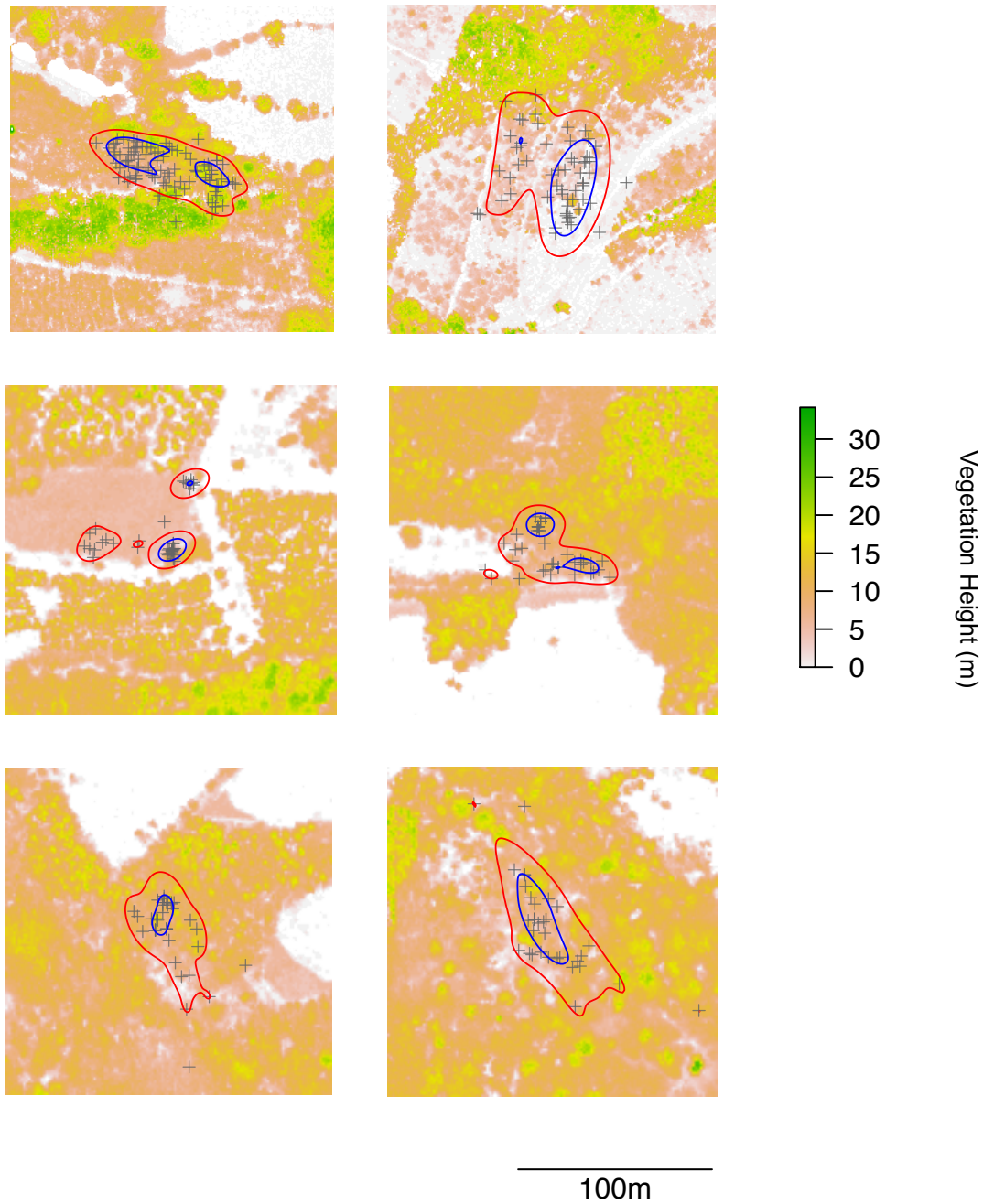


Figure 5.3. Examples of radio-tracked dormouse home ranges. 95% outer contours of Kernel Density Estimates are shown in red and 50% core ranges are shown in blue. Used location records are shown by grey crosses. LiDAR vegetation structure data are also shown: colours indicate vegetation height in metres (m) and all vegetation < 0.5m was excluded from analysis. Scale is the same in all panels.

Habitat and species preferences

The Simpson's index of vegetation species diversity ranged between 0.61 and 0.89 within dormouse ranges, with a mean of 0.76 (0.20 SE). Tree species were consistently used to different extents by dormice (LR test = 50.8; $p < 0.001$, Fig. 5.4, Appendix 8). Yew *Taxus baccata* (7.24 - 9.75 95% CIs difference between use and availability), rowan (1.00 - 3.00 95% CIs), and hazel (1.00 - 12.23 95% CIs) were especially favoured relative to availability. There were no differences among dormice in their relative use of tree species (LR test = 14.4; $p = 0.57$), however, different species of tree were available to different dormice (LR test = 57.0; $p < 0.001$).

Within dormouse ranges, the average canopy height was 8.3m (0.5 SE) and mean canopy density was 83% (3% SE) and mean vegetation heights within dormouse ranges varied from 4.5m to 12.1m, while variation (standard deviation) in heights ranged from 2.7m to 5.6m, and canopy density from 46% to 96%.

Several aspects of vegetation structure (based on LiDAR-derived PCs) had a strong effect on whether areas were selected by dormice during night-time ranging (Fig. 5.5). Areas selected by ranging dormice had higher canopy density and a lower proportion of vegetation heights <5m (LiDAR PC1); a greater proportion of 5-10m trees, less variation in canopy height and a lower proportion of trees over 10m (PC2); a higher proportion of 0-1m and 5-10m vegetation heights in conjunction with less vegetation of 2-5m (PC4); and a higher proportion of 0-1m vegetation in conjunction with less vegetation of 1-2m (PC5). The fact that dormice ranged in woodland patches that contained both 0-1m vegetation and 5-10m vegetation within a 5m radius represents the use of areas with both open and mid-height vegetation. These areas are therefore edge habitats and could represent fine-scale mosaic structuring within the woodland, internal edges between woodland stands, and external woodland edges. This model fitted well and had high predictive power ($R_s = 0.83$ (0.81, 0.84 95% CIs); $p < 0.01$; Appendix 9) and the R_s correlations for used habitat were much higher than for available habitat ($t_{115} = 26.2$, $p < 0.001$), signifying that the model could accurately predict whether woodland habitat was used compared to a random sample.

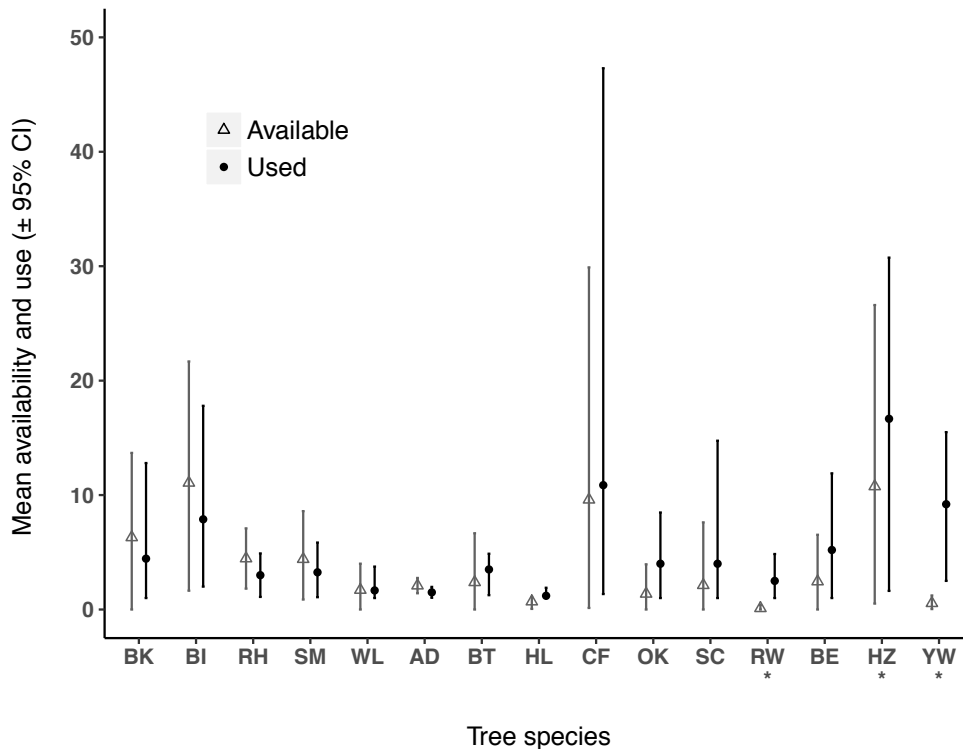


Figure 5.4. The availability of tree and plant species and their use by dormice on two woodland sites in Kent and Devon, England. The mean count and 95% CIs of trees used by dormice were calculated from the locations of active, radio-tracked dormice. Species are ranked by the mean difference between their use and availability. The mean and 95% CIs of available trees were calculated from bootstrap samples of availability on transects surveyed from the centre of each dormouse's home range. Only species that were used by at least two individual dormice are shown. Species which had zero use or availability counts were excluded. RW=Rowan, YW=Yew, HL=Holly, OK=Oak, AD=Alder, WL=Willow, BT=Buckthorn, RH=Rhododendron, BE=Beech, SC=Sweet Chestnut, SM=Sycamore, BK=Bracken, CF=Conifer, BI=Birch, HZ=Hazel. Significance of the difference between use and availability 95% CIs of species is denoted by *.

Analysis of original individual LiDAR measures supported the main results for LiDAR PCs. The proportion of habitat vegetation 0-1m (Effect size = 0.14 (0.06, 0.22 95% CIs); RI = 1) and 5-10m high (Effect size = 0.20 (0.11, 0.29 95% CIs); RI = 1) were higher in areas selected by ranging dormice. The proportion of vegetation between 1-2m high (Effect size = -0.25 (-0.39, -0.11 95% CIs); RI = 1), and the variation in canopy height (Effect size = -0.23 (-0.34, -0.12 95% CIs); RI = 1), were both lower in areas

preferred by ranging dormice. The local ‘clumpiness’ of vegetation (RI = 0.3), and the proportion of vegetation between 2-5m (RI = 0.2) and over 10m (RI = 0) had no effect on ranging habitat selection.

The selection by dormice of habitat for daytime resting sites was also strongly affected by LiDAR-derived vegetation structure PC2 (Fig. 5.5). Areas selected by dormice for daytime resting had a greater proportion of 5-10m trees, less variation in canopy height and a lower proportion of trees over 10m. This model also had significant predictive power ($R_s = 0.60$ (0.57, 0.63 95% CIs); $p < 0.05$; Appendix 9), but was not as strong as the model for ranging habitat preference, and the R_s correlations for used habitats were higher than for available habitats ($t_{115} = 15.0$, $p < 0.001$). No individual original LiDAR measure was associated with day-time resting habitat selection.

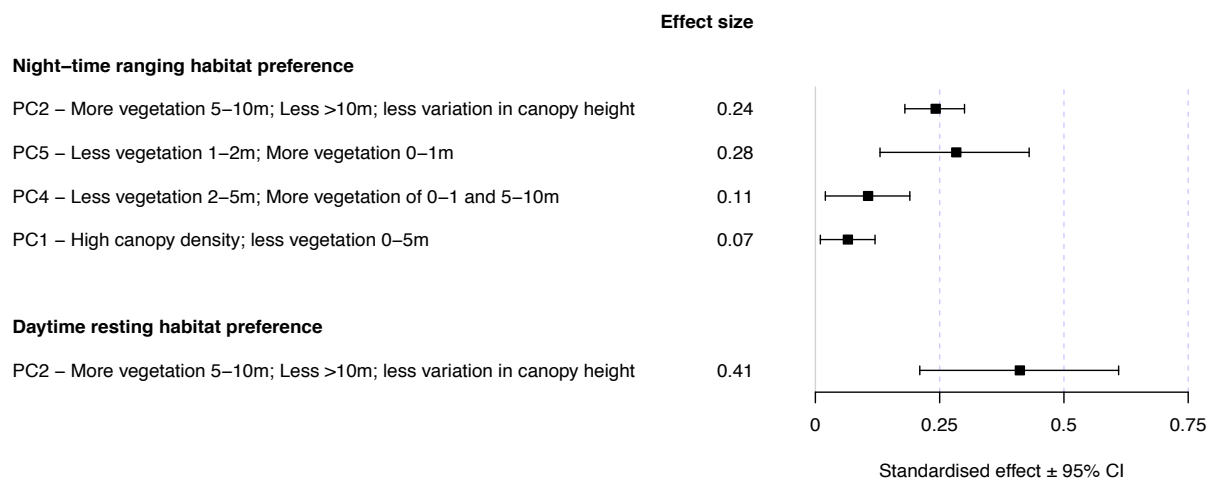


Figure 5.5. *Habitat preferences of radio-tracked hazel dormice on sites in Kent and Devon, England. The effects of vegetation structure on the relative intensity of use are shown separately for night-time ranging and daytime resting. Vegetation structure is described by Principal Components (PCs) from analysis of LiDAR data. The standardised effect sizes (\pm 95% Confidence Intervals) are derived from mixed-effect binary logistic model averaging logit estimates of effect sizes across the top model set. Relative importance across the top model sets of all the terms shown is 1. Terms are shown in order of the strength of effect (as derived through effect size and accuracy of effect size estimation (CIs)).*

Effects of felling

The distances travelled by dormice from the resting site did not differ before and after felling, or between sites with and without felling ($RI = 0.24$; Fig. 5.6). The ranges of dormice in areas where felling was conducted shifted to a lesser extent than those in areas where no felling was conducted (Effect size = 0.81 (0.12, 1.50 95% CIs); $RI = 1$; Fig. 5.7). Dormice were found in the same locations immediately before and after felling in 23 of 26 occasions. Of the three instances of movement, one dormouse moved 35m from a nest box surrounded by tree removal work to a small oak tree, while another individual moved 43m between nest boxes on two days when felling was being carried out in the vicinity.

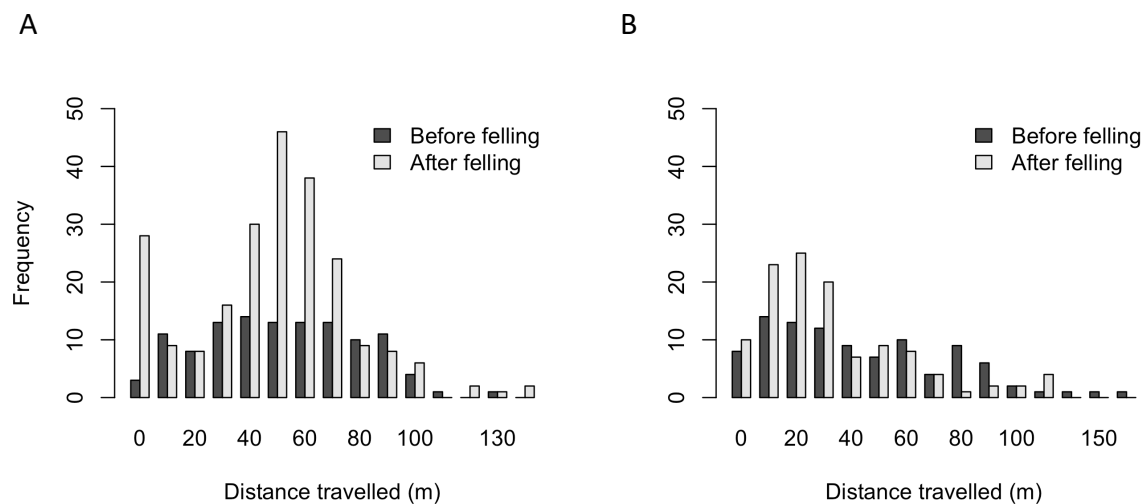


Figure 5.6. The frequency at which dormice were recorded at night at different distances from their daytime resting site, before and after felling periods, in areas where felling was conducted (A) and control areas where felling was not conducted (B).

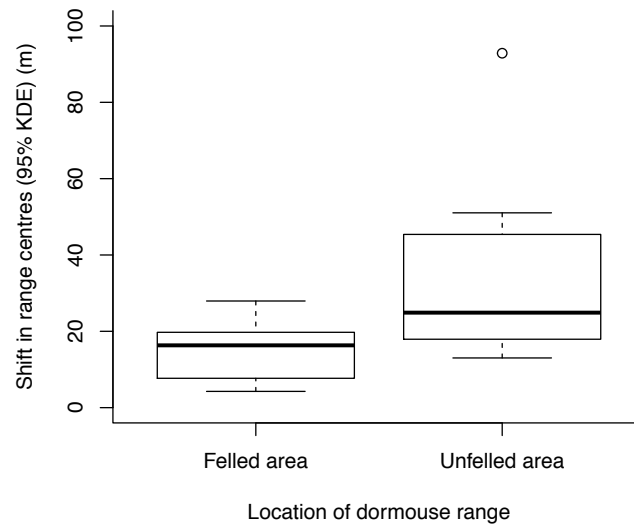


Figure 5.7. A comparison of the extent of the home range shift* between radio-tracked hazel dormice in areas with tree felling and areas with no tree felling. The box plot indicates the median displacement distance with the box indicating the 50% range and the whiskers indicating the 75% range in overall distances (m). *the distance between home range centroids calculated in pre- and post- felling periods

Discussion

Habitat preferences of dormice

The night-time ranging habitat preferences of tracked dormice were for higher proportions of vegetation of 5-10m, lower proportions of high forest and lower variations in canopy density. These vegetation structures have also been found to be a consistent indicator of relatively high dormouse abundance and breeding frequency at a site level (Chapter 3), suggesting the local, individual preferences observed here can be scaled up to a population level. The positive associations of tracked dormice with low variation in canopy density reflect their selection of a particular canopy density and, although not established empirically, dormice have been reported to require habitat with high branch-connectivity between trees and shrubs in order to enable ranging and dispersal (Bright & Morris 1994, Bright 1998). Dormice also preferred to range near edge habitats. Dormice have been associated with woodland edge habitats through other survey methods (Bright et al. 1994, Berg & Berg 1998, Ramakers et al. 2014), but not previously through direct observation of their ranging behaviour. There is increased light and warmth from greater insolation at woodland edges and both promote fruiting and flowering, providing food for dormice (Juškaitis 2007a).

The selection of vegetation at certain heights and densities will clearly depend on their availability (Aarts et al. 2013). Although not markedly different from the findings in this study that dormice used canopy heights of between 5-10m, Bright and Morris (1991) found dormice to use lower tree heights of 4.14m to 5.19m corresponding to a lower woodland canopy height overall of 5-6m. In very different woodland habitats, habitat preferences might therefore vary in relation to the available structures and species. Even within this study, there are differences in habitat preference based on the habitats available to each dormouse. The high predictive ability of these models, however, suggests that the habitat preferences I found are consistent between individuals (Boyce et al. 2002, Johnson et al. 2006).

Dormouse populations have also been shown to be positively associated with a variety of habitat types (Goodwin et al., 2018; Berg and Berg, 1998), some of which were likely under-represented on our study sites. Dormouse populations may be more flexible in their habitat use when more, or different, habitats are available.

Furthermore, hedgerows and more woodland connections in the landscape have been found to be important for dormice (Bright et al., 1994; Goodwin et al., 2018). While we know little of the effects of variations in hedgerow habitat, these beneficial habitat features in the landscape may mitigate or affect the influence of habitat change within a woodland.

Bright & Morris (1992) found that in woodland with different vegetation layers (i.e. an understorey and canopy layer), dormice used different vegetation heights depending on the seasonal availability of food resources. Woodland in this study, however, was of one layer, either mixed, shrubby woodland or beech or conifer high woodland without an understorey, therefore dormouse activity would have predominantly been in the canopy. This cautions against applying the habitat preference findings of this work to such woodland habitats, with understorey and canopy layers. The use by dormice of different layers within woodland would have proved difficult to examine using my methodology. It would be necessary to employ a tracking methodology to identify the position of dormice in a vertical dimension and to measure the vertical vegetation structure of woodlands, e.g. through the use of waveform LiDAR (Anderson et al. 2016) or terrestrial laser scanning (Eichhorn et al. 2017).

Resting site selection is in part determined by proximity to suitable ranging habitat, creating a likelihood of identifying a similar preference for both (Guo et al. 2008). Resting sites were, however, associated with only one preferred ranging habitat, where there was more vegetation of 5-10m, fewer high trees, and less variation in canopy heights, suggesting that these sites tended to be more in the core areas of the animals' ranges, further from edges and more likely to be protected from weather and predation (Rader & Krockenberger 2006, Chutipong et al. 2015). Dormouse preference for nest sites within woodland interiors is supported by other studies (Williams et al. 2013).

While dormouse resting site preference may be for areas with a higher proportion of 5-10m trees, actual dormouse nests were often situated in features associated with old growth; 67% of natural nests (38% of all nests) were in tree cavities or squirrel dreys and bird nests in mature trees. This presents a necessity to preserve mature trees and old-growth features in order to provide adequate nesting sites, particularly

in woodlands with less bramble and other dense shrub habitat (as also found by Hurrell & McIntosh 1984).

The preferences of dormice for particular tree species can guide management, though their value and preferences will clearly change seasonally as species produce flowers, fruit and seeds and their insect populations fluctuate (Bright & Morris 1992). Preferences for hazel and yew shown by dormice in this study are consistent with the work of Bright and Morris (1993), in which yew was preferred in late summer, while hazel was preferred in early autumn. Bright and Morris (1993) also identified preferences for honeysuckle which I did not replicate here. The use of climbing species, such as honeysuckle, may be generally under-recorded, as its use cannot strictly be distinguished from that of the tree in which it is climbing. Otherwise, discrepancies between this study and the earlier work likely arise from differences in species composition among sites. Rowan, which I found to be preferred by dormice, was not present on the study sites of Bright and Morris (1993) but is similar to other soft-masting trees they identified, such as wayfaring tree *Viburnum lantana*.

Effects of tree-felling

Perhaps counterintuitively, dormice living adjacent to felled areas shifted their ranges to a lesser extent than dormice in non-felled areas. This reduction in resting site mobility could represent a 'hiding' response (Escobar et al. 2015), perhaps associated with a perception of increased risk arising from the noise and habitat change caused by forestry operations. However, the nightly distances travelled by dormice after felling did not differ, suggesting that dormice movement was not substantially restricted within their range. Rather, I suggest the ability or willingness for dormice to disperse to other resting or ranging habitats was reduced. This might be due to felling reducing either connectivity and/or the availability of nest sites in the surroundings (Spring et al. 2008). Habitat change may have particularly prominent effects on individual dormice due to their small range size. Dormouse ranges in these woodlands were small but consistent with other studies, even considering the variable lengths of time for which dormice were tracked (Bright & Morris 1991, 1992). Sensitivity to habitat connectivity has also been identified at larger scales, where fragmentation leads to reduced dispersal of dormice (Buchner 2008, Mortelliti et al. 2013).

Tree removal in this study was small-scale and was oriented towards woodland conservation. Felling practices are, however, very variable. Commercial felling affects wide areas leading to more vegetation disturbance, habitat loss and fragmentation (Trout et al. 2012b, Bogdziewicz & Zwolak 2014), with likely greater consequences for dormouse survival and emigration (Connette & Semlitsch 2015, Escobar et al. 2015). Experimental manipulation of forestry intensity and practices (e.g. the % of canopy removed) is challenging to implement in a real-world forestry context, however experiments would help guide recommendations for forestry and woodland management practise. Although in the UK, under the Forestry Act, there is a stipulation that forests and woodlands must be re-created and so the loss and fragmentation of woodland is, in principle at least, of short duration. The noise and disturbance of even small-scale felling is considerable; in this study chainsaws were used directly adjacent to occupied nest boxes. Perhaps surprisingly, the majority of dormice did not flee from this disturbance, suggesting that large-scale, contiguous felling could have impacts on dormouse survival (Blumstein 2010, Escobar et al. 2015). In addition, at other times of year dormice are often in torpor during the day and so might be more vulnerable to felling events. From this study, however, it is not possible to determine the effects of more direct physical disturbance to the nests of dormice (such as that caused by a large number of falling trees). It is possible that more direct disturbance would elicit a fleeing response in dormice. Further research into the behavioural responses exhibited by dormice to different degrees of noise and physical disturbance would be useful in predicting their response to large-scale felling.

Woodland management leads to immediate changes in vegetation structure and species composition, affecting individual animal range quality (Guo et al. 2008), though populations might nonetheless be resilient over the longer term (Converse et al. 2006). Studies have found little effect of management interventions in parts of a woodland on the abundance of dormice across the entire woodland (Juškaitis 2008, Trout et al. 2012b). Negative effects of habitat alteration for dormice in the short term may be offset by immigration and increases in survival once succession progresses and habitats rapidly become suitable (Juškaitis 2008, Sozio et al. 2016). In fact, some forms of felling, such as thinning and Continuous Cover Forestry, can increase habitat suitability in the longer term by creating glades, a more open canopy (Berg & Berg

1998, Juškaitis & Šiožinytė 2008), and over time the dense, mid-height vegetation and edge habitats which ranging dormice prefer.

Implications for woodland management and dormouse conservation

The promotion and preservation of mid-height trees of 5-10m and edge habitats, and reductions in high forest, will increase the provision of resting and ranging habitats for dormice, although old growth features should also be retained to provide adequate nesting opportunities. Maintaining a dense, highly connected layer between trees will also allow for increased ranging movements. Preserving yew, rowan and hazel trees will also provide preferred autumn habitats for dormice. As dormouse range sizes are small and may lack the flexibility to encompass more resources where required, preferred food plants should be distributed across woodlands to increase their carrying capacity and population abundance.

The lack of behavioural response of dormice to tree removal work could have implications for reduced survival of individual dormice. These effects could be mitigated by the scale of patch removal and the maintenance of some connectivity (Lehmkuhl et al. 2006). However, dormouse preferences for mid-height, scrubby habitats that arise after felling and clearance, emphasise the need for active management to maintain their preferred habitats. Therefore, management will need to find an optimum between felling, which is essential for both silvicultural purposes and for dormouse conservation, and the creation and maintenance of dense and productive understorey, while retaining old growth features. This will inevitably include a trade-off between the likely short-term negative consequences of forestry operations for individual dormice and the long-term positive effects of management for dormouse populations.

Chapter 6

Discussion

Chapter 6: Discussion

Woodland ecosystems have been subject to rapid loss and change over the last 200 years, across Europe and the UK, and indeed globally (Farrell et al. 2000, Hopkins & Kirby 2007, Hansen et al. 2013), due to various anthropogenic pressures and land use change (Young et al. 2005). These habitat variations, combined with the re-structuring of ecological communities and broader climatic shifts, have altered woodlands dramatically, with consequences for the functioning of woodland ecosystems and the populations of many woodland species (Fuller & Gill 2001, Fuller et al. 2007b, Kirby et al. 2017). It is therefore important to assess the status and habitat responses of woodland species to these changes in order to understand the need for conservation action and likely responses to further change (Sutherland et al. 2004). Moreover, once a species' requirements are understood, it is possible to identify synergies and conflicts with the conservation of other species and competing management objectives (Lindenmayer 1999, Rodrigues & Brooks 2007, Cook et al. 2017). If the needs of species align it is then possible to propose indicator and flagship species that can be used to conserve wider habitats and biodiversity (Caro & O'Doherty 1999, Mortelliti et al. 2009).

The hazel dormouse is a protected species and has traditionally been associated with woodland and management systems that, in the UK, have been in decline over the last 100 years (Bright & Morris 1996, Harmer & Howe 2003, Bright et al. 2006). It has also been used as a flagship species for these woodland habitats (Morris 2003). In this thesis, I aimed to i) assess dormouse population change; ii) understand the drivers of hazel dormouse population status in UK woodlands; iii) evaluate the trophic ecology of dormice in relation to woodland habitat; and iv) examine the habitat preferences of dormice in relation to woodland species composition and structure.

In this chapter I will review how I have addressed these research objectives, how the findings of this thesis contribute to knowledge of dormouse conservation, and set the work within the wider context of woodland conservation, change and management.

Dormice and citizen scientists

A major strength of this work is the appraisal and use of citizen science data from the National Dormouse Monitoring Programme (NDMP). The Programme provides a wealth of data across many different woodland contexts. However, due to the challenges of survey design and implementation that are inherent in citizen science schemes, the Programme must be validated to ensure it can adequately represent real population change (Crall et al. 2011, Reynolds 2012, Burgess et al. 2017). I have been able to do this by checking the scheme for potential survey biases in **Chapter 2**. I found no evidence for biases, and thus the NDMP appears to be a robust method of tracking dormouse population change, as well as a source of recreational and social benefits for its volunteer participants.

In **Chapter 3**, using these validated data, I was able to assess environmental influences on populations at a spatial and temporal scale that would not have been possible without citizen scientists (Bonney et al. 2014). The amount of data and length of time over which they were collected have allowed me to quantify more fully the effects of habitats on the abundance, breeding and trends of dormouse populations. This moves beyond the presence-absence approach, a coarser measure of habitat suitability, applied in other studies (Bright et al. 1994, Mortelliti et al. 2011, Reiners et al. 2012, Mortelliti 2013, Amici et al. 2015, Becker & Encarnação 2015).

Furthermore, the selection and use of sites with established dormouse populations in **Chapters 4 and 5** was made possible through information provided by the NDMP and with the help of programme volunteers. The Programme can therefore act as an information resource and starting point for more detailed research of dormouse populations in the UK.

Hazel dormouse habitat requirements

My findings on the habitat requirements of dormice range from those that support established elements of dormouse habitat suitability, to those that provide new insights. The positive effects I found of larger, more connected woodlands on populations have been echoed across habitat suitability studies (Bright et al. 1994, Bailey et al. 2002, Mortelliti et al. 2011, 2014). Other results build on findings

concerning dormouse habitat suitability in other landscape and habitat type settings in Germany and Italy; for example, the negative association of conifers and positive association of open canopy habitats (Bright & Morris 1992, Reiners et al. 2012, Mortelliti 2013, Becker & Encarnação 2015). I have also substantiated evidence for many putative drivers of hazel dormouse population status in the UK (Bright & Morris 1996). These include the positive effects of warm temperatures in spring and summer, and their negative effects in the winter, and the importance of successional habitats within woodland. Some of my findings reveal new elements of dormouse habitat interactions, such as the direct importance of woodland management and presence of particular plant species.

There are some differences between the habitat associations of dormice found in this study and those in continental Europe. For example high summer temperatures had a negative impact on dormouse detection probability in Italy (Mortelliti et al. 2014), it appears that the generally cooler temperatures in the UK did not elicit these effects on detection probability. In contrast to my findings, woodland species diversity was linked to benefits for dormouse populations in Germany and Italy (Mortelliti et al. 2014, Becker & Encarnação 2015). This discrepancy could be due to the fact that the estimated value of habitats will depend on the value of habitats with which they are compared. While this study was able to include many sites, they were all situated in woodland, often where conservation is a principal objective (see **Chapter 3**), and are therefore likely to represent woodland of 'higher conservation value' than the average across the UK. This cautions against uncritically applying these findings on dormouse habitat in all contexts, both on the population level in **Chapter 3** and individual level in **Chapter 5**. On the other hand, many findings in this thesis are consistent with other studies and these seem likely to benefit dormouse conservation when applied across most habitat contexts (Fuller et al. 2007a).

Dormouse decline and environmental change

The habitat associations of dormice I established in **Chapters 3, 4 and 5** provide insight into why the dormice population might be declining nationally, as shown in **Chapter 2**. The prevalence of habitat and climatic characteristics associated with abundant and stable or increasing populations has decreased over the last century.

Climatically, I found that dormice benefit from drier, warmer weather across the active season and consistently cold weather over the winter. While spring and summer temperatures have increased in the UK, precipitation and the occurrence of extreme precipitation events has risen (Horton et al. 2010), which is likely to have affected dormouse activity patterns and survival (Bright et al. 1996, Juškaitis 2014). Perhaps more critically, however, winter temperatures and the frequency of temperature extremes, have increased. Higher temperatures during hibernation increase the metabolic rate of dormice, which may have led to the expedited loss of winter fat reserves, increased winter mortality and reduced dormouse abundance (Juškaitis 1999c, Horton et al. 2010, Bieber et al. 2012).

The extent of semi-natural wooded habitats and size of woods, wooded habitat corridors, glades, successional woodland patches and structural diversity have all decreased in Europe and the UK (Fuller et al. 2007a, Mihók et al. 2009, Kirby et al. 2016). All these features were positively associated with dormouse population abundance, breeding and/or trend in **Chapter 3**, and with favoured ranging and nesting habitats in **Chapter 5**. At the same time, habitats that were negatively associated with dormouse population status, principally even-aged high forest and conifer plantation, have increased (Farrell et al. 2000, Fuller et al. 2007b, Hopkins & Kirby 2007).

Hazel dormouse habitat requirements at multiple scales

Many findings on habitat preferences of dormice were similar across different temporal and spatial scales in **Chapters 3, 4 and 5**. These scales ranged from variation among individuals in their habitat preferences; to dietary variation within and between individuals and populations over different seasons; up to the responses of populations to habitat, landscape, climate and woodland management.

Woodland structural characteristics that were beneficial at the population level in **Chapter 3** were echoed in the habitat structure preferences of individuals in **Chapter 5**. Individual dormice exhibited both ranging and resting preferences for the successional stages and structural diversity of woodlands that were associated with greater dormouse abundance and higher breeding rates across many woodlands.

High forest had equally negative effects at both the individual and the population level. Ranging individuals selected areas of edge habitat, reflecting the positive population association with successional habitats and plant species. There was, by contrast, a negative effect of habitat edges in the population level analysis. However, this is most likely due to the coarser spatial scale on which they were measured. Woodland edges on this scale represented at least 25m of open habitat separating woodland patches, and were therefore more indicative of woodland fragmentation.

If a population study had been conducted in isolation, it might be argued that some of the species that were positively correlated with aspects of dormouse population status could simply be more likely to occur in better habitat and were not important in their own right. However, many of the plant species positively associated with dormouse abundance or breeding, were also preferred by ranging individuals in **Chapter 5**, or were important in the diet of dormice in a high-quality woodland in **Chapter 4**. Two of three species that were preferred by ranging dormice in autumn in **Chapter 5**, hazel and yew, were also associated with higher population abundance and breeding in **Chapter 3**. Willow, associated with higher breeding in **Chapter 3**, was also part of the tree flower group that was important in spring diet in **Chapter 4**, a similar finding to that made by (Juškaitis & Baltrūnaitė 2013). Honeysuckle made a significant contribution to the diet of dormice in the autumn in **Chapter 4**, and was associated with greater population abundances across woodlands in **Chapter 3**, and was most probably under-recorded in the habitat use of ranging dormice in **Chapter 5**, so any preference might have been missed. The only species where consistency in effect could not be demonstrated was birch. Although this species was associated with high dormouse abundance in **Chapter 3**, it may have acted as an indicator of successional habitat types, and therefore was not preferred by individual dormice in **Chapter 5** (Becker & Encarnação 2015). It could not be entered in its own right into diet models in **Chapter 4** as it was not isotopically distinctive from other shrubs, and so preference, if any, could not have been detected.

Conversely, it might be argued that preferences for woodland tree and shrub species at fine temporal and spatial scales, should not be generalised across longer time frames and larger areas. The preferences of dormice in two woodlands over three weeks in autumn, as in **Chapter 5**, might not apply across seasons and woodlands.

There is, however, evidence in **Chapter 3** that hazel and yew are valuable over different woodland habitats and seasons in multiple years. The lack of apparent importance of hazel in the diet models of **Chapter 4** is most likely due to the timing of sample collection as diet was characterised in summer when hazel is not yet producing ripe nuts. Rowan, which is preferred by ranging dormice in autumn, did not appear to be important on the population scale across woodlands and years. This could be because it is specifically valued in autumn when it bears fruit, or that it is not common enough for its beneficial effect to be detected on the population scale.

Woodland management for dormouse conservation

The formation of woodland management recommendations, from the landscape to the stand level, was a strong motivating force behind this work. I found in **Chapters 3 and 5** that woodland management is beneficial for dormice. In **Chapter 4**, I also found that woodland management has the potential to improve resource distribution for dormice. These findings, however, are conditional on the fact that the sites and types of woodland management studied were predominantly conservation orientated. Therefore, while I have found small-scale and conservation management practises to have positive implications for dormice, this may not extend to all forest management, especially more commercial practises.

In **Chapter 5**, I showed that the removal of trees around the home ranges of dormice restricted the extent to which they shifted their ranging areas, and could have dispersal and survival consequences when felling is carried out in contiguous blocks and/or on a large scale. Dormouse preferences are for habitats that result from management interventions, however, and so active management is required for the creation of favourable habitat in the long term. This beneficial effect is echoed in **Chapter 3** on the population level, where active woodland management had a positive effect on dormouse abundance across many woodland sites and over long timeframes. Furthermore, the habitats associated with higher population abundances, breeding rates and trends were often the successional vegetation species and younger woodland habitats which result from management.

Alongside the importance of younger habitats, I have briefly identified the importance of old-growth features, such as cavities and dead trees, for dormouse resting sites in **Chapter 5**. These old growth features should be preserved, and the emphasis for dormouse conservation placed on the maintenance of a heterogeneity of habitat structures and ages within woodland. Therefore, the need for woodland management is nuanced, and should include consideration of the specific features of certain stands. This argument has also been made for other species groups which have diverse habitat needs, such as woodland birds (Quine et al. 2007). It was not possible to look at old growth features in isolation from vegetation height in **Chapter 3**, but this would be beneficial in future work.

The small ranges of dormice identified in **Chapter 5** and in other studies (Bright & Morris 1991, 1992), and fine scale at which food availability affected dormouse trophic niches in **Chapter 4**, suggests that resources should be distributed throughout a woodland in order to increase its dormouse population density. The consumption over summer of a range of plant food sources, illustrated in **Chapter 4**, also places emphasis on maintaining the availability of a range of plants across the season (Hopkins & Kirby 2007).

Forest systems in Europe and the UK will continue to experience changing climate, species composition and disease pressures (Lawrence 2017). This uncertainty emphasises the importance of habitat improvement to buffer and strengthen dormice populations in the face of this change (Lindenmayer 1999, Fuller et al. 2007b).

Legislative protection of dormice in woodlands: help or hindrance?

Considerable time and financial resources are devoted to abiding by legislation for dormice when performing routine forestry and woodland management activities (Hartley 2002, Hauer et al. 2010). This is especially true in woodlands and forestry plantations, which contain multiple protected species, whose legislation must be considered in tandem. While legislation therefore provides effective protection from habitat removal, it may create barriers to the implementation of desirable woodland management (Bright et al. 1994). Species protective legislation has been unsuccessful in preserving other species suffering from habitat deterioration or subtle changes in

habitat quality (Wulf 2003, Santangeli et al. 2013, Jokinen et al. 2015, Rossi et al. 2015).

Consequently, there have been calls for a shift from individual to population-level consideration of the effects of disturbances on European Protected Species; as individual protection may not result in population-level benefits (Wulf 2003, Heydon et al. 2010).

A shift towards maintaining the 'Favourable Conservation Status' of dormice populations, rather than simply preventing the destruction of individuals and their habitats, could encourage more pro-active conservation (Russell et al. 2013, Mölder et al. 2014, Jokinen et al. 2015). This shift to population-level measures has been suggested for other species, such as the Siberian flying squirrel *Pteromys volans* where the protection of individuals and their nest sites has not adequately conserved the species in forest systems (Santangeli et al. 2013, Jokinen et al. 2015). Moreover, forest managers may be deterred from establishing favourable dormouse habitat in their woods due to an unwillingness to take on the responsibility, and associated resource demands, of protecting the dormice that will reside there.

As well as focusing on populations, integration of habitat management measures into species protection could benefit dormice (Pärtel et al. 2005). Such approaches are sometimes delivered legislatively through compensation payments to land managers for implementing certain management regimes (Kleijn & Sutherland 2003, Wätzold & Schwerdtner 2005). This is particularly relevant to extensive land-cover types, such as woodland, as habitat designation (e.g. as nature reserves) does not adequately conserve these habitats (Ostermann 1998). Policy changes to integrate forest and woodland into the CAP have been proposed by stakeholders in the UK (Sutherland et al. 2010). These measures, however, are extremely costly to assess, implement and enforce and their cost-effectiveness has been little examined (Wätzold & Schwerdtner 2005).

Threats facing the hazel dormouse arise from habitat changes that are broadly similar across Europe (Rudel et al. 2005, Mölder et al. 2014, Rossi et al. 2015, Ranta et al. 2016). Consequently, issues surrounding dormouse conservation legislation are likely

to apply in many national contexts. Conflicts have been reported between EU legislative requirements of agricultural, water and conservation policies (Young et al. 2005, Ranta et al. 2016). Studies into the perception of these conflicts by woodland managers, and an understanding of how different management priorities are balanced in multi-functional forests would help direct future conservation efforts (Primmer & Karppinen 2010, Lawrence 2017).

Woodland conservation and management implications

A more detailed knowledge of the habitat management requirements of dormice allows their conservation to be delivered more efficiently alongside other woodland management priorities. The fact that dormice have been impacted by widespread changes in woodland habitat types, configuration and structure supports the case for their continued use both as indicators of woodland change and as a flagship species for woodland habitats (Caro & O'Doherty 1999, Morris 2003, Hunter et al. 2016). The popularity of the species could allow the dormouse to be a symbol of the effects of woodland change in the UK and Europe. The associations of dormice with the pre-industrial landscapes and habitats of over 200 years ago may even enhance its appeal and flagship status (Grant & Edwards 2008).

Many species have been shown to suffer from the loss and fragmentation of woodland habitats that also affect dormouse populations (Macdonald & Rushton 2003, Bailey 2007, Mortelliti et al. 2011, Mortelliti 2013). Woodland birds have been similarly negatively impacted by the loss of successional habitats and structural diversity, canopy closure and increased deer densities (Fuller et al. 2007a, Hewson et al. 2007). Furthermore, their declines have been connected to related changes in management practices (Fuller et al. 2007b, Quine et al. 2007). Equally, woodland butterflies and moths have suffered from habitat fragmentation, canopy closure and the loss of more open and transitional habitats (Fartmann et al. 2013, Fox 2013). In stored coppice, particularly, butterflies and moths have suffered from the abandonment of management and require rotational systems to maintain diversity (Broome et al. 2011, Fartmann et al. 2013). Some species, for example some moth and bird species, however, benefit from mature closed-canopy woodlands and the microclimates these create (Broome et al. 2011, Quine et al. 2011). While generally these species have

not experienced declines, as their habitat has become more prevalent, their requirements must also be considered in habitat planning (Quine et al. 2007). Further study of the coincidence of dormouse population status with the status of different taxa and threatened species will quantify the extent that conserving dormice would fully conserve other species. The conservation of woodlands for dormice could also increase their recreational and aesthetic value by introducing more structural, floristic and species diversity, features which are preferred by people (Dhakal et al. 2012, Filyushkina et al. 2017). On the other hand, recreational demands on woodlands do not always coincide with conservation objectives. For instance, the heavy use of paths by dogs and people has the potential to disturb nesting and hibernating dormice, which might in turn have detrimental impacts on survival and population persistence.

As well as conservation and recreation, the management of increasingly multifunctional forests often has to consider timber production. This often involves a trade-off between different extents of conservation and production (Faith et al. 1996, Nalle et al. 2004, Hauer et al. 2010, Brockerhoff et al. 2017). The results of this thesis do not warn against silvicultural management *per se*, and in fact the removal of trees, even in forestry production systems, will open canopies and result in mid-successional habitats, benefiting dormice (**Chapter 3 and 5**). However, the effects of tree removal on individual ranges will alter their dispersal capabilities, and could affect survival, as illustrated in **Chapter 5**. This will have greater ramifications in forestry systems where felling is conducted at larger scales. Hence the detrimental effect of felling trees needs to be balanced with the beneficial effects of the creation of new habitats. For example, research into how individual effects translate into population consequences; the optimal balance of age structures within a woodland; thresholds of habitat removal; and the effects of the timing of forestry operations would inform how to achieve this balance.

While the sites in this study are generally conservation-orientated, broad habitat principles found to benefit dormice can be applied in sites with alternative management objectives, including those more oriented towards commercial production (Hartley 2002, Lindenmayer et al. 2006). Moreover, commercial conifer systems are less valuable dormouse habitats, and the introduction of more broadleaf species and structural diversity would increase their value for dormice, as well as

benefit wider biodiversity (Hartley 2002, Smith et al. 2007, Calladine et al. 2015). The introduction of these measures, however, may compete with economic aspects of forestry and the costs of habitat improvement measures must be considered (Nalle et al. 2004, Naidoo et al. 2006).

Concluding remarks

Effective conservation of a species requires knowledge of its status, requirements and the influence of changing environmental conditions. An understanding of these dimensions allows the conservation of a species to be considered alongside the conservation of other species, habitats and ecosystem service delivery. This is particularly useful in increasingly multifunctional forest systems, which must also balance other land-use demands such as the provision of wood products. In this thesis, I have quantified the changing status of dormice populations in UK woodland through the use of validated citizen science data. Further use of these data has allowed assessment of the environmental influences on dormouse populations at large temporal and spatial scales across different habitat settings. I have also examined the habitat associations of dormice at multiple scales, highlighting the importance of understanding the effects of habitat on individuals, between individuals within different populations, and across populations. The outcomes of the research in this thesis provide recommendations for the preservation, configuration and management of woodlands to aid dormice conservation. Moreover, this work highlights the importance of assessing the status of species protected by international and national legislation, and appraising the success of this legislation in promoting effective conservation. Dormouse declines are symptomatic of wider environmental and management changes that have affected a large raft of declining woodland species. Thus, conservation of this endearing and popular mammal can be central to a change in attitude towards conserving wider woodland biodiversity.

Appendices

Appendix 1: Methodological details of model selection procedure (chapter 3)

Prior to analyses, correlations between explanatory variables were explored using Pearson's correlation or Spearman's rank correlation tests. Correlated explanatory variables (> 0.5 correlation coefficient) included habitat proportions within the area covered by the nest boxes and the woodland site, and the amount of Ancient woodland and total woodland within the surrounding 1km. Correlated variables were precluded from appearing together in models and a single variable was selected that was the best predictor of the response variable (Austin 2002).

Model selection was performed using an information theoretic approach and the effects of explanatory variables were derived through multi-model inference via model averaging using the MuMIn package (Bartoń 2017). This approach involves assessing all candidate models comprised of all possible combinations of explanatory variables and ranking these by Akaike's Information Criterion (AIC), adjusted for sample size (AICc) (Whittingham et al. 2006, Lindberg et al. 2015). These models were fitted by Maximum Likelihood for Generalised Least Squares and Restricted Estimate Maximum Likelihood for GAM analysis. The models selected to be the most likely to explain variation in dormouse population measures were all those within $2 \Delta AIC$ of the top model (Burnham & Anderson 2002). Model averaging was performed across this top model set, weighted by their relative AICc values, to calculate effect sizes and confidence intervals. The relative importance (RI) of each variable is the proportion of models within the top model set that included that term.

Conditional or 'natural' model averaging averages the effect of a variable only across models in which it is present, whereas full or 'zero-method' averaging sets that effect to be zero when it is not present in models and is thus more conservative (Grueber et al. 2011).

Appendix 2: Details of data acquisition, processing and analysis (chapter 3)

A. Landscape and habitat data acquisition and processing

The National Forest Inventory classifies woodland habitat areas of >2ha based on Ordnance Survey imagery. EC Forest data are based on CORINE land cover maps and Landsat imagery (Spot4; Spot5 and IRS-P6) of 25m resolution, spatial types were classified as follows: edge, within 25m of forest exterior; isolated, surrounded by less than 25m woodland and over 25m from other woodland; and interior, surrounded by over 25m woodland on all sides.

Environment Agency LiDAR data are gathered through aerial surveys using lasers to map the ground (terrain layer) and above ground level (surface layer). Coverage was incomplete on around half the sites for which LiDAR data were downloaded (n=109); all sites with over 90% coverage and enough dormouse population data to derive indices were used.

The area of a woodland site was defined as the area of contiguous woodland (classified by NFI as not separated by more than 20m) in which the nest boxes were located. The landscape surrounding a site was defined as within 1km around the perimeter of sites. I determined this method of classifying 'wooded site' and 'landscape' by comparing three different scales of classification for each (20m, 30m and 70m; 50m, 500m and 1km respectively), fitting a Generalised Additive Model with an interactive smoothed term describing location (see statistical analysis section for full model description) and selecting the spatial scale in the model that best described variation in population indices.

B. Derivation of dormouse population indices

To obtain site indices, a Generalized Additive Model (GAM; using the R package mgcv (Wood 2011)) was fitted to the adult dormouse count with year as a smoothed term, site as a factor and an offset for the number of nest boxes on site to control for survey effort. Only counts of adult dormice were used as different age classes are not consistently recorded and any young and juveniles have high winter mortality and are less representative of year-to-year population size (Juškaitis & Büchner 2013). The

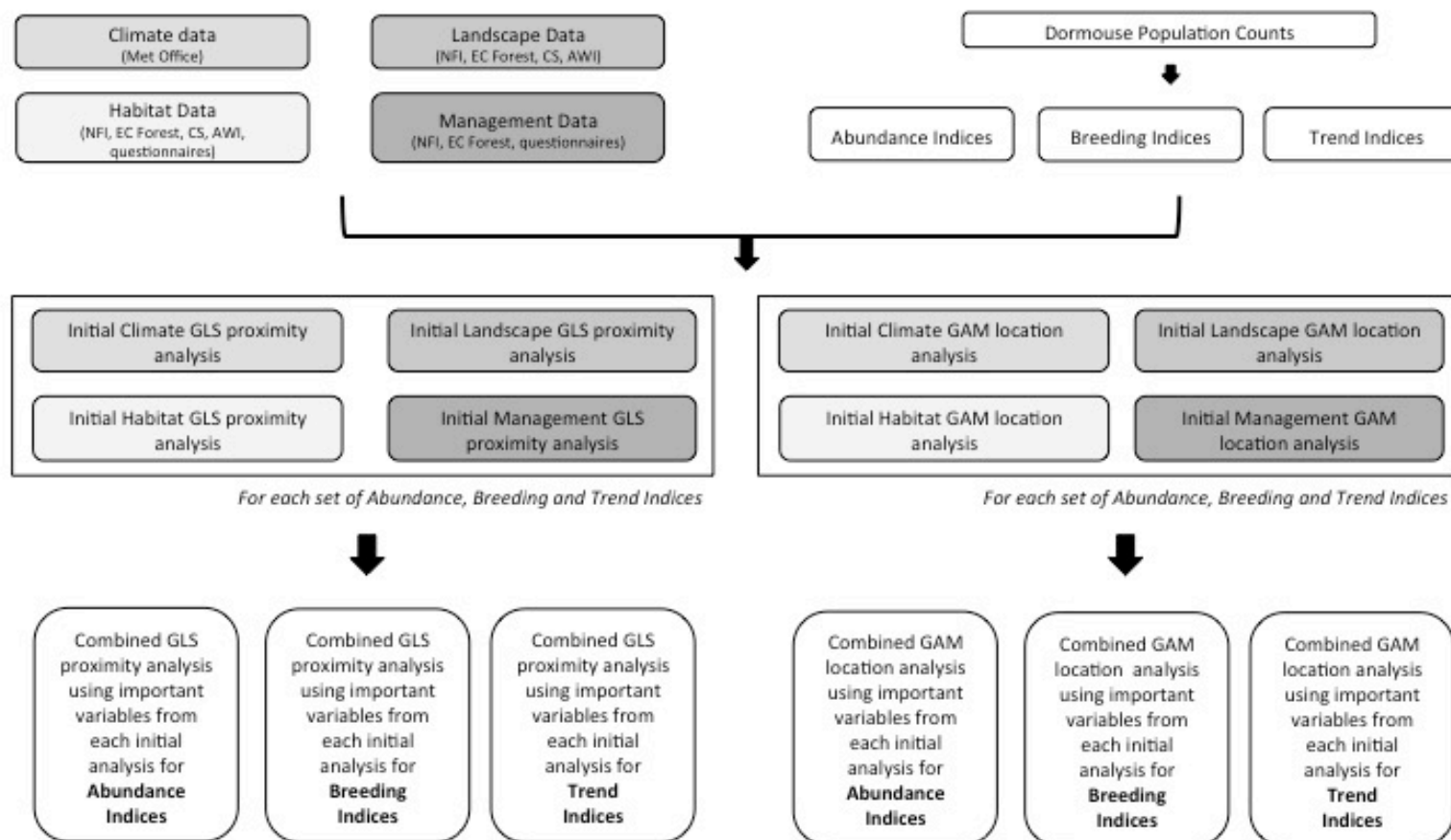
intercepts for each site were extracted and used as a site-level index of dormouse abundance (“Abundance index”). I used a similar approach of fitting a GAM to counts of the number of litters to derive a site-level, time independent index of breeding frequency (“Breeding index”). I checked whether the inclusion of nest box density improved the fit of these two models but found it did not explain significant variation in the dormouse abundance, whether it was used in addition to or instead of the number of boxes. Abundance and Breeding indices were log-transformed in all further analyses to normalize their distribution.

A similar generalized linear model (GLM) was then used to derive population trends for each site. Five sites were excluded from this analysis as trends could not be estimated due to a sparsity of count data, leaving 295 sites. The trend was obtained by including a site*year interaction term in the model. The slope coefficient for each site was then extracted to produce a “Trend index”. This index represents the average annual change in dormouse numbers on sites relative to an index of 1 in a baseline year; i.e. a trend of 0.5 signifies an average 50% decline in dormouse numbers each year while a trend of 1.5 represents a 50% increase (Goodwin et al. 2017).

Table S2.1. Variables used in initial analyses of the effects on dormouse Abundance Indices, Breeding Indices and Trend indices. ECF = EC FOREST remotely sensed datasets. NFI = National Forest Inventory remotely sensed datasets. ‘Edge habitat’ is habitat on the edge of a woodland patch >100m² and >25m from another woodland patch. ‘Isolated woodland habitat’ is part of a small woodland patch <100m² and >25m from another patch.

Climate variables translated into 8 PCs	Plant species (questionnaire) data on DAFOR scale	Broad scale habitat variables (ECF 2006; NFI 2012)
Daily minimum winter temperature (°C)	Simpsons diversity index	Proportion of woodland in surrounding 1km
Daily winter temperature range (°C)	Abundance of hazel	Proportion of ancient woodland in surrounding 1km
Daily minimum spring temperature (°C)	Abundance of willow	Mean length of hedgerow in surrounding 1km (Km)
Mean daily spring sun hours	Abundance of ash	Size of site (km ²)
Total spring rain (mm)	Abundance of oak	Proportion of broadleaf habitat in woodland site
Daily minimum summer temperature (°C)	Abundance of birch	Proportion of mixed broadleaf/conifer habitat in woodland site
Mean daily summer sun hours	Abundance of conifer	Proportion of edge habitat in woodland site
Total summer rain (mm)	Abundance of honeysuckle	Proportion of isolated woodland habitat in woodland site
Daily minimum autumn temperature (°C)	Abundance of bramble	Proportion of ancient woodland in woodland site
Mean daily autumn sun hours	Abundance of sycamore	Proportion of shrub habitat in woodland site
Total autumn rain (mm)	Abundance of yew	Proportion of broadleaf habitat in nest box area
		Proportion of mixed broadleaf/conifer habitat in nest box area
		Proportion of edge habitat in nest box area
		Proportion of isolated woodland habitat in nest box area
Management (questionnaire) data	Change in woodland habitat (ECF; NFI)	Proportion of ancient woodland in nest box area
Total area managed (ha)	Change in woodland configuration 2000-2006 (ECF)	Proportion of shrub habitat in nest box area
Whether site reported management	Any change in habitat proportion 2011-2014 (NFI)	

Figure S2.1. Schematic diagram illustrating the analytical pathway for initial and final assessment of the effect of climate, landscape, habitat and management features on Dormouse Abundance, Breeding and Trend Indices of sites. EC Forest = EC FOREST remotely sensed datasets. NFI = National Forest Inventory remotely sensed datasets. AWI=Ancient Woodland Inventory, CS = hedgerow Countryside Survey. Questionnaires were sent out to site dormouse monitors. GLS = Generalised Least squares. GAM = Generalised Additive model with interactive smoother for x and y spatial coordinates.



Appendix 3: Principal Component tables for climate and LiDAR data (chapter 3)

Table S3.1. Principal Component Analysis of climate variables on National Dormouse Monitoring Programme sites. The rotation (R) and the Proportional Loading (PL) (the amount of variation) associated with different climate variables for each Principal Component (PC) used in the analysis of the effect of between site variation in climate on dormouse abundance indices. % of variation attributed to each PC is also shown. PCs explaining the large majority (76%) of observed climate variation among NDMP sites are in red.

	PC1		PC2		PC3		PC4	
	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>
Mean daily max winter temp	-0.24	0.08	0.10	0.04	-0.52	0.24	0.20	0.08
Mean daily winter temp range	0.21	0.07	-0.40	0.15	-0.78	0.37	-0.04	0.02
Mean minimum summer temp	-0.52	0.18	0.04	0.02	0.02	0.01	0.06	0.02
Total summer rainfall	0.13	0.04	0.46	0.18	-0.14	0.07	-0.50	0.19
Mean daily summer sunshine hrs	-0.35	0.12	-0.09	0.04	0.02	0.01	0.39	0.15
Mean minimum spring temp	-0.36	0.12	0.11	0.04	-0.19	0.09	-0.15	0.06
Total spring rainfall	0.07	0.02	0.49	0.19	-0.20	0.10	0.31	0.12
Mean daily spring sunshine hrs	-0.26	0.09	-0.02	0.01	-0.04	0.02	-0.62	0.24
Mean min autumn temp	-0.36	0.12	0.15	0.06	0.02	0.01	0.07	0.03
Total autumn rainfall	0.05	0.02	0.56	0.22	-0.14	0.07	0.08	0.03
Mean daily autumn sunshine hrs	-0.37	0.13	-0.16	0.06	-0.06	0.03	-0.20	0.08
% variation explained	51		25		8		4	
	PC5		PC6					
Mean daily max winter temp	0.11	0.04	-0.07	0.03				
Mean daily winter temp range	-0.03	0.01	0.17	0.06				
Mean minimum summer temp	0.20	0.07	-0.20	0.07				
Total summer rainfall	0.04	0.01	-0.01	0.00				
Mean daily summer sunshine hrs	-0.46	0.16	0.29	0.11				
Mean minimum spring temp	0.45	0.16	-0.21	0.08				
Total spring rainfall	-0.18	0.06	-0.21	0.08				
Mean daily spring sunshine hrs	-0.32	0.11	0.33	0.12				
Mean min autumn temp	0.26	0.09	0.62	0.22				
Total autumn rainfall	-0.32	0.11	0.13	0.05				
Mean daily autumn sunshine hrs	-0.47	0.16	-0.50	0.18				
% variation explained	4		2					

Table S3.2. Principal Component Analysis of LiDAR data from National Dormouse Monitoring Programme sites. The rotation (R) and the Proportional Loading (PL) (the amount of variation) associated with different LiDAR vegetation structure variables for each Principal Component (PC) used in analysis of vegetation structure on dormouse abundance and breeding indices. % of variation attributed to each PC is also shown.

Site area	PC1		PC2		PC3		PC4	
	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>	<i>R</i>	<i>PL</i>
Variation in canopy density (5m)	0.44	0.17	-0.16	0.08	0.28	0.12	0.25	0.13
Prop of open ground	-0.20	0.08	0.77	0.40	0.17	0.07	0.04	0.02
Prop of 0-1m vegetation	-0.35	0.13	- 0.58	0.31	- 0.18	0.08	- 0.02	0.01
Prop of 1-2m vegetation	0.32	0.13	0.08	0.04	- 0.67	0.30	0.24	0.13
Prop of 2-5m vegetation	0.43	0.17	0.13	0.07	- 0.38	0.17	0.15	0.08
Prop of 5-10m vegetation	0.46	0.18	-0.02	0.01	0.06	0.03	- 0.85	0.44
Prop of over 10m vegetation	0.38	0.15	- 0.16	0.08	0.52	0.23	0.37	0.19
% variation explained	59		20		17		2	

Appendix 4: Site composition details (chapter 3)

Information on all environmental characters was available for 180 sites for Abundance, 140 for Breeding and 182 for Trend Indices. The most widespread habitat type was broadleaf woodland, occurring on 99% of sites, and comprising an average of 69% ($\pm 2\%$) of site area. Ancient woodland occurred on 77% of sites, and on these an average of 64% ($\pm 2\%$) of site area was ancient woodland. Conifer woodland occurred on 48% of sites, and on these an average of 14% ($\pm 2\%$) of site area was conifer-dominated habitat. Isolated woodland, mixed broadleaf and conifer, and shrub occurred in 69%, 39% and 36% of woodland sites respectively. Hazel was the most common species, reported at 99% of sites. Oak, bramble, honeysuckle, ash and birch were all found at $> 90\%$ of sites while willow, sycamore, conifer, sweet chestnut and yew were reported on between 50 and 90% of sites.

Appendix 5: Food source groupings and availabilities (chapter 4)

Table S5.1. The food source groups, constituent samples and sample sizes used in dormouse dietary assessment of Bradfield Woods. All samples were mentioned as dormouse dietary sources in the literature.

Source groups	Constituent samples					
	Spring	(n)	Total n	Autumn	(n)	Total n
Hazel	Hazel leaf buds	41	41	Hazelnut	40	40
Honeysuckle	Honeysuckle flowers	27	37	Honeysuckle flowers	16	50
	Honeysuckle leaf	10		Honeysuckle berries	34	
Shrubs	Birch catkins	19	65	Birch catkins	10	166
	Bramble flower	30		Bramble berry	38	
	Hawthorn berries	16		Hawthorn berries	86	
				Sloe berries	8	
				Rose hip	24	
Trees	Oak flower	28	43	Acorn	40	48
	Willow flower	15		Ash seeds	8	
Lepidoptera	Larvae	13	17	Larvae	12	12
	Adults	4				
Omnivorous	Hemiptera	2	61	Hemiptera	6	91
Invertebrates	Coleoptera	15		Coleoptera	37	
	Aranae	39		Aranae	38	
	Dermaptera	4		Dermaptera	10	
	Ephemeroptera	1				

Appendix 6: Estimates of range size for tracked dormice (chapter 5)

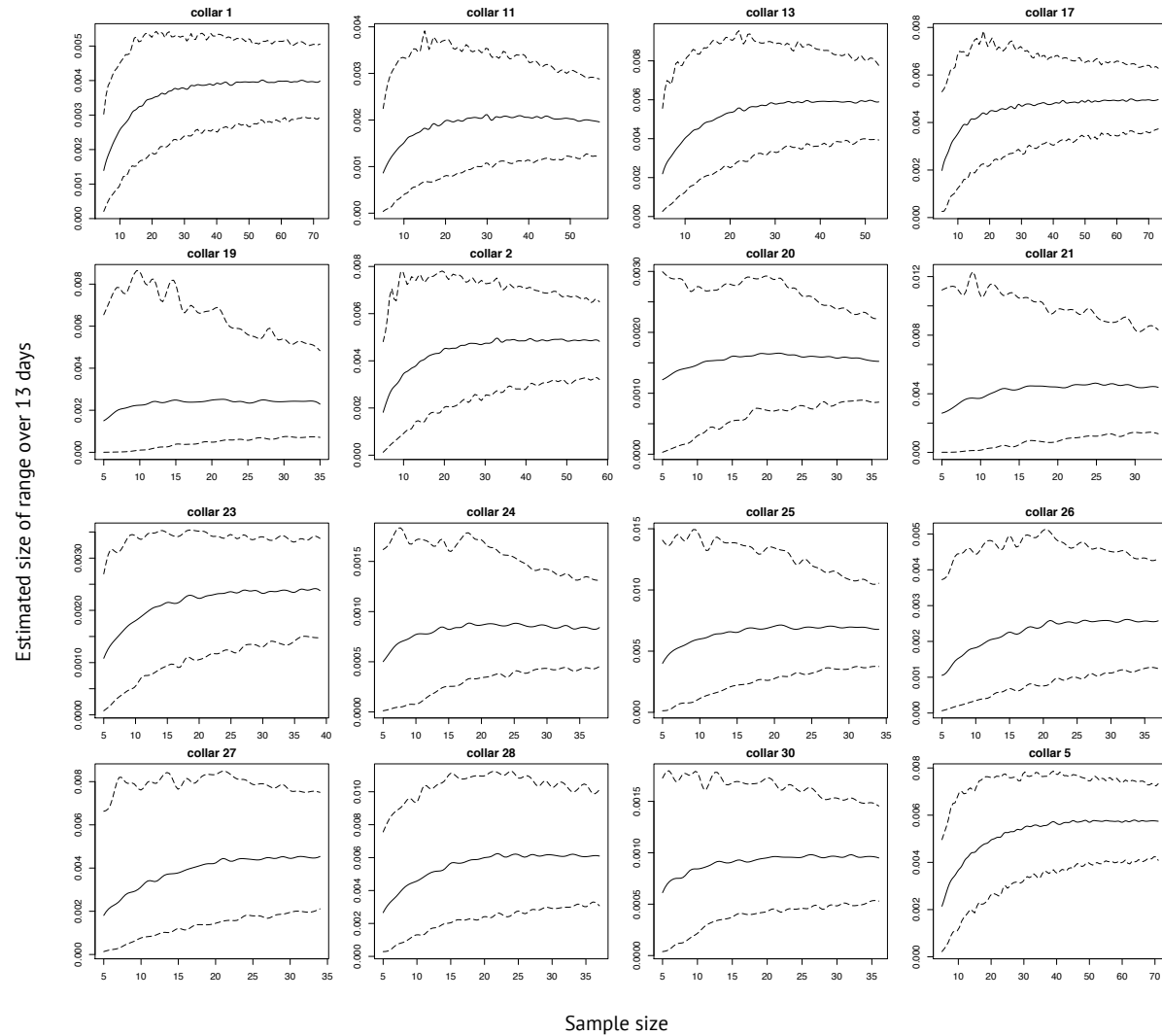


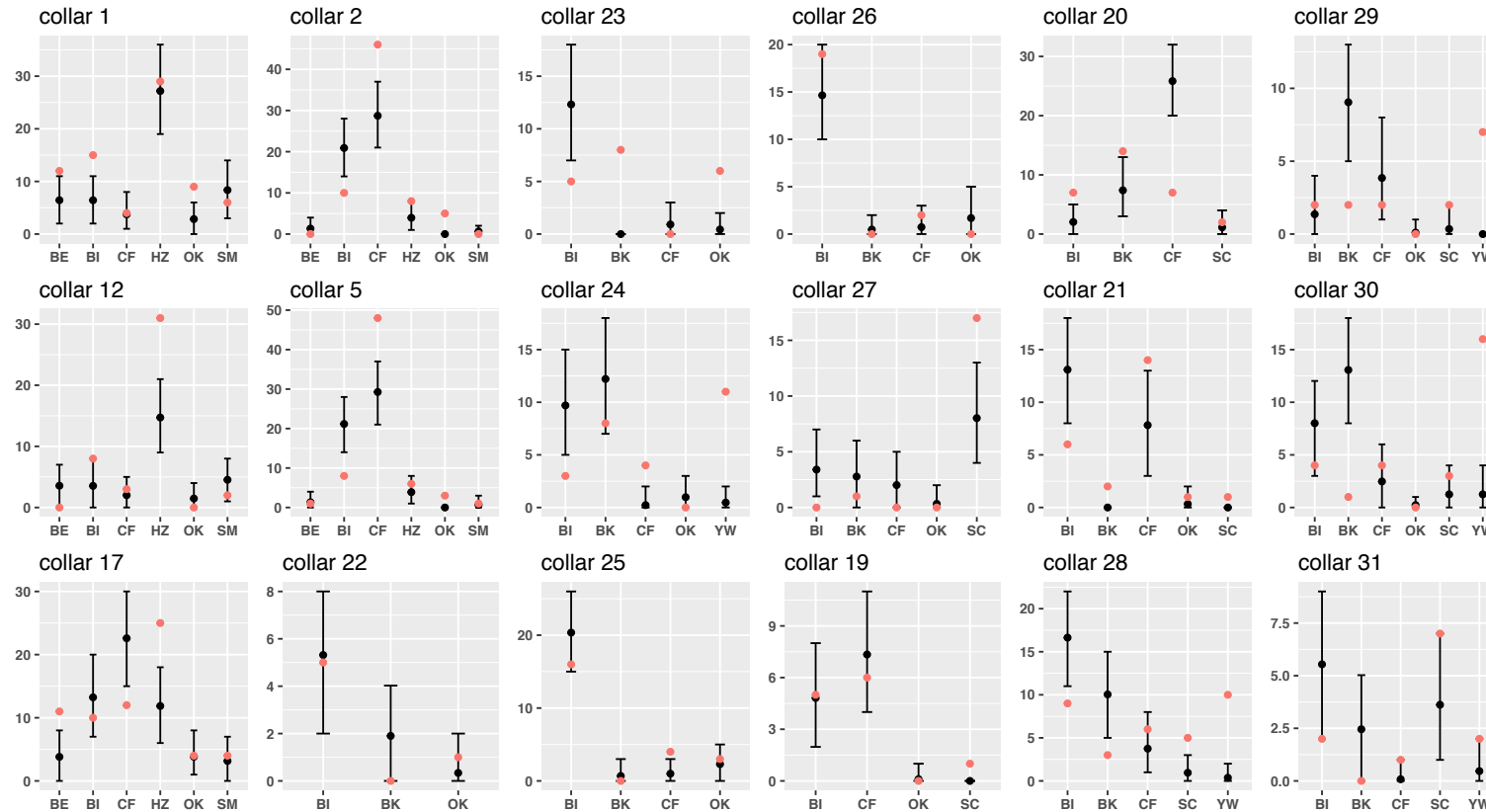
Figure S6.1. Estimates of the range sizes of dormice (in km²) over 13 days, using increasing numbers of fixes. Means and 95% Confidence Intervals are calculated from 1000 bootstrap samples for each number of fixes. Graphs illustrate asymptotic distributions but wide margin of error. 95% CIs for collar 19 and 21 are particularly wide, and asymptotes low, due to a high proportion of time spent in nestboxes overnight.

Appendix 7: Principal Component tables for LIDAR data (chapter 5)

Table S7.1. PC tables for LIDAR values of used and available canopy areas for A) ranging areas and B) resting sites. The rotation (R) and the Proportional Loading (PL) (the amount of variation) associated with LIDAR vegetation structure variables is shown for each Principal Component (PC) used in preference analysis for nighttime ranging and daytime resting. % of variation attributed to each PC is also shown.

	PC1		PC2		PC3		PC4		PC5		PC6	
A) Nighttime ranging points	R	PL	R	PL	R	PL	R	PL	R	PL	R	PL
Variation in canopy height	-0.04	0.02	-0.53	0.22	-0.51	0.23	0.14	0.06	-0.04	0.02	-0.66	0.29
Canopy density	0.55	0.22	0.10	0.04	-0.15	0.07	-0.03	0.01	-0.10	0.05	0.05	0.02
Local var. in canopy density (1m)	-0.24	0.09	-0.08	0.03	-0.74	0.33	-0.19	0.09	0.04	0.02	0.60	0.27
Prop of 0-1m vegetation	-0.39	0.16	-0.22	0.09	0.17	0.08	0.56	0.25	0.43	0.23	0.19	0.08
Prop of 1-2m vegetation	-0.40	0.16	-0.12	0.05	0.15	0.07	0.04	0.02	-0.85	0.46	0.08	0.04
Prop of 2-5m vegetation	-0.39	0.16	0.22	0.09	0.03	0.01	-0.65	0.29	0.23	0.12	-0.31	0.14
Prop of 5-10m vegetation	0.08	0.03	0.60	0.26	-0.33	0.15	0.41	0.18	-0.13	0.07	-0.15	0.07
Prop of over 10m vegetation	0.41	0.16	-0.48	0.20	0.13	0.06	-0.19	0.09	-0.03	0.01	0.20	0.09
% variation explained	38		23		16		11		8		4	
B) Daytime resting points	R	PL	R	PL	R	PL	R	PL	R	PL	R	PL
Variation in canopy height	0.03	0.01	-0.48	0.21	-0.59	0.28	0.18	0.08	-0.28	0.13	-0.55	0.24
Canopy density	-0.51	0.21	0.16	0.07	-0.13	0.06	-0.02	0.01	-0.12	0.06	0.09	0.04
Local var. in canopy density (1m)	0.25	0.10	0.00	0.00	-0.70	0.33	-0.21	0.09	0.18	0.08	0.60	0.26
Prop of 0-1m vegetation	0.40	0.16	-0.27	0.11	0.15	0.07	0.51	0.23	0.50	0.24	0.03	0.01
Prop of 1-2m vegetation	0.43	0.17	-0.16	0.07	0.23	0.11	0.04	0.02	-0.76	0.36	0.33	0.14
Prop of 2-5m vegetation	0.40	0.16	0.16	0.07	0.02	0.01	-0.68	0.31	0.11	0.05	-0.41	0.18
Prop of 5-10m vegetation	0.03	0.01	0.66	0.29	-0.24	0.11	0.40	0.18	-0.17	0.08	-0.10	0.04
Prop of over 10m vegetation	-0.42	0.17	-0.43	0.19	0.07	0.03	-0.17	0.08	0.02	0.01	0.20	0.08
% variation explained	43		22		15		9		5		4	

Appendix 8: Use and availability of tree species for each dormouse (chapter 5)

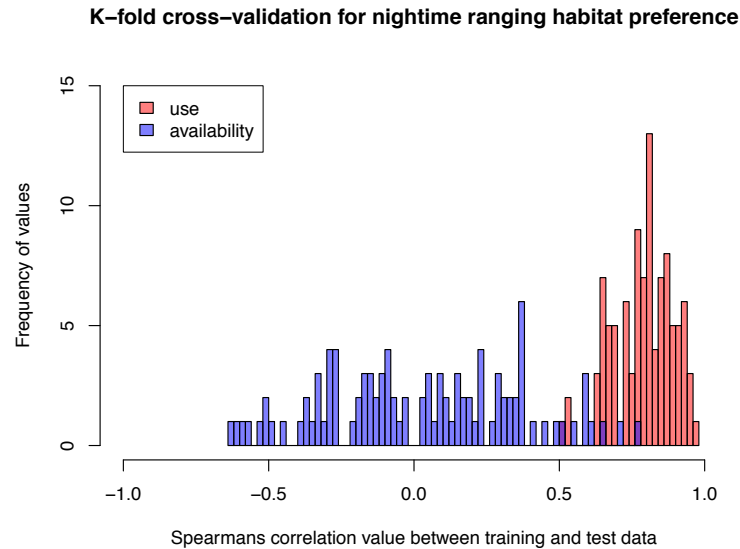


YW=Yew, OK=Oak, BE=Beech, SC=Sweet Chestnut, SM=Sycamore, BK=Bracken, CF=Conifer, BI=Birch, HZ=Hazel.

Figure S8.1. Counts of the use and availability, for individual dormice, of the main tree species on each site (three to six tree species per dormouse). Collars 1, 2, 5, 12, 17 were on the Devon site, and collars 22 - 31 were on the Kent site. Red points indicate the counts of each tree that were used by the dormice, black points and error bars indicate mean availability from 1000 bootstrap samples (\pm 95% Confidence Intervals).

Appendix 9: K-fold cross validation for models of habitat preference (chapter 5)

A)



B)

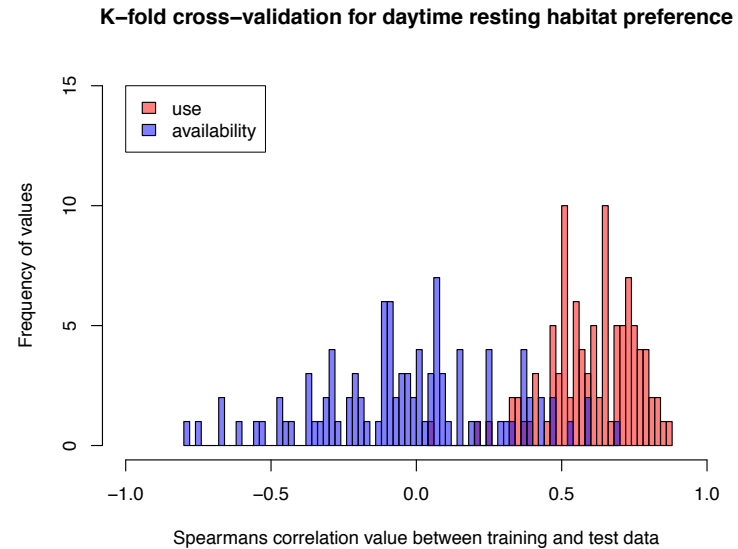


Figure S9.1. Results of k-fold cross-validation procedures for binary logistic regression models of habitat preference based on use and availability data for dormouse A) nighttime ranging and B) daytime resting. Histograms of Spearman's rank correlation values between model predictions based on 100 samples of training data and test data are shown for used habitat (red) and available habitat (blue).

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