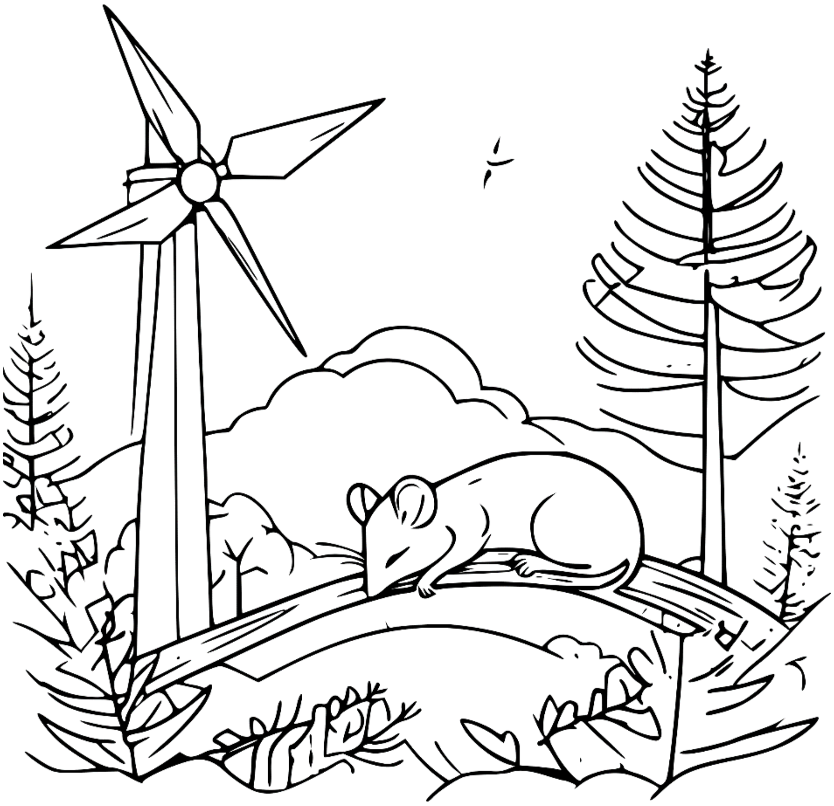
# Conservation of the hazel dormouse on the edge of the species’ range

Submitted by Charlotte Armitage to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, December 2023.



I certify that all material in this thesis which is not my own work has been identified and that no material any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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# Abstract

Species declines are both widespread and worsening, and climate change is predicted to become one of the biggest drivers. Populations living at the edge of species' distributional ranges are projected to be particularly vulnerable under future climate change scenarios. Life history strategies, such as dormancy, will play a role in how variation in species resilience and persistence, especially in non-typical habitats at the peripheries of their range, becomes manifest. Energy conservation strategies, such as dormancy, might gain particular significance in the context of a changing climate, potentially affording individuals of some species a competitive advantage. Understanding the energetic and ecological requirements of species, particularly those at the range margins, is likely to become more useful for effective conservation.

In this thesis, I have investigated the patterns, drivers, and consequences of daily torpor use in populations of hazel dormice *Muscardinus avellanarius* in Britain. I have then assessed how this behaviour might change in response to climate change, and what the implications are for dormouse populations. I evaluate new tools for effective conservation of dormice in marginal landscapes by testing species distribution models at different resolutions. I then explore dormouse ecological requirements in these landscapes through dietary analysis.

My study reveals that rates of daily torpor are influenced by factors such as the presence of ancient woodland, connectivity of broadleaf habitat, geographic location, and climate. I reveal relationships between torpor, dormouse abundance, and breeding events, directly impacting population dynamics.

I then predict the future frequencies of daily torpor in Britain. Projections suggest a reduction in torpor use as local climatic conditions change, potentially leading to increased fecundity among dormouse populations in England and Wales. However, under worst-case climate scenarios, elevated torpor rates are expected in certain years, posing a risk to small populations, especially those at the distributional edge. Conservation strategies should focus on preventing declines at range margins, fostering resilience, and averting range constriction.

At a landscape scale, I examined the accuracy of predicting dormouse distribution in non-typical habitats, particularly conifer plantations at the edge of their range in North Wales. Regional and national species distribution models could not accurately predict dormouse presence in non-typical habitat, highlighting the need for increased knowledge of dormouse subsistence in conifer plantation.

At a finer-scale, I investigate the persistence of dormouse populations in conifer plantations at the edge of their range. I conducted stable isotope analysis to compare diets between non-typical and optimal habitats. Results indicate varying niche breadths among dormouse populations, with the ability to subsist on a restricted diet in coniferous habitats. The study highlights site-specific food sources, including invertebrates, and underscores the importance of plant diversity and high invertebrate numbers in conservation management.

Finally, I collated the findings of this thesis and discuss them within the context of edge of range populations and future threats from climate change. My work aids understanding of hazel dormice energy budgets, habitat requirements, and diets, offering diverse conservation recommendations, particularly in the face of ongoing climate change.

# Acknowledgements

There are many people who have supported, guided, and helped me during the course of my PhD. I would firstly like to thank my supervisors for all their guidance. I would like to particularly thank Jon Bennie for his invaluable knowledge of statistics and for his support while finishing the PhD. I am grateful to Robbie McDonald for giving me the opportunity to work on such a fascinating project that has allowed me to take regular trips up to North Wales, the beauty of which I am sure I will fully appreciate when I am no longer making the seven hour journey!

None of my thesis would have been possible without the funding from RWE, but the staff have always been incredibly supportive and enthusiastic about my work. A special mention to Kristen Liptrot for her endless energy and positivity, which has always provided me with great comfort. I would also like to thank Brian Rumble, and Richard Couzens for always considering the dormice at Clocaenog in all their work.

I am particularly indebted to everyone who helped with training for me to obtain my dormouse licence in record time, without which my fieldwork would not have been possible. Particular thanks to Dave Groves for providing a reference, but also to everyone else who let me attend surveys; Leo Gubert, Matt Parkins, Laura Snell, Elizabeth Coleing, and Emma Weller.

Many thanks to everyone who helped me with data collection in the field. Special mention to Nicola Rae for her sheer hard work, and amazing tree beating skills, without which collecting invertebrates would have taken a lot longer. Rhian Hughes and Lucy Boyett were instrumental during my first field season and in subsequent years, I am extremely grateful. I would also like to thank all the staff at Natural Resource Wales for allowing me to conduct studies on their sites, and providing friendly faces while I was out in the field.

I express my gratitude to the individuals at the People’s Trust for Endangered Species, specifically Ian White and Nida Al-Fulaij, for their valuable assistance in providing data, and facilitating productive discussions. I must also thank Regan Early for providing knowledge, data, and support with regards to Species Distribution Models, without who I would have been truly lost.

I am very appreciative of those friends who offered me shelter, kept me sane and have provided a sounding board while I have completed this PhD, particularly Alice and Alex Snell, Emily and Rob Haley, Victoria Whitehead, Kate Macpherson, Emma Fish, George Noad, Ellie Scopes, and Emily Strong.

Huge thanks go to my parents, Richard and Mo who have provided constant advice and unhesitating offers of help throughout my studies. To my partner Kristian for acting as my unofficial research assistant in North Wales on multiple occasions, for offering unwavering support, and for a constant supply of sweet treats. And to Ripley for being the best fat ginger purring companion anyone could want, especially while trying to start a PhD during a global pandemic.

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# Author’s declaration for co-authored manuscripts

Chapters 2 and 3 have been 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 Jon Bennie (JB).

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 RM and JB. Eleanor Scopes (ES) provided site level variables and dormouse population metrics for chapter 2.

I designed all the fieldwork for chapter 4, and conducted it with field assistance from Nicola Rae (NR). I gathered the data to build a regional Species Distribution Model with guidance from Regan Early (RE). I processed and analysed the data. RE provided data and results from a national Species Distribution Model.

I designed all the fieldwork for chapter 5 and conducted it with assistance from NR. Stable isotope sample processing was done by myself, I analysed the data.

I wrote all 4 manuscripts, then amended and revised them in response to comments, suggestions and advice from RM and JB.

The cover illustration for this thesis was kindly provided by Kristian Butler, who conceived and edited the image. The image was generated through Artificial Intelligence.

Photographs in this thesis were taken by myself.

# Chapter 1

## Introduction

# Chapter 1: Introduction

## *Biodiversity declines*

Biodiversity is declining globally (Pimm et al. 1995; Ceballos and Ehrlich 2002; Schipper et al. 2008; Pereira et al. 2010) with evidence suggesting we are approaching a sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015). Determining the drivers behind this decline is challenging, although anthropogenic land use change and climate change are frequently cited (Hoffmann et al. 2010; Pereira et al. 2010; Manes et al. 2021; Habibullah et al. 2022). Despite commitments to halt biodiversity loss, targets are often unmet, and it is estimated that 48% of species are experiencing population declines, which will in turn contribute to biodiversity loss (IPBES 2019; Rounsevell et al. 2020; Xu et al. 2021; Finn et al. 2023). The loss of biodiversity is not only important for functioning ecosystems, but also to human society. Biodiversity offers benefits in the provision of ecosystem services, for example flood protection, timber, and food (Mace et al. 2012). Certain species and ecosystems also hold cultural and aesthetic significance (Justus et al. 2009; Clark et al. 2014) as well as contributing to human health and well-being (Lachowycz and Jones 2013).

## *Climate change and biodiversity decline*

Throughout the 20th century, global temperatures have exhibited a consistent rise, with implications for both natural and human systems. These consequences span ecosystem function, food production, livelihoods, and health. While habitat loss due to human-driven land use changes and overexploitation are acknowledged currently as the main drivers of species declines, there is a growing recognition that climate change is likely to emerge as a key driver in the future (Pereira et al. 2010; Caro et al. 2022). It is imperative for effective species conservation strategies to integrate species responses to climate change.

The responses of species to a warming climate such as distributional shifts, alterations in phenology, adaptations, and physiological changes, are the easiest to predict (Walther et al. 2002). As temperatures rise, it is anticipated that species will adjust their ranges by moving towards higher latitudes and/or altitudes, seeking refuge in cooler environments (Walther et al. 2002; Root et al. 2003). The timing of biological events such as reproduction or hibernation is also shifting, with potentially detrimental consequences for populations (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2016). Climate-induced alterations in species behaviour and physiology have the potential to cascade into population-level effects.

Predicting the indirect consequences of warming temperatures becomes challenging; a number of additional threats may arise, particularly as climate interacts with other stressors like habitat loss and fragmentation (McCarty 2001; Berteaux et al. 2006). The anticipated expansion of non-native species into novel areas poses a heightened risk, potentially leading to adverse outcomes for native flora and fauna due to altered species interactions (Walther et al. 2009). Species that have previously not been invasive could have a competitive advantage under warmer temperatures putting native wildlife at risk (Hellmann et al. 2008). The redistribution of species ranges driven by warming temperatures holds the potential to reshape community structures, triggering the loss or gain of natural enemies (Wallingford et al. 2020). Indirect climate-induced effects have the capacity to influence the abundance of species at the local scale, arising from modified trophic interactions mediated through alterations in species physiology and behaviour (Van der Putten et al. 2010).

The consideration of increases in extreme weather events is important in the examination of climate change impacts on species. In a recent review, of 519 observational studies conducted, it was found that 38% of species or ecosystems did not return to pre-disturbance levels after experiencing an extreme weather event (Maxwell et al. 2019). Extreme weather encompasses phenomena like droughts, floods, and extreme high and low temperatures (Jentsch et al. 2007). These events have the capacity to alter species distribution and composition but assessing their importance can be challenging (Jentsch et al. 2007). Temporal cascades, characterised by delayed effects on a species physiology and development, are frequently linked with extreme events (Gutschick and BassiriRad 2003). It is expected that modified competition and diversity will arise from extreme events if the fitness of individuals within species diminishes (Gutschick and BassiriRad 2003). Mortality after extreme weather events could lead to local extinctions, particularly for species with small population sizes that struggle to recover (Román-Palacios and Wiens 2020).

The exploration of climate change effects on ecosystem processes poses a complex challenge; indirect effects mediated by biotic interactions are often more important than direct effects from abiotic drivers (Ockendon et al. 2014). The intricacies of studying interdependent relationships and processes across different temporal and spatial scales with regards to climate change, and predicting species responses can be challenging. While global reviews effectively capture overarching risk patterns, such as the advancement of spring and northward range shifts (Walther et al. 2002; Root et al. 2003; Parmesan 2007), they lack generality in predicting national responses due to biases in available data, particularly the underrepresentation of plants and endothermic animals (Feeley et al. 2017). To predict climate change responses with confidence, irrespective of the scale, we may need to integrate information about multiple impact pathways (Dawson et al. 2011). The consequences for species of a changing climate is multifaceted, requiring attention of all aspects of vulnerability; exposure, sensitivity, and adaptive capacity (Dawson et al. 2011). To fully assess the vulnerability of taxa to climate change behavioural, physiological and genetic data is often required, all of which is rarely available (Huey et al. 2012). Focusing on a particular taxonomic group at a finer spatial scale may therefore provide more useful predictions of the likely effects of climate change, and generate effective conservation action.

### ***Edge of range species and climate risk***

Globally, species are estimated to be shifting elevations at a median rate of 11 metres per decade and higher latitudes at a median rate of 16.9 kilometres per decade (Chen et al. 2011). Historical data analysis has already established range-shift responses across multiple taxa (Hickling et al. 2006; Bradbury et al. 2011; Chen et al. 2011). Range-edge populations play a critical role during climate-driven range shifts (Rehm et al. 2015). Individuals at the edge of their species’ range must possess the capability to shift at a rate that tracks climate change, to not adversely impact their behavioural and physiological attributes and avoid range contraction. Life history traits significantly influence a species' adaptability to range shift, with those most exposed to a changing climate often being the least able to colonise new areas (Morrison et al. 2018). Species with more specialised habitat and dietary requirements, and slow reproductive strategies are less able to shift their ranges as temperatures rise (Estrada et al. 2016; Estrada et al. 2018; Morrison et al. 2018). Range-edge populations will be critical in the maintenance and expansion of species geographic distributions under future climate change and therefore warrant conservation attention (Rehm et al. 2015).

From a species perspective, range edge environments, often have a high frequency and severity of climatic extremes when compared to the range core and are important in defining species distributions (Rehm et al. 2015). The increasing unpredictability of climate patterns raises concerns, particularly for range-margin populations that demonstrate heightened sensitivity to both extreme and non-linear environmental shifts (Thomas et al. 1994; Westerbom et al. 2019). Populations at the edge of their range often act as early indicators for species responses to climate change (Wiens 2016; Fogarty et al. 2017). If conditions are good, range-edge populations are on the front line of species expansion, if the environment deteriorates they are often the first to go extinct (Kanda et al. 2009; Furrer and Pasinelli 2016; Goel and Keitt 2022). Under future climate change scenarios, increased rarity and population declines at the range edge inhibit range expansion and may result in less resilience among species populations (Gibson et al. 2009). However, in one review of empirical studies 70% of mammals studied (n=100) exhibited greater persistence along the periphery than in the core of their range. This observation suggests that locations along the boundary of the range might present valuable opportunities for species conservation (Channell and Lomolino 2000).

### *Range margin sites*

Species at the range edge face unique challenges, and exploring the dynamics of range-margin sites is essential to address comprehensively the vulnerability of species in the face of climate risks. Populations situated at the range edge serve as a threshold of environmental variation beyond which a species cannot expand (Böhme et al. 2007). Appropriate data to achieve positive conservation outcomes for species at the edge of their range is often lacking because of their tendency towards non-typical habitat and sparse distribution (Sexton et al. 2009). In comparison to core populations, those at the range edge often encounter different threats and exist in geographic isolation (Thakur et al. 2018). Additionally, populations at the range margin are commonly associated with poor habitat quality and smaller patch sizes (Caissy et al. 2020). These edge populations are therefore more susceptible to local extinctions due to lower overall abundance when contrasted with the core (Lawton 1993; Fisher 2011; Fristoe et al. 2023). Species experiencing declines are therefore predicted to survive longer near the centre of their ranges where conditions are more optimal (Fisher 2011). For example greater declines in Wood Thrush (*Hylocichla mustelina*) on the periphery of their range have been observed in Canada due to lower habitat quality and immigration rates when compared to the core (Torrenta et al. 2022).

Species positioned at the edge of their range frequently constitute small, isolated populations, influenced by factors such as habitat quality and remoteness, rendering them susceptible to inbreeding and genetic drift (Ellstrand and Elam 1993; Lesica and Allendorf 1995; Brown et al. 1996; Caissy et al. 2020). Edge populations have been thought to be less important to species long-term persistence and resilience (Bunnell et al. 2004). Despite this, conservation interventions for globally common species' peripheral populations are expected to become increasingly crucial under future climate scenarios, as evidenced by adaptive differentiation at the edge of their range (Lesica and Allendorf 1995; Thakur et al. 2018; Angert et al. 2020). Under a changing climate the preservation of these adaptations may be beneficial for species persistence and expansion (Rehm et al. 2015). Unique conditions associated with edge populations often give rise to genetic variants distinct from central populations (Lesica and Allendorf

1995; Rehm et al. 2015). Morphological differences (Hudson et al. 2016), changes in population dynamics (Aikens and Roach 2014; Chuang and Peterson 2016), and variations in behaviour (Hudina et al. 2014; Liebl and Martin 2014; Gruber et al. 2017; Johnston and Smith 2018) are frequently observed when comparing marginal populations with those found in the core.

### ***Climate change and dormancy***

Dormancy, a crucial life history strategy for some endotherms, could become increasingly important for species at the range edge. A key aspect of species response to climate change is their capacity to survive short-term extreme climatic events or periods of unfavourable weather. Energetic constraints affect all aspects of species biology including distribution, survival and breeding success. Energy budgets and therefore life history strategies are likely to be heavily influenced by a changing climate through changes in species behaviour and physiology, which is key to individual success and could alter species richness, diversity and composition (Wells et al. 2022). Many endotherms employ heterothermy as a life history strategy, allowing them to conserve energy when environmental conditions are unfavourable and resources are scarce (Geiser and Cooper 2023). Dormancy emerges as a vital adaptive mechanism, enabling these species to survive climatic extremes and variability, a necessity amplified in the face of future climate change scenarios, especially for range-edge populations.

Hibernation, defined by prolonged periods of dormancy lasting typically more than one week with infrequent arousals (Geiser and Körtner 2010), is particularly beneficial as a life history strategy in seasonal climates. This strategy permits taxa to become inactive during extended periods of harsh environmental conditions when resources are scarce (Juškaitis 2005; Ruf and Geiser 2015). Monito del monte (*Domiciops gliroides*) can conserve up to 88% of their energy during hibernation (Mejías et al. 2022). Despite the trade-off between energy conservation and the physiological costs of metabolic depression, hibernators exhibit higher annual survival rates than predicted for their body mass, potentially owing to the protective benefits of hibernation (Humphries et al. 2003; Turbill et al. 2011).

Species that enter hibernation are reliant on internal-time keeping, circannual rhythms, but also rely on external cues such as photoperiod and ambient temperatures for entering hibernation and subsequent emergence (Helm et al. 2013). However, concerns arise when the timing of hibernation deviates from resource availability, posing risks upon emergence. External cues are sensitive to rapid environmental change. Due to increasing temperatures, marmots (*Marmota flaviventris*) in Colorado have been emerging from hibernation  before the onset of the plant growing season, raising the chance of starvation due to inadequate resources (Inouye et al., 2000). However early emergence, for some species, also potentially lengthens the active season, providing more foraging opportunities, increasing individual fitness as body size increases (Phelps 2008; Ozgul et al. 2010). This introduces uncertainties regarding the overall impact of climate change on the life history events of hibernators (Wells et al. 2022).

Warming ambient temperatures during winter are associated with increased arousals during hibernation (Wells et al. 2022; Findlay-Robinson et al. 2023). Such arousals incur substantial energy costs and could prove detrimental if resources are insufficient to compensate, resulting in lower body condition in spring (Buck and Barnes 2000; Pretzlaff and Dausmann 2012). As winters become milder, a reduction in the probability of overwinter survival and potential impacts on the fitness of surviving individuals are predicted (Findlay-Robinson et al. 2023),  with subsequent effects on adult populations, breeding success, and overall population resilience during the active season.

Climatic extremes, particularly when unpredictable conditions coincide with emergence dates, could influence hibernators. Increased frequency of late-season snow storms in Alberta, Canada has delayed snowmelt, leading to the later emergence of Columbian ground squirrel (*Urocitellus columbianus*) and associated decreases in individual fitness (Lane et al. 2012). Additionally, a 2012 heatwave in Canada prompted the early emergence of a captive population of Richardson's ground squirrels (*Urocitellus richardsonii*) in Winnipeg, resulting in breeding before many of the males were physiologically prepared (Kucheravy et al. 2021).

In contrast to hibernation, daily torpor is restricted to a period of less than 24 hours when animals lower their body temperature to less than 32ºC and reduce their metabolic rate (MR) (Wilz and Heldmaier 2000; Geiser 2020). Daily torpor is advantageous as it increases species chance of survival through energy conservation when there is short-term unpredictable variability in climate during a species' active season (Geiser and Turbill 2009; Hanna and Cardillo 2014; Ruf and Geiser 2015). Bushbabies (*Galago moholi)* can save up to 10% of their energy by reducing body temperatures during daily torpor (Nowack et al. 2023).

In areas of increasing climate variability, species capable of employing heterothermy are anticipated to exhibit reduced rates of extinction, attributed to their ability to evade environmental hazards and enhanced tolerance to unpredictable environments (Geiser and Turbill 2009; Vuarin et al. 2013; Nowack et al. 2017; Blanco et al. 2018; Nowack et al. 2020). Echidna (*Tachyglossus aculeatus)* utilise torpor to avoid fire (Nowack et al. 2016) and sugar gliders (*Petaurus breviceps)* to escape storms (Nowack et al. 2015). If climatic extremes increase, taxa employing dormancy gain a substantial advantage, reducing exposure to environmental stressors and unpredictable food supplies, thereby increasing their chances of survival (Liow et al. 2009; Hanna and Cardillo 2014; Norin and Metcalfe 2019; Fuller et al. 2020). As a consequence, it is expected that species relying on daily torpor may exhibit increased frequency of its use if local weather patterns become more changeable.

Cooler ambient temperatures are often associated with the adoption of daily torpor, especially when foraging and maintaining body temperature become energetically demanding (Ruf and Geiser 2015). The anticipated trend of warming ambient temperatures is expected to ease thermoregulation for many species, diminishing the relative energetic benefits of daily heterothermy (Alston et al. 2022). Studies suggest that warming temperatures may lead to the shortening of the length and frequency of daily torpor in bats (Stawski and Geiser 2012; Sherwin et al. 2013). However, each species possesses an optimal thermotolerance threshold, and if temperatures surpass this, energy expenditure may paradoxically increase (Lovegrove et al. 2014). In some instances, reduced fitness is anticipated, leading to compromised functions such as reproduction and growth as animals cope with heat stress. Consequently, in some cases there may be an increase in the frequency of daily torpor to compensate for warming temperatures (Lovegrove et al. 2014).

### ***Breeding and dormancy***

Energetic constraints and the adaptation of dormancy become essential factors in understanding how species, especially those relying on hibernation or daily torpor, navigate the challenges associated with a changing climate and its impact on breeding strategies. Reproduction incurs significant energetic costs, demanding substantial investment, with species having evolved to synchronize breeding with the peak availability of resources, typically occurring in the spring (Bieber and Ruf 2009; Lebl et al. 2011). Across diverse taxa, the onset of spring events is accelerating in response to rising temperatures (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2016). Predictions indicate an advancement of spring by 2.8 days per decade across the Northern Hemisphere (Parmesan 2007). Studies have shown the earlier occurrences of spring events within specific groups such as spawning dates in amphibians (Beebee 1995), first flowering dates (Menzel et al. 2006), and the first appearances of butterflies (Roy and Sparks 2000). This plastic response to warming temperatures varies among species, leading to potential desynchronization across trophic levels (Plard et al. 2014; Thackeray et al. 2016). Evidence suggests that species at lower trophic levels are advancing more quickly, contributing to phenological mismatches (Thackeray et al. 2016). Hibernating species, given their shortened active seasons, face heightened vulnerability to phenological mismatch, as the demanding lactation phase must align with the availability of high-quality resources for reproductive success (Boutin and Lane 2014), however specific examples of this manifesting among wild hibernators are lacking. Climatic variation is likely to be more influential. For example, a delayed emergence from hibernation due to late snowfall can impede juvenile weight gain for first hibernation, diminishing their likelihood of survival. Instances of this have been observed in yellow-bellied marmots (Monclús et al. 2014) and little brown myotis (*Myotis lucifugus)* (Frick et al. 2010).

Animals found in seasonal but unpredictable environments are often required to utilise daily torpor during the reproductive season (McAllan and Geiser 2014; Geiser and Cooper 2023). Some species are able to utilise torpor during pregnancy or lactation such as dunnart (*Sminthopsis macroura*) (Geiser et al. 2005) and Rafinesque's big-eared bats (*Corynorhinus rafinesquii*) (Johnson and Lacki 2014). In contrast, for certain species breeding and torpor are mutually exclusive events such as male pouched mice (*Saccostomus campestris*) (Mzilikazi and Lovegrove 2002) and edible dormice (*Glis glis*) (Fietz et al. 2010). A decrease in the need for daily torpor amid a changing climate could prove advantageous for species, freeing them from energetic constraints imposed by cooler temperatures and enabling greater investment in breeding. For example, in bats, a projected reduction in daily torpor frequency may lead to earlier parturition and accelerated juvenile development, ultimately enhancing reproductive success (Sherwin et al. 2013). However for species that are predicted to increase the frequency of daily torpor under a changing climate, the overall fecundity of the population might decrease if torpor limits individuals' ability to breed. The intricate interplay between climate change, dormancy, and breeding strategies highlights the multifaceted nature of species responses to environmental shifts. As we explore these interactions we can gain valuable insights for effective conservation strategies in the face of climate change.

### ***British mammals and climate change***

The UK is predicted to experience warmer, wetter winters and hotter, drier summers with an increased likelihood of weather extremes under future climate scenarios (Kendon et al. 2020). Notably, 2022 marked the warmest year in the UK since systematic monitoring started in 1884 (Kendon et al. 2023b). This temperature trend raises concerns for biodiversity across the UK, which is already facing pressure. The State of UK Nature report, released in 2019 reveals that 41% of species have decreased in abundance since 1970 (Hayhow et al. 2019). Despite a 24% rise in expenditure by non-governmental organisations (NGOs) since 2010/2011 and a 46% increase in volunteer hours since 2000, the UK has fallen short of meeting 14 out of the 19 Aichi targets for biodiversity (Hayhow et al. 2019; Environmental Audit Committee 2021). In the ecological landscape of Britain, mammals play a pivotal role, constituting a substantial proportion of apex predators, such as otters (*Lutra lutra*) and foxes (*Vulpes vulpes*), in ecosystems otherwise deprived of top predators, and serving as indicator species, including bats and hazel dormice (*Muscardinus avellanarius*), for the health of ecosystems.

The preservation of British mammals is important due to their unique assemblage that is genetically isolated from their counter-parts in continental Europe, as a consequence of pre-historic climatic variation (Schreve 2001). Throughout and after the last ice age many mammals in Europe survived in southern refugia and subsequently underwent a rapid range expansion north, shaping the current flora and fauna of Britain (Hewitt 1999). After the last glacial maximum (LGM) cold-tolerant mammals quickly established themselves but then (mostly) disappeared due to rapid warming (Montgomery et al. 2014). The arrival of warm-adapted mammals via the North Sea land bridge, submerged approximately 8,000 years ago, underscores the geographical challenges faced by terrestrial mammals in Britain, many of which now find themselves on the northern or north-western edge of their distributional range (Montgomery et al. 2014). British bat species, harvest mice (*Micromys minutus*), hazel dormice, and yellow-necked mice (*Apodemus flavicollis*) are all at the edge of their distributional range in Britain. A recent review by Natural England stresses that nearly one in five mammals in Britain now face a high risk of extinction, requiring urgent conservation attention (Mathews et al. 2018). Conservation strategies may involve safeguarding specific species from the impacts of built development and agricultural changes (bats and water vole (*Arvicola amphibius*)), ensuring genetic integrity (wildcat (*Felis silvestris*)), and enhancing the viability of small populations through translocation (pine marten (*Martes martes)*) (Mathews et al. 2018).

Climate change could drive a reduction in species abundance and in turn an increase in extinctions (Thomas et al. 2004). Species at the greatest risk of extinction are those with low population densities, large home range requirements, late weaning, narrow geographical distributions, and substantial overlap with human territories (Cardillo et al. 2008). Attributes associated with mammal adaptability to a changing climate include those found in more generalist species, and those capable of persisting under adverse conditions that employ fast reproductive strategies, such as short inter-birth intervals, larger litter sizes, and quicker attainment of sexual maturity (Pacifici et al. 2017; Estrada et al. 2018; Morrison et al. 2018). Larger-bodied mammals are considered more vulnerable to extinction due to associated life history events, including increased resource requirements and larger home-range sizes (Cardillo et al. 2005; Isaac 2009).

Four consequential effects of climate change- habitat change, altered disease exposure, thermoregulatory compromise, and changes in food availability, are of particular concern for British mammals (Newman and Macdonald 2015). Despite a relative lack of empirical studies on the influence of climate change on British mammals, existing studies on specific taxa provide insights. For example a long-term study of red deer (*Cervus elaphus*) on the Isle of Rum in Scotland has demonstrated advancements in six breeding traits and their associated phenology, indicating potential risks such as mismatches in temporal changes between males and females that could negatively impact breeding success (Moyes et al. 2011).

British mammals with specialist life history traits may be particularly susceptible to the adverse impacts of a changing climate. Those with more generalist characteristics might experience advantages from increasing ambient temperatures. Studies on bat populations suggest that warming temperatures, particularly over the winter, could be beneficial (Park et al. 2000; Hope and Jones 2012). Greater horseshoe bats (*Rhinolophus ferrumequi)* in Cheddar Gorge in Southwest England exhibited greater arousal duration at temperatures above 10$^{o}$C, likely due to increased foraging opportunities in warmer conditions (Park et al. 2000). Similar results were observed for Natterer’s bats (*Myotis nattereri*) in Basingstoke in Hampshire, indicating that warmer winter temperatures could lead to increased body condition, survival rates, and breeding success for bats as a result of an extended active season and enhanced foraging opportunities (Hope and Jones 2012).

In Wytham Woods in Oxfordshire, badger populations have shown an increase in response to more favourable climatic conditions; warmer and wetter winters, creating more foraging opportunities (Macdonald and Newman 2002). Counter-intuitively warmer winter conditions have been shown to have a disadvantageous effect on individual survival due to increased road traffic accidents as badgers forego torpor (Macdonald et al. 2010). This underscores the importance of considering the interactions between climate change and anthropogenic factors. Despite these insights, much of the information available for British mammal taxa relies on supposition and conjecture, limiting confidence in projections for populations and undermines capacity to plan conservation and management (Newman and Macdonald 2015). By considering the specific traits and vulnerabilities of British mammals, we can enhance our ability to formulate effective conservation strategies in the face of climate change.

### ***Hazel dormice***

As climate change raises concerns about the future of British mammals, the hazel dormouse (referred to henceforth simply as ‘dormice’), emerges as a critical focal point for understanding the intricate interplay between climate change, dormancy patterns, and the strategies necessary for effective conservation. Dormice are a small nocturnal, arboreal mammal belonging to the family Gliridae. Dormice inhabit the north-western edge of their distributional range in Britain (Hutterer et al., 2021) (Figure 1.1).  The conditions in Britain pose notable challenges and suboptimal environments for dormice (Pretzlaff and Dausmann 2012). Despite substantial conservation efforts and intervention, dormouse populations have declined by 78% from 1994 to 2020 (Goodwin et al. 2017; Scopes et al. 2023). Dormice in Britain are experiencing range contractions, yet their global status remains Least Concern according to the International Union for Conservation of Nature (IUCN) Red List and European Regional Assessment, owing to their extensive European distribution (Hutterer et al., 2021) (Figure 1.1). Dormice have become extinct over half of their previous range in England and Wales (Hurrell and McIntosh, 1984), and the species is currently listed as Vulnerable in Britain (Mathews and Harrower 2020). The hazel dormouse holds protected status under the UK Habitats Regulations (1994) and is recognised as a European Protected Species, listed under Annex IV of the European Habitats Directive (1992).

Dormice, active from April to October in Britain, are relatively long-lived for a small mammal with lifespans of up to four years (Juškaitis and Büchner 2013). The reproductive pattern of female dormice is dependent on local conditions, yielding one or two litters annually, each with three to six young (Bright et al. 2006). Throughout every month of their active season, dormice employ daily torpor, although this varies temporally with fluctuations in the frequency of torpor across years. Daily torpor in dormice is dictated by a combination of intrinsic and extrinsic factors. Within the British context, torpor is presumed to manifest during cool, wet periods, acting as an energy-saving mechanism (Bright et al. 2006). Beyond Britain, dormice exhibit an increased likelihood of torpor on colder days, earlier in the year, and among individuals with lower body mass (Juškaitis 2005; Pretzlaff et al. 2014).

In response to Britain's seasonality, dormice undergo an extended hibernation phase from November to March, avoiding harsh climatic conditions and limited food availability. In contrast, hazel dormice in more Mediterranean climates forego hibernation altogether (Panchetti et al. 2004). Rising winter temperatures in Britain raise concerns for dormice, prompting increased arousal frequency in dormice during milder winters, ultimately leading to decreased body condition at the end of the hibernation period (Pretzlaff and Dausmann 2012). Dormice are specialist feeders, unable to digest cellulose and must exploit plants at different life stages throughout the season, specifically buds and pollen in the spring (Richards et al. 1984). Premature emergence from hibernation, prior to the availability of these resources, poses a risk of compromising body condition just before the breeding season. Notably, body condition and litter size are directly correlated, as lighter females tend to produce smaller litters (Naim et al. 2011). Consequently, the early emergence from hibernation holds the potential for direct consequences on breeding success and overall population growth.

Dormice in Britain are typically associated with broadleaf woodland with an understory that is dense and diverse (Bright and Morris, 1996, 1993; Hutterer et al., 2021; Juškaitis, 2008; Juškaitis and Augutė, 2008). The presence of honeysuckle (*Lonicera periclymenum*), bramble (*Rubus fruticosus*), and hazel (*Corylus avellana*) are seen as indicator species for suitable woodland for dormice (Bright and Morris 1990; Morris et al. 1990; Bright and Morris 1992).

Given their specialised diet, dormice rely heavily on diverse woodlands for highly nutritional food throughout the active season (Richards et al. 1984; Bright and Morris 1996; Goodwin et al. 2020). Consequently, the loss of habitat and the decline of traditional management techniques, such as coppicing, pose significant threats to dormice in Britain (Bright and Morris 1996; Bright et al. 2006).

The conservation efforts for hazel dormice in England and Wales have primarily concentrated on raising awareness about the species and its associated habitats, accompanied by the development of guidelines for effective woodland management with regards to dormice (Bright et al. 2006). To engage the public, and gain deeper insights into dormouse distribution, The Great Nut Hunt was implemented in 1993, involving the search for feeding signs (Bright et al. 1996a). Additionally, dormice are also part of a captive breeding programme with subsequent reintroductions aimed at reclaiming lost areas of their range (Mitchell-Jones and White 2009; White 2019).

The National Dormouse Monitoring Programme (NDMP) was first established in 1988 to monitor the status of populations of a few ‘key sites’ for dormice in England (Bright and Morris 1995). Currently coordinated by The People’s Trust for Endangered Species (PTES), the program spans over 400 sites across England and Wales (Scopes et al. 2023).  NDMP sites contain dormouse nest boxes positioned at head height spaced at 20m grids throughout woodland (Morris et al. 1990; White 2012). These sites undergo checks at least twice a year, often with monthly surveys (White 2012). During surveys, biometric data including, sex, mass, age, and activity status (torpid or not), are recorded for individuals encountered (PTES 2022). With the involvement of at least 1200 licensed volunteers, the scheme provides a unique opportunity for people to engage with this charismatic yet elusive woodland mammal (White 2012). The NDMP represents a rare large-scale, long-term dataset, offering valuable insights into questions surrounding dormice ecology and life history strategies.

Evidence already suggests that dormice alter their behaviour in response to ambient temperatures, producing more litters and being more abundant on sites with warmer, sunnier springs (Goodwin et al. 2018a). Additionally, dormice adopt a diurnal foraging routine in response to lower ambient summer temperatures, heightening their vulnerability to predation (Bright et al. 1996b; Bright and Morris 1996). It is generally acknowledged that climate change could be detrimental to dormice as a hibernating species, but little consideration has previously been given to their dormancy patterns during the active season. This gap in understanding raises questions about how climate change influences the hazel dormouse's propensity for daily torpor and, consequently, shapes key life history events. The connections between torpor utilisation, survival and breeding success under varying conditions remain poorly understood. Bridging these knowledge gaps is essential for predicting how hazel dormice will respond to climate change in Britain. This lack of understanding is not unique to dormice; other British mammals, including bats, are also subject to similar knowledge gaps regarding climate change and daily torpor.

Considering the broader ecological context, investigations into the interplay between environment, energetics, and torpor use could offer valuable insights into how species ranges are manifest. The utilisation of heterothermy, allowing endotherms to persist in energetically challenging environments (Dausmann and Warnecke 2016), emerges as a potential avenue for understanding dormouse adaptations. In the specific context of hazel dormice in Britain, the frequency of daily torpor could be a decisive factor influencing the growth or contraction of dormouse populations, especially at the range edge. In Britain dormice have increasingly been found in a wider range of habitat such as conifer plantation, roadside margins, and coastal scrub (Bright 1995; Chanin and Woods 2003; Chanin and Gubert 2012; Trout et al. 2012), with little known about their distribution and subsistence in these non-typical environments. The populations of hazel dormice at the periphery of their British range, may hold heightened significance under future climate scenarios. These populations could potentially contribute to range expansion and bolster population resilience. Understanding the distribution, behaviour, and adaptations of these populations in non-typical habitats is crucial for informed conservation strategies and effective management of hazel dormice in the context of climate change.

**Figure 1. 1.** *The distribution of the hazel dormouse across Europe, yellow shading on the map represents dormouse presence. Great Britain is at the north-western edge of the dormouse range. Reproduced from Hutterer et al, (2021)*

### ***The Thesis***

The primary objective of my thesis is to enhance understanding of dormouse life history strategies during the active season and their potential adaptation to a changing climate, with a specific focus on populations at the periphery of their range in non-typical habitats in Britain. The aim is to inform conservation management decisions, particularly in light of climate change, to prevent local extinctions.

Specifically I aim to:

I. Investigate the drivers of daily torpor during the dormouse active season and explore the subsequent consequences of this on life history events.

II. Understand how the frequency of daily torpor might change under future climate scenarios and assess the implications for dormouse populations in Britain.

III. Evaluate the effectiveness of a species distribution model (SDM) as a conservation tool for dormice at the edge of their distributional range in the UK.

IV. Assess dormouse diets in non-typical habitats.

These objectives will be approached through a combination of NDMP data collected by volunteers, habitat and climatic data, and empirical fieldwork data. Following this introduction the thesis is structured into four chapters, each corresponding to the objectives above, followed by a general discussion.

In **Chapter 2**, I use observational data from the NDMP to assess the variation in the use of torpor in woodland sites with differing climate, landscape, and habitat characteristics. I evaluate the relative importance of intrinsic and extrinsic factors driving daily torpor use in dormouse individuals across England and Wales. I then analyse relationships between rates of torpor and metrics for population dynamics across NDMP sites to understand how torpor impacts on dormouse life history events.

In **Chapter 3**, I investigate how the frequency of torpor use amongst populations of hazel dormice might change under future climate scenarios. I do this by using a predictive model created in Chapter 2 and future climate projections obtained from the Met Office.

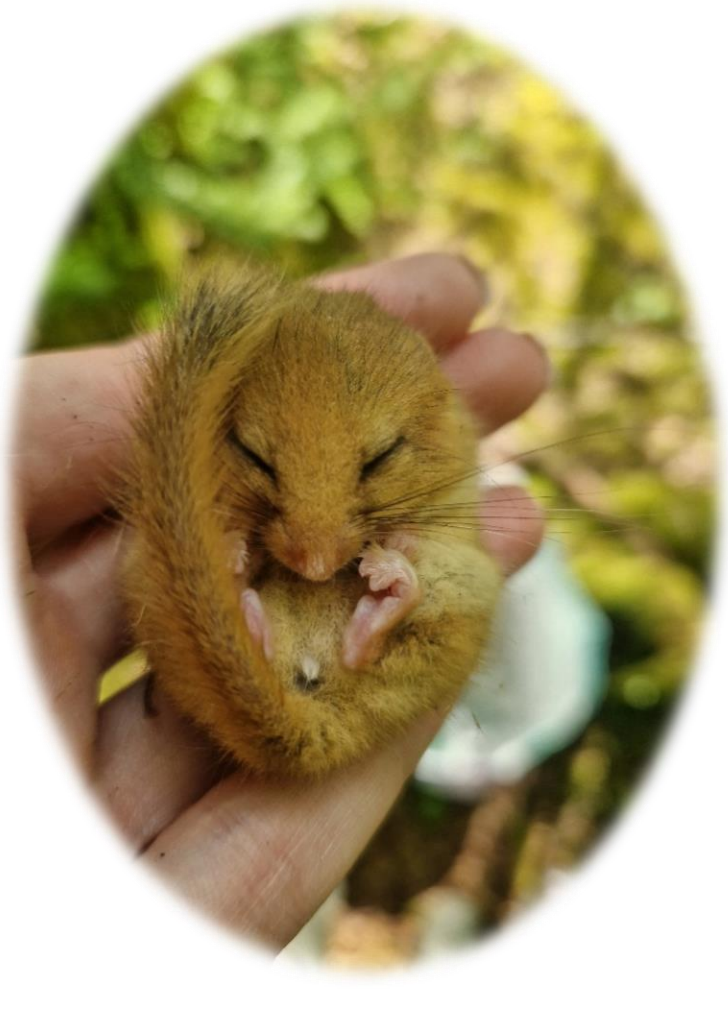
In **Chapter 4**, I assess whether species distribution models (SDMs) can produce effective predictions of dormouse distributions in non-typical habitat at the northern periphery of their range in Wales. I build an SDM for two counties in north Wales and then test the model by collecting independent validation data in the field.

In **Chapter 5**, I focus on the diets of dormice in non-typical habitats when compared to broadleaf woodland. I use stable isotope analysis to examine dietary variation between locations and seasons to test the effects of habitat types on dormouse diets.

In **Chapter 6**, my general discussion provides a synthesis of my findings, and contributions to knowledge of dormouse life history strategies, and ecology. The chapter also discusses the wider implications for dormouse populations and conservation in Britain under a changing climate.

# Chapter 2

# Environmental causes and population consequences of variation in daily torpor in hazel dormice (*Muscardinus avellanarius*)



# Chapter 2: Environmental causes and population consequences of variation in daily torpor in hazel dormice (*Muscardinus avellanarius*)

## *Abstract*

Torpor is an endotherm life history strategy for conserving energy, particularly during unfavourable conditions, and is manifest in the three mammalian subclasses (monotremes, marsupials and placentals). Daily torpor is less than 24 hours in duration, occurs between bouts of activity, and is characterised by reductions in metabolic rate and body temperature. While hazel dormice *Muscardinus avellanarius* are well-known for their profound, seasonal torpor (hibernation), they also use daily torpor to save energy when not hibernating. In Great Britain, where dormice are at the edge of the species' range, there is marked spatial and temporal variation in their use of daily torpor, though the causes and consequences of this variation are not well understood. Using the National Dormouse Monitoring Programme, comprising 53,953 observations of dormice at 381 sites over 25 years, we modelled intrinsic and extrinsic correlates of variation in daily torpor at individual and population (site) levels. Rates of torpor are greater in sites towards the west of Britain and increase with site elevation, at sites with a greater proportion of ancient woodland, and greater connectivity of broadleaf woodland habitat. Dormice were torpid more frequently on colder and wetter days, and within colder and wetter seasons. Individuals found in boxes where breeding was in evidence were rarely torpid, while animals found by themselves were more likely to be torpid. The relative effects of body mass and sex on the likelihood of an individual being torpid varied with time of year. Lighter individuals were more likely to be torpid earlier in the year (April-August) and heavier individuals later in the year (September-October). Males were more likely to be torpid in August and females in September. Sites with higher rates of torpor had a lower abundance of dormice and fewer breeding events. My results suggest torpor may be an important mediator of environmental drivers of dormouse population dynamics, especially with varying environmental conditions under future climate change scenarios. This is of particular concern for

populations at the edge of their range, such as those in Great Britain, which already experience sub-optimal environmental conditions.

## ***Introduction***

Endotherms maintain high and consistent body temperatures, though this comes at a high energetic cost, particularly during periods when environmental conditions are unfavourable or resources are scarce. To mitigate these energetic costs, some mammals exhibit temporal heterothermy (Geiser and Cooper 2023) during dormancy, of which there are three major types, each with distinct implications for life history (Wilsterman et al. 2021). *Hibernation* comprises prolonged and profound bouts of torpor, typically lasting more than a week, with infrequent arousals (Geiser and Körtner 2010). Hibernation in temperate zones is seasonal and occurs during periods of sustained cold and food shortage, when heat production is harder to sustain (Vuarin and Henry 2014). *Aestivation* comprises periods of dormancy when ambient temperatures are high, typically occurs in the tropics, and is thought to enable avoidance of extreme heat and drought (Geiser 2010). *Daily torpor* is when an animal reduces its metabolic rate and its body temperature, and is limited to durations of less than 24 hours (Wilz and Heldmaier 2000; Geiser 2020). In this study, I focus on daily torpor, hereafter referred to simply as torpor.

By reducing body temperature closer to ambient and lowering metabolic rate, individuals can save considerable energy during torpor (Geiser and Cooper 2023). Skin temperatures of male Daubenton's bats (*Myotis daubentonii*) dropped from 37.2 $^{o}$C to 16.8$^{o}$C whilst torpid (Dietz and Kalko 2006). When entering torpor, young desert hamsters (*Phodopus roborovskii*) reduce their metabolic rate by up to 90% (Geiser et al. 2019). Mouse lemurs (*Microcebus danfossi*) in Madagascan rain forests can reduce their energy expenditure by up to 11% when torpid (Schmid and Speakman 2009). Torpor is not only an approach to energy-saving but can also be associated with avoidance of hazards, such as predators (Bieber and Ruf 2009), storms (Nowack et al. 2015), and fire (Nowack et al. 2016). Moreover, comparative analyses suggest that mammals utilising hibernation and torpor are more resilient to extinction because of their reduced exposure to environmental stressors (Geiser and Turbill 2009; Liow et al. 2009; Hanna and Cardillo 2014).

Knowledge of the causes and consequences of torpor might enable better understanding of the adaptive benefits of daily torpor. The drivers of torpor in small mammals and birds have often been investigated experimentally in captive populations under controlled conditions, enabling examination of the interactions between temperature and food resource availability. With reduced food availability, captive African woodland dormice (*Graphiurus murinus)* reduced their activity levels at 25°C and entered torpor at 10°C (Webb and Skinner 1996). In captive populations of edible dormouse (*Glis glis),* spectacled dormouse (*Graphiurus ocularis)* and Djungarian hamster (*Phodus sungorus*), reduced ambient temperatures drove individuals into daily torpor (Ruf et al. 1991; Perrin and Ridgard 1999; Wilz and Heldmaier 2000). Information on the determinants of torpor use for temperate species in the field is somewhat limited (Doucette et al. 2012; Vuarin and Henry 2014), though direct and indirect field observations suggest that temperature and food availability are also correlates of torpor in wild populations of both birds and mammals in diverse biomes (Körtner and Geiser 2000; Smit and McKechnie 2010; Smit et al. 2011; Doucette et al. 2012).

The interacting costs and benefits of torpor are manifest in multiple aspects of population ecology, as constrained energy budgets often require individuals to trade-off survival and energetically-costly breeding. Species that employ daily torpor during their reproductive period are often found in highly seasonal, unpredictable environments with associated variation in food supplies (McAllan and Geiser 2014). Edible dormice invest heavily in reproduction during tree mast years, when resources are abundant, but exhibit prolonged dormancy when foraging opportunities are few (Bieber and Ruf 2009; Lebl et al. 2011). Conversely, edible dormice avoid torpor during testosterone production, but form sleeping groups to reduce energy expenditure through social thermoregulation (Fietz et al. 2010). Unusually, male edible dormice appear to present some constraint upon breeding success, as the number of males producing testosterone directly correlates with the number of litters produced (Fietz et al. 2004). Torpor is also suppressed in male pouched mice (*Saccostomus campestris*) when they are producing testosterone to facilitate opportunistic breeding, but this compromises energy conservation (Mzilikazi and Lovegrove 2002). During pregnancy, incubation, and lactation, some small mammals also employ torpor (McAllan and Geiser 2014; Geiser and Cooper 2023). Torpor during reproduction in females has been documented through observational studies in several small mammal species; mulgaras (*Dasycercus blythi*) will enter torpor during gestation but not after (Körtner et al. 2008). Whereas other species such as dunnarts (*Sminthopsis macroura*) and little brown bats (*Myotis lucifugus*) will enter torpor during all stages of reproduction including lactation (Geiser et al. 2005; Dzal and Brigham 2013). While torpor expression when an individual is actively breeding results in an extended reproductive period, this is counter-balanced by greater success in production of offspring and increased fitness of the parent (Geiser and Cooper 2023).

Hazel dormice *Muscardinus avellanarius* (referred to henceforth simply as 'dormice') utilise daily torpor during every month of the active (and reproductive) season, which, in Great Britain, is April to October. Female dormice in Britain usually have one litter later in the season but, if conditions are favourable, they can also breed earlier in the season and have two litters (Bright et al. 2006). Hazel dormice in Britain are at the edge of the species' distribution range, where climatic conditions are likely to be more energetically demanding (Pretzlaff and Dausmann 2012). Local weather conditions alter hazel dormice activity and in Britain individuals are thought to enter torpor during cool, wet periods (Bright et al. 2006). In their continental range, dormice are more likely to be torpid on colder days, earlier in the year, and in individuals with lower body mass (Juškaitis 2005; Pretzlaff et al. 2014). Dormice are opportunistic feeders but cannot digest cellulose and so must exploit plants at different life stages throughout the season; they are therefore particularly sensitive to seasonal food shortages and are thought to employ daily torpor to save energy during lean periods (Bright et al., 2006; Goodwin et al., 2020; Richards et al., 1984). Dormice therefore represent a useful model for investigating the drivers of torpor during the active/reproductive season and the associated consequences for populations.

Hazel dormouse is also a species of conservation concern. It is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992) and, in the UK, is afforded protection under the Habitats Regulations (1994). It is categorised as Least Concern under the International Union for Conservation of Nature (IUCN) Red List and European Regional Assessment, however this assessment states that in parts of its northern range it is declining and there is cause for concern (Hutterer et al. 2021). Dormouse populations are in chronic decline in England and Wales, with an overall decline of 78% from 1994-2020 (Goodwin et al. 2017; Scopes et al. 2023), and they are categorised as Vulnerable on the UK Red List (Mathews and Harrower 2020).

While the overall trend in dormouse populations in Britain is one of decline (Goodwin et al. 2017; Scopes et al. 2023), local numbers fluctuate between years, suggesting that sites experience good and bad years. Hazel dormice have also been shown to be more abundant and produce more litters on sites with warmer, sunnier springs (Goodwin et al. 2018a). The connections between torpor utilisation, survival and breeding success under varying conditions remain poorly understood. I used the National Dormouse Monitoring Programme (NDMP), which is an extensive, national, long-term dataset of hazel dormouse records from nestbox monitoring, to explore intrinsic and extrinsic, habitat and climate-related correlates of spatial and temporal variation in torpor with a view to understanding causes and consequences for hazel dormouse populations in Britain. I hypothesised that torpor frequency would be affected by environmental conditions, and would, in turn, affect breeding events and dormouse counts, in-year and in the subsequent year.

## *Methods*

### *National Dormouse Monitoring Programme*

Hazel dormice are monitored throughout England and Wales as part of the National Dormouse Monitoring Programme (NDMP). Licenced volunteers conduct nestbox surveys during the dormouse active season from April to October. Permanent nest boxes are set up across sites, usually in a grid formation depending on habitat and topography. For a more detailed description of the survey protocol, see PTES (2022) and for an analysis and validation of the programme, see Goodwin et al. (2017).

Only observations of adult dormice were used in this analysis as it has been shown that juveniles are less likely to enter torpor (Juškaitis 2005). Individual observations were excluded from analysis if they omitted details of sex, mass and torpor state (torpid/not torpid), or contained erroneous data, for example negative mass. Records (n= 1,604) of hibernating animals and aberrant records of active animals from outside the active season (November-March) were removed. Records from 1993-2018 were included in the programme data, but data from 1988 to 1992 were excluded as the programme included only a few sites (n <30) in its early years (Goodwin et al. 2017). Records from a site were removed from the dataset if fewer than 15 dormice were recorded over the whole study period. After this cleaning, of the original 77,048 observations of adult dormice, 53,953 from 381 sites were used in the analysis.

### *Statistical analysis*

All analysis was completed in R version 4.2.2 (R Core Team 2022).

#### Correlates of torpor in dormouse populations

To investigate spatial variation in torpor, I first created a site-level index of torpor, which controlled for variation arising from month, year and sex. To derive this torpor index, I used a generalised linear model (GLM) with torpor as a binary response (torpid or not torpid) and a family link ‘logit’, and site, month, year and sex as predictor variables.

Torpor ~ Month + Year + Sex

To prevent zero inflation in the models, if no torpid individuals were recorded at a site over the study period, a single “simulated” torpid observation was added at the earliest survey date. This process ensured that no sites had unrealistically fitted probabilities of torpor very close to zero, as it was considered that the true probability of torpor was non-zero. The coefficient for each site was extracted from the model (and inverse-logit transformed) and was used as the torpor index, relative to an arbitrary reference site; hence the higher the torpor index, the greater the fitted likelihood of finding a dormouse in torpor at that site on any given day or year. The reference site coefficient is, by default, zero, and therefore the (inverse-logit transformed) index for the reference site is 0.5. The reference site was NDMP site 450; it is located in Wiltshire (grid reference SU247689) and was chosen as this is the site closest to the mean latitude and longitude co-coordinate of all the sites in the dataset. Model performance was tested by calculating K-fold score and McFadden’s R squared.

Habitat and climate variables are known to effect dormice populations across NDMP sites (Goodwin et al. 2018a). To investigate relationships between torpor and relevant environmental characteristics, GLMs were constructed using the raw torpor index score (coefficients from the model before transformation) as a response, with a Gaussian error structure. Predictor variables were: latitude, longitude, elevation, solar index, proportion of ancient woodland, proportion of broadleaf trees, and woodland connectivity.

Raw torpor index score ~ elevation + latitude + longitude + proportion of broadleaf + proportion of ancient woodland + broadleaf connectivity + ancient woodland connectivity

The dredge function was used in R package MuMIn to obtain the most parsimonious combinations of these variables (Barton, 2022). The importance of variables (the proportion of models within the top set within 2 AIC containing each variable) were compared to identify the variables likely to affect the relative probability of torpor at a site.

All NDMP sites have recorded point locations, though only a subset (n=264) have georeferenced polygon data that identify the sampled area in which surveys take place. Only sites with this polygon information were included in the subsequent analysis. Location (latitude and longitude) for each site was obtained from the centroid of each polygon. To determine the proportion of broadleaf woodland at each site, the Forestry Commission's National Forest Inventory (NFI) 2010-2020 was used (Forestry Commission 2022). For each of the NDMP sites, woodland area was calculated as the total area of connected woodlands not separated by >20 m of non-woodland habitat, taken as the mean over the period 2010-2020. This area may exceed the area of the sampled NDMP polygon, as it also includes any adjacent woodland lying outside the polygon. The mean proportion of broadleaf cover for the woodland areas was obtained from 2011-2020 and used as the independent variable. The proportion of each woodland area classified as ancient woodland was calculated as a separate variable (Spencer and Kirby 1992). These data were obtained from the Ancient Woodland Inventory, provided by Natural England and Natural Resource Wales (Welsh Government 2021; Natural England 2023). Connectivity was expressed as the total area of (i) broadleaf woodland and (ii) ancient woodland within a 1 km radius of the centroid of the site.

Topographical information was extracted from Terrain 50 digital terrain models from Ordnance Survey at a resolution of 50 m (Ordnance Survey 2022). From this we calculated the mean elevation, aspect and slope for each site. The elevation data were centred (mean-subtracted) and scaled (divided by standard deviation) across sites. For each site and year, we calculated the 'solar index'. This is a measure of the proportion of direct sunlight an area receives, using the R package 'microclima' (Maclean et al. 2019). For each site, the mean slope and aspect were obtained and the solar index calculated. A measure at 12pm on the first day of each month was calculated and then a mean was taken for each site per year. The solar index is calculated using the digital terrain model for a particular latitude, time of day, and day of the year, and varies between zero (the ground surface is in full shade) and one (the solar beam is perpendicular to the ground surface).

### Correlates of torpor in individual dormice

To investigate the extrinsic and intrinsic factors affecting torpor in individual dormice, a binomial GLM was created. To explore the effects of local weather, I fitted a binomial GLM, using daily (short term), weekly (medium), monthly (long) and seasonal (90 days, very long) mean minimum temperatures (°C) and total rainfall (mm) as explanatory variables.

I also analysed characteristics, that potentially impact dormouse thermoregulation, and life history events that subsequently could influence torpor use (Juškaitis 2005; Pretzlaff et al. 2014). Body mass (g), sex (F, M), number of adults in the box, whether the dormouse was in a breeding (1) or non-breeding (0) nestbox, and if so, the number of juveniles (young of the year independent of the mother) and number of dependent young in the box, were included as explanatory variables. The interactions between body mass and month, and between sex and month, were included to test sex-specific variation in life history and the effect of individual fitness, across the active season. I analysed variation in torpor as a binary response with the family link ‘cloglog’ because of asymmetry in the distribution of 1s and 0s (Thomas 2015), since many more dormice were found to be active than in torpor.

Torpor ~ month * mass + month * sex + breeding + number of adults + number of juvenile + daily minimum temperature + average week minimum temperature

+ average month minimum temperature + average season minimum temperature + day total rainfall + week total rainfall + month total rainfall + season total rainfall

For this analysis, slightly different data were used to that above: only observations with adult mass above 10g were included as any below this are likely to have been recording errors, and sites were included if as few as 2 or more dormice had been recorded during the monitoring period, as this was an individual level analysis. This resulted in 53,494 adult dormouse observations for analysis.

Minimum daily temperature and total daily rainfall for all NDMP sites for every survey year were obtained from the UK Met Office HadUK-Grid dataset, gridded at 1 x 1 km horizontal resolution (Met Office et al. 2021). To investigate the short, medium, long and very long term effects of local climate on dormice across a season, daily data climate variables were collated and then summarised for the 7, 30 and 90 days preceding and including the observation date, for each dormouse observation. This provided daily, weekly, monthly and seasonal average daily minimum temperature and total rainfall. These variables were chosen in accordance with climate variables found to be informative by (Goodwin et al. 2018a) when investigating variation in dormouse populations. A 30-year (1990-2020) baseline for central England was then subtracted from the climate data obtained from HadUK, resulting in site-level residuals from the England mean.

### Consequences of torpor

To establish how torpor frequency might affect dormouse populations, I used site-level indices of dormouse abundance and of population trend, that controlled for survey effort and between-year variation in counts, and derived these indices following the approaches applied by Goodwin et al., (2017) and updated by Scopes et al., (2023). I tested relationships between the raw torpor index score (coefficients from the model before transformation) as a predictor and first the dormouse abundance index ($\log_{10}$ site-level index of dormice counted), and second an exponent of population trend index (site-level slope of population counts over time) as responses. For both analyses, a linear regression was built with Gaussian error structure.

Raw torpor score (beta) ~ dormouse population metric

To examine the potential impact of variation in torpor on hazel dormouse populations, I derived a torpor index similar to that above, but for each year of the survey, and for males and females separately (based on 27,292 observations of female and 29,286 male dormice). Treating the sexes separately, two binomial GLMs were built with site and year as an interaction term. The coefficients from the models were inverse logit to scale yearly torpor scores, resulting in a score between 0 (no torpor) and 1 for each site in each year.

Similar torpor indices were also created for early and late season. These were created in the same way as described above but only observations of dormice from April-July were included in the early season model and observations from August-October in the late season model. This resulted in four additional sets of scores; early and late season for males and for females.

Torpor ~ month + site:year

I used eight measures as response variables to evaluate the effects of torpor on hazel dormouse populations in both the current and the subsequent season. I tested: total adult counts within a survey season; adult counts in the early and late season; counts of young, where these were the totals of all four age-classes of young; young counts in the early and late season; number of breeding events (defined as any instance where young dormice were found in a nestbox); litter size; mean adult dormouse mass for each site and year (as a proxy for fitness) and mean mass of young. The mean young dormouse mass for each site was calculated using just the greys-eyes-open age class. I chose this age class as it represents the most frequently encountered category among young dormice. These measures were analysed using GLMs, with yearly torpor scores as predictor variables.

Dormouse population measure ~ yearly torpor score

Further details on the model structures are available in the appendix (Appendix 1).

## ***Results***

Of 53,953 observations, 23% were of dormice in torpor. Monthly frequency of torpor varied from 0.1% (September 2011) to 100% (e.g. April 2010).

### *Torpor indices*

The torpor index was highly variable among NDMP sites (Figure 2.1). The predictive power of the model used to create the torpor index was tested using K-fold score which gave an accuracy of 83.6% (0.833-0.8391 95% CI). The McFadden's R squared for the model is 33%.

The best performing model of variation in the torpor index based on site characteristics contained four variables; longitude, elevation, proportion of ancient woodland, and broadleaf connectivity. Ancient woodland connectivity, proportion of broadleaf, solar index, and latitude were not included in this model. The top model set contained 36 models and the four variables in the top model had the highest importance in this set (Table 2.1). Sites with high torpor index scores were more likely to be in the west of Britain and at sites at higher elevations (Figure 2.2). Sites with a large proportion of ancient woodland and with higher connectivity of broadleaf habitat were also more likely to have higher torpor index scores (Figure 2.2).

When daily temperature is no different from the 30-year (1990-2020) baseline for central England, when all other variables are held constant, the likelihood of finding a dormouse torpid is 72% (95% CI: 68-75%) and if daily temperature is 4$^{o}$C warmer than this baseline this decreases to 55% (95% CI: 51-59%) (Table 2.2, Figure 2.3). When seasonal temperature is the same as the 30-year (1990-2020) baseline for central England, the likelihood of finding a dormouse torpid is 72% (95% CI: 69-76%) and if seasonal temperature is 4$^{o}$C warmer than this baseline this decreases to 48% (95%CI: 43-52%) (Table 2.2, Figure 2.3). Weekly and monthly temperature variation did not significantly affect torpor.

When daily rainfall is no different from the 30-year (1990-2020) baseline for central England, when all other variables are held constant, the likelihood of finding a dormouse torpid is 72% (95% CI: 68%-76%) and if daily rainfall is 40 mm greater than this baseline this increases to 83% (95% CI: 76%-88%) (Table 2.2, Figure 2.3). When seasonal rainfall is the same as the 30-year (1990-2020) baseline for central England, the likelihood of finding a dormouse torpid is 70% (95% CI: 66%-74%) and if seasonal rainfall is 300mm greater than this baseline this increases to 82% (95%CI: 79%-86%). (Table 2.2, Figure 2.3). Weekly and monthly total rainfall variation did not significantly affect torpor.

The relationship between mass and the likelihood of being in torpor varied by month; from May-August lighter individuals were more likely to be in torpor, whereas in September and October this pattern reversed and heavier individuals were more likely to be in torpor (Table 2.2, Figure 2.4). The relationship between sex and the prevalence of torpor varied by month; males were more likely than females to be in torpor in August, though this effect reversed in September, when females were more likely torpid. Across other months, April-July and October, there was no significant difference between the sexes in their torpor.

Dormice found in breeding nestboxes were significantly less likely to be in torpor than those not in breeding boxes, with a 91% reduction (95% CI: 89%-94%) in the incidence of torpor (Table 2.2). As the number of adults ($P < 0.001$) or juveniles ($P < 0.001$) found in the box increased, then the probability of torpor decreased (Table 2.2). The number of young found in the box did not significantly affect torpor.

An ROC curve was plotted to validate the drivers of torpor model, and the resulting area under the curve was 86%.

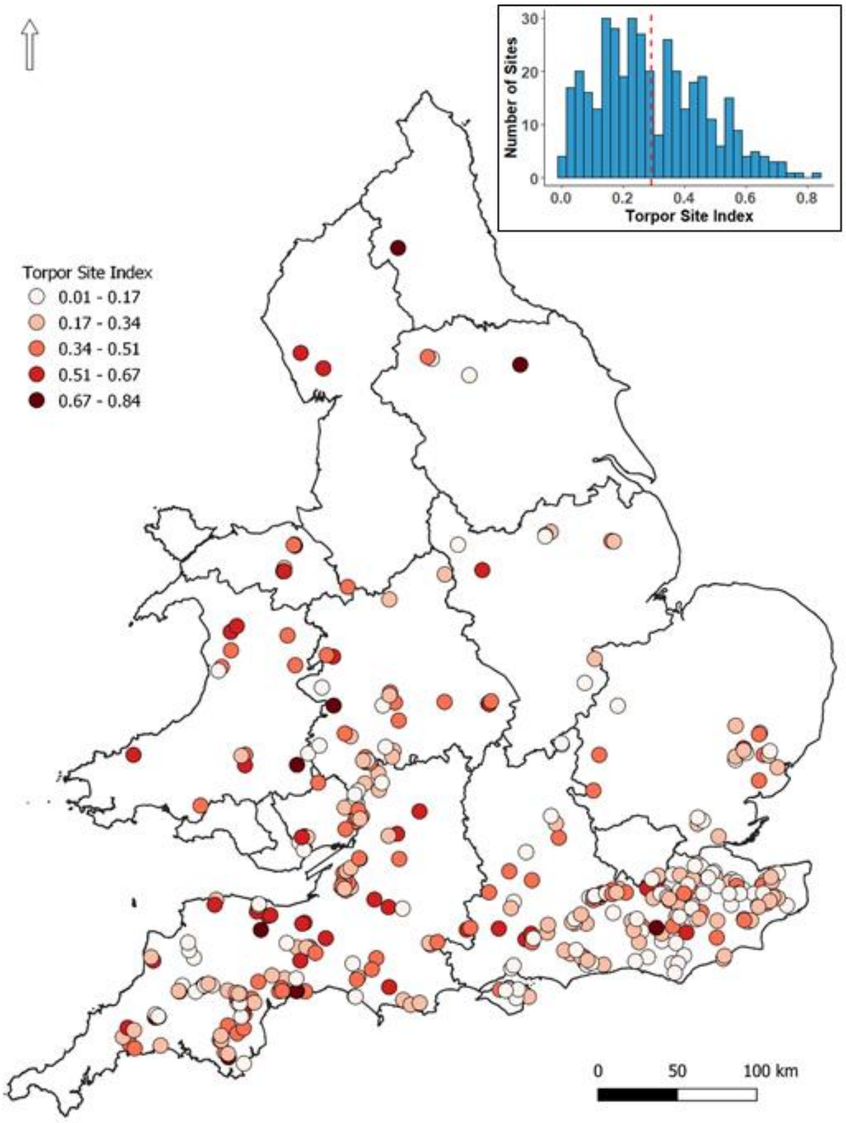


**Figure 2. 1.** *Locations of 381 National Dormouse Monitoring Programme sites in England and Wales and variation in the site-level index of daily torpor frequency.. Torpor index represents the inverse-logit transformed model coefficient for each site; the higher site index, the higher the fitted likelihood of finding a dormouse in torpor at that site on any given day or year. Observations are of dormice in nest-boxes from the NDMP. Shade indicates the likelihood of finding a torpid dormouse at a site when compared to reference site 450. Darker sites represent more torpor at a site and lighter sites less torpor. Inset: Frequency histogram of torpor index across all NDMP sites. Reference site 450 (central site), has a torpor index of 0.5. The dotted red line denotes the mean torpor index value across all NDMP sites that were analysed.*

| **Response Variable** | **Importance** | **Weighted average of the co-efficient** |
|---|---|---|
| Longitude | 1 | -0.11 |
| Proportion of Ancient Woodland | 0.67 | 0.0028 |
| Elevation | 0.67 | 0.0014 |
| Broadleaf Connectivity | 0.61 | 0.14 |
| Latitude | 0.53 | 0.06 |
| Solar Index | 0.39 | -0.48 |
| Ancient Woodland Connectivity | 0.34 | -0.01 |
| Proportion of Broadleaf | 0.08 | 0.0001 |

**Table 2.1**. *Results of top model set of relationships between dormouse site-level torpor index and environmental conditions. Observations are of dormice in nest-boxes from the NDMP. 36 models were in the top model set (within 2 AIC of the top performing model), the importance denotes the proportion of times each variable appeared in the top model set to indicate their relative influence over torpor. The four variables that appeared most often in the top model set were also the four variables in the top performing model.*

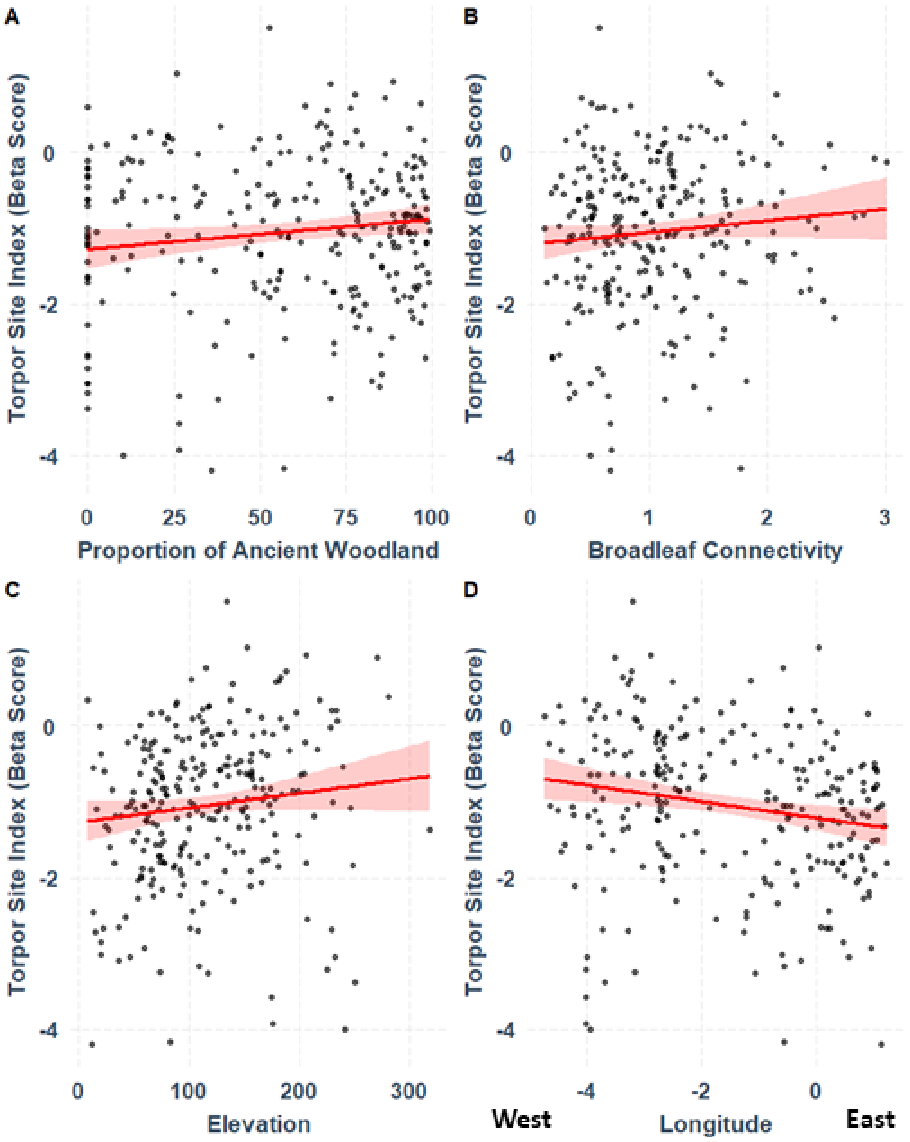


**Figure 2. 2.** *Relationships between dormouse site-level torpor index and environmental conditions. The torpor index is a site-level summary of the frequency of torpor from the National Dormouse Monitoring Programme. The response variables in the top performing model were: A) Proportion of ancient woodland, B) connectivity of broadleaf woodland to a site, C) elevation, and D) longitude. Red lines denote the model prediction for each variable and bands illustrate the estimated standard error of the effect. Raw data for sites are plotted in black.*

| | **Co-efficient** | **Standard Error** | **Hazard Ratio** | **P Value** |
|---|---|---|---|---|
| April | | *Reference* | | |
| May | -0.2102 | 0.2211 | 0.8104 | 0.3417 |
| June | 0.0393 | 0.2269 | 1.0401 | 0.862 |
| July | 0.3654 | 0.3041 | 1.4410 | 0.2295 |
| August | -1.9246 | 0.4529 | 0.1459 | 0.0002 |
| September | -5.6565 | 0.4453 | 0.0035 | <0.0001 |
| October | -4.9837 | 0.2215 | 0.0068 | <0.0001 |
| Mass(g) | -0.0369 | 0.0113 | 0.9638 | 0.0011 |
| Female | | *Reference* | | |
| Male | -0.1851 | 0.0648 | 0.8310 | 0.0048 |
| Not Breeding Box | | *Reference* | | |
| Breeding Box | -2.5216 | 0.1619 | 0.0803 | <0.0001 |
| Number of Adults | -0.1272 | 0.0120 | 0.8805 | <0.0001 |
| Number of Juveniles | -0.5805 | 0.0585 | 0.5596 | <0.0001 |
| May*Mass (g) | -0.0166 | 0.0130 | 0.9835 | 0.2015 |
| June*Mass (g) | -0.0504 | 0.0134 | 0.9508 | 0.0002 |
| July*Mass (g) | -0.1161 | 0.0177 | 0.8904 | <0.0001 |
| August*Mass (g) | -0.0611 | 0.0244 | 0.9407 | 0.0123 |
| September*Mass (g) | 0.0973 | 0.0223 | 1.1021 | <0.0001 |
| October*Mass (g) | 0.1249 | 0.0121 | 1.1331 | <0.0001 |
| May * Males | 0.0905 | 0.0724 | 1.0947 | 0.2113 |
| June*Males | 0.0841 | 0.0731 | 1.0877 | 0.2500 |
| July*Males | 0.1179 | 0.0890 | 1.1252 | 0.1849 |
| August*Males | 0.3920 | 0.1542 | 1.4800 | 0.0110 |
| September*Males | -0.4169 | 0.1748 | 0.6591 | 0.0171 |
| October*Males | -0.0205 | 0.0843 | 0.9797 | 0.8081 |
| Daily minimum temperature | -0.1175 | 0.0035 | 0.8891 | <0.0001 |
| Seasonal average minimum temperature | -0.1715 | 0.0102 | 0.8424 | <0.0001 |
| Daily Rainfall | 0.0081 | 0.0020 | 1.0081 | <0.0001 |
| Season Rainfall | 0.0012 | 0.0001 | 1.0012 | <0.0001 |

**Table 2.2.** *Summary of model analysing variation in the tendency of hazel dormice to be found in torpor as predicted by intrinsic and extrinsic factors. Model coefficients denote the effect size of predictor variables, standard error measures how precise the model estimates are, hazard ratio denotes the probability of torpor relative to the reference conditions, and P statistics denote the significance of each variable.*

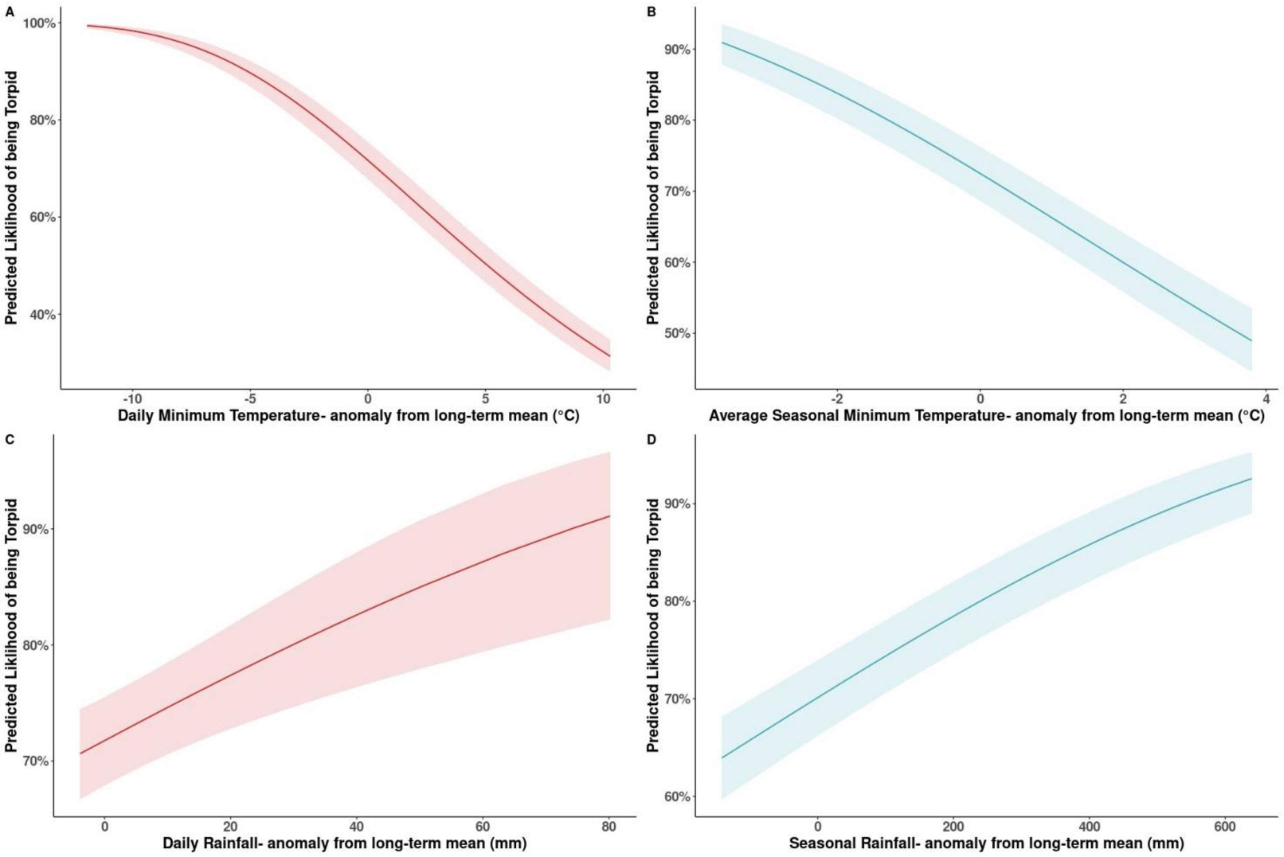


**Figure 2. 3.** *Effects of daily and seasonal variation in environmental conditions on the likelihood of finding hazel dormice in daily torpor. Plots indicate the predicted likelihood of finding a torpid dormouse at different temporal scales for total rainfall and minimum temperature, when all other variables are held constant (references in Table 2.2). Predictions are from binomial GLM investigating the intrinsic and extrinsic factors effecting torpor in dormice. Observations of torpid dormice were obtained from the National Dormouse Monitoring Programme. All climatic variables are expressed as the difference from the central England 30-year baseline, so denote whether a site is cool/warm and dry/wet relative to the baseline. Shading around the line denotes the 95% confidence interval in the model predictions. Short (daily) (A), very long (seasonal) (B) minimum mean temperature and short (daily) (C), very long (seasonal) (D) total rainfall.*

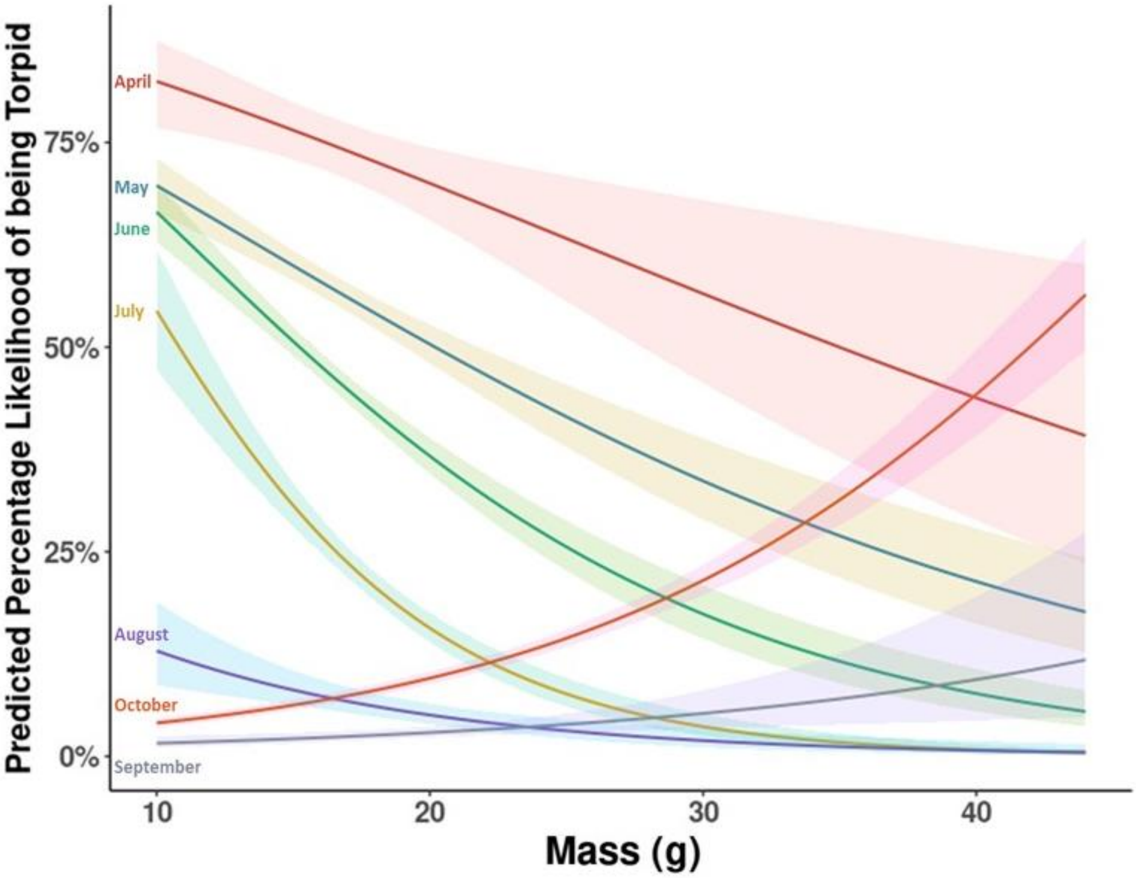


**Figure 2. 4.** *Interacting effects of body mass and month upon the likelihood of an individual dormouse being found torpid. Observations of torpid dormice were obtained from the National Dormouse Monitoring Programme. The plot indicates the predicted likelihood of finding a torpid dormouse during different months of the dormouse active season (April- October) based on an individual's mass (g), when all other variables are held constant. Predictions are from binomial GLM investigating the intrinsic and extrinsic factors affecting torpor in dormice. Shading around the line denotes the 95% confidence interval in the model predictions.*

| Month | Female 15g | | Female 20g | | Male 15g | | Male 20g | |
|---|---|---|---|---|---|---|---|---|
| | Breeding box | Non-breeding box | Breeding box | Non-breeding box | Breeding box | Non-breeding box | Breeding box | Non-breeding box |
| April | 11 | 75 | 9 | 69 | 9 | 69 | 7 | 62 |
| May | 7 | 59 | 5 | 49 | 6 | 55 | 5 | 46 |
| June | 5 | 50 | 3 | 36 | 5 | 46 | 3 | 33 |
| July | 3 | 30 | 1 | 15 | 3 | 28 | 1 | 14 |
| August | 1 | 8 | 0 | 5 | 1 | 10 | 0 | 6 |
| September | 0 | 2 | 0 | 3 | 0 | 1 | 0 | 2 |
| October | 1 | 6 | 1 | 9 | 0 | 5 | 1 | 8 |

***Table 2. 3** Effects of different mass, sex, and months on the likelihood of finding hazel dormice in daily torpor. Table denotes the model predictions of finding a torpid dormouse as a percentage, when animals are solitary and temperature and rainfall variables are the same as the central England 30-year baseline. Predictions are from binomial GLM investigating the intrinsic and extrinsic factors effecting torpor in dormice. Observations of torpid dormice were obtained from the National Dormouse Monitoring Programme.*

### *Consequences of torpor for dormouse populations*

There was a significant, negative relationship between the site-level indices of dormouse torpor and dormouse abundance (p=0.0014; Figure 2.5), but no significant relationship between torpor indices and population trend.

The magnitudes of effects are described by comparing predicted outcomes when there is a torpor score of 0 (very infrequent torpor) and a torpor score of 1 (very frequent torpor) between the sexes (Figure 2.6).

Relationships between torpor frequency and adult dormouse counts differed between the sexes. Frequent torpor in males was associated with an 11% (95%CI: 8-13%) decrease in adult counts in the same active season, while frequent torpor in females was associated with a 4% (95%CI: 1-6%) increase. Frequent torpor in males was associated with a 5% (95%CI: 3-7%) decrease in counts of adults in the subsequent year, though female torpor had no similar effect.

The relationship between torpor frequency and adult counts in the subsequent year varied over the course of the active season. High rates of torpor in males and females resulted in a reduction in counts of adults early in the season in the subsequent year of 17% (95%CI: 14-21%) and 10% (95%CI: 6-13%), respectively. In contrast, high rates of torpor in males and females resulted in an increase in counts of adults late in the season in the subsequent year of 6% (95%CI: 2-10%) and 9% (95%CI: 6-13%), respectively.

Frequent torpor in males and females was associated in the same year with reductions in counts of young of 38% (95%CI: 35-40%) and 33% (95%CI: 30%-35%), respectively. Frequent torpor in females resulted in a 5% (95%CI: 1%-9%) increase in counts of young in the subsequent year, though male torpor had no similar effect.

Frequent torpor in males in the early season was associated with a 44% (95%CI: 38%-49%) reduction in counts of young, while frequent torpor in females in the early season was associated with a 55% (95%CI: 50%-61%) reduction. Frequent torpor in males and females in the late season was associated with reductions in counts of young of 20% (95%CI: 17%-23%) and 18% (95%CI: 14%-21%), respectively.

The relationship between torpor frequency and counts of young varied over the course of the active season in the following year. High rates of torpor among males resulted in a reduction in counts of young early in the season, in the following year, by 24% (95%CI: 18%-35%), female torpor had no similar effect. In contrast, later in the season, high rates of torpor in males and females resulted in an increase in counts of young the following year by 21% (95%CI: 11%-32%) and 20% (95%CI: 12%-28%), respectively.

Frequent torpor in males and females was associated with reductions in the number of breeding events in-year of 36% (95%CI: 30-41%) and 31% (95%CI: 25-36%), respectively. Frequent torpor in females was associated with an increase in the number of breeding events in the subsequent year of 16% (95%CI: 7%-25%), though male torpor had no similar effect.

Frequent torpor in males was associated with a reduction in litter size in-year of 5% (95%CI: 0%-9%), though female torpor had no similar effect. Torpor frequencies for both sexes had no effect on litter sizes in the subsequent year.

Frequent torpor in males was associated with a decrease in mean adult male mass of 0.7 g (95%CI: 0.4-1.0 g), and in females with a decrease of 1.2 g (95%CI: 0.9-1.5 g). Torpor frequency had no effect on adult masses in the subsequent year. Torpor had no effect on the masses of young in either the same year or the following year, irrespective of sex.

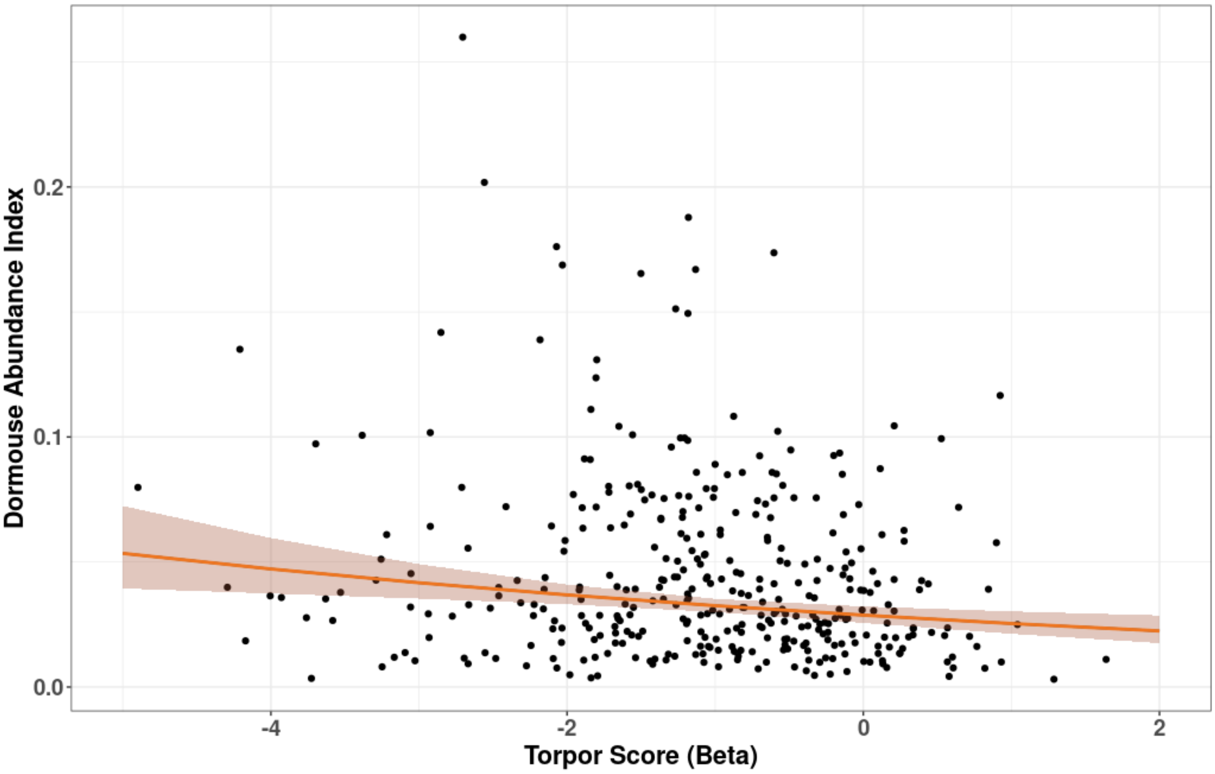


**Figure 2. 5.** *Relationship between indices of daily torpor frequency and dormouse abundance at sites of the National Dormouse Monitoring Programme. Site-level indices of dormouse abundance that controlled for survey effort and between-year variation in counts were calculated using observations of dormice from the National Dormouse Monitoring Programme. The relationship between indices of torpor and abundance is shown as the orange line and the Dormouse Abundance Index has been back transformed in the plot to illustrate results. Confidence intervals are denoted by lighter orange shading and raw data are black points. The higher the torpor index the greater the likelihood of dormice being observed in torpor.*

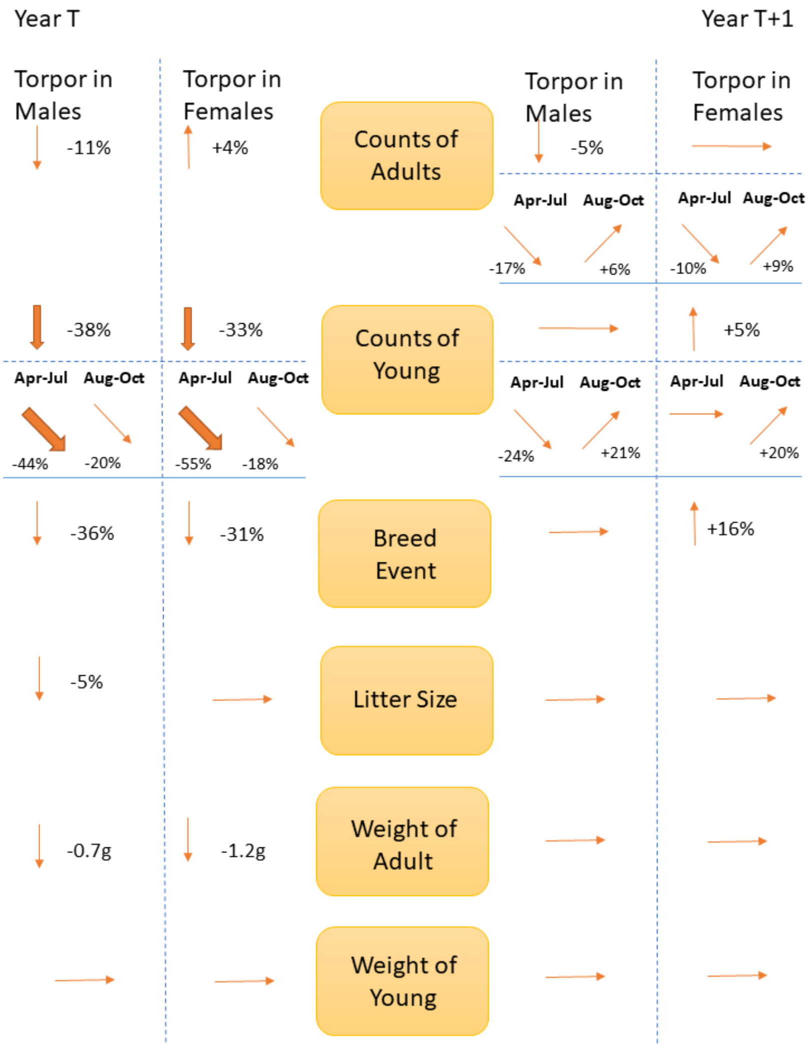


**Figure 2. 6.** *Diagram of the summary of relationships between dormouse torpor and population metrics. Dormouse observations from the National Dormouse Monitoring programme were used, treating the sexes separately, two binomial GLMs were built with site and year as an interaction term. Central boxes denote the population metric that was tested as a response variable. Columns on the left denote the relationship between high rates of torpor in either males or females and the corresponding population metric. Columns on the right denote the relationship between high rates of torpor in either males of females in year T and the corresponding population metric in the following year. A horizontal line denotes that there was no relationship between the response and predictor variables. An upward arrow signifies a positive relationship, a downward arrow a negative relationship. Numeric values are comparing differences of the population metric at sites with a torpor score of 0, very low torpor, and a torpor score of 1, very high torpor.*

### *Discussion*

Using a uniquely extensive database of direct observations of individual hazel dormice in Great Britain, I highlight the multiple correlates of daily torpor, identifying the environmental conditions associated with torpor frequency, how torpor then relates to population characteristics and how these effects differ between the sexes. This is not an experimental study, rather it is based on variation in a great many direct observations of free-living animals across a wide range of conditions, over an extended period, providing insight into effects that, while sometimes subtle, are relevant to understanding the adaptive consequences of torpor and, in the case of this declining species, population change as the environment itself changes.

I show that cold, wet conditions, expressed at daily and seasonal (but not weekly or monthly) temporal scales and at local and regional spatial scales, were associated with more frequent daily torpor. Moreover, I show that sites and years experiencing such conditions, and more frequent torpor, were characterised by reduced counts of adults and reduced productivity. Sites where dormice were more frequently in torpor appear to indicate climatic and habitat conditions that are relatively unfavourable for dormice and thus sustain smaller populations.

Daily temperature and rainfall both affected torpor, signifying that dormice respond quickly to short-term conditions to save energy. Hazel dormice reduce their nightly activity when there is high rainfall, ostensibly because of heat loss due to their sparse guard hairs (Bright et al. 1996b). Instead of foraging in these costly conditions dormice mitigate losses by utilising torpor. While temperature and rainfall during the week and month preceding the observation date had no effect on torpor, over a longer time span, seasonal conditions were influential likely due to their generalised impact on plant productivity and food availability.

Environment and energetics, and how these relate to torpor use have the potential to aid in our understanding of how species ranges are manifest. Species at the edge of their range exist in areas that are often associated with declining suitability and abundance of habitat (Caissy et al. 2020) and have a higher severity and frequency of extreme climatic events when compared with the core (Rehm et al. 2015). The edge of the range is therefore often more energetically demanding and unfavourable conditions prevent further expansion in these challenging environments. Employing heterothermy may enable endotherms to persist in areas that would otherwise be energetically unfavourable (Dausmann and Warnecke 2016).  Torpor might even aid in the colonisation of new areas as energy requirements are reduced during challenging conditions and thereby enable a population to become established (Nowack and Dausmann 2015). This is particularly important under a changing climate as areas in a landscape might become more or less energetically favourable. In the case of hazel dormice in Britain, if conditions improve at the cooler and wetter margins a reduction in the frequency of daily torpor could be a factor that allows growth of dormouse populations, where appropriate habitat is available.

The impact of a high frequency of torpor on adult hazel dormouse populations appears to be dependent on sex. High rates of torpor in males were associated with lower counts of adults, while conversely, a high frequency of torpor among females was associated with greater counts, in the same season. This could reflect distinct patterns of dispersal, foraging and survival. If females enter torpor as an energy saving technique it might be expected that in high torpor years more adults would be found during monitoring. If males employ a different life history strategy and continue to attempt to forage and utilise torpor as a last resort then their mortality could be higher. Differing physiological and behavioural patterns with regards to torpor have been documented in other species, male kalutas (*Dasykaluta rosamondae*) expend more energy than females while foraging and during rest phases, with shorted shallower bouts of torpor (Körtner et al. 2010).

The dynamic patterns of trade-offs faced by males and females were particularly apparent later in the season. Relative to females, male dormice were more likely to be in torpor in August but less likely in September (Juškaitis 2005; Pretzlaff et al. 2014), suggesting that reproductively active females might not routinely utilize daily torpor. My results show that torpor use presents a trade-off with reproduction in dormice. Fewer young are found in years with higher torpor rates due to a combination of fewer breeding events and a reduction in litter sizes. Somewhat counterintuitively, litter size is only affected by male torpor rates and not females, perhaps because dormice exhibit multiple paternity in their litters (Naim et al. 2011). Other studies have suggested that there is a relationship between potential male partners and litter sizes in mammal species that employ multiple paternity (Gayet et al. 2016; Dobson et al. 2018). As torpor frequency increases among males, there are fewer breeding opportunities for females resulting in reduced litter sizes.

The prevalence of daily torpor in hazel dormice is influenced by the number of individuals found in nest boxes during monitoring. Solitary animals are more likely to exhibit torpor compared to those found in multiple occupancy boxes. Little is known about the social structure and behaviour of hazel dormice so it is difficult to surmise why this might be (Glass 2017). One possibility is that lowering metabolic rate and basal temperature when entering torpor is more easily done when solitary.

Hazel dormouse are opportunistic feeders and their diets are highly variable driven by variation in food availability (Juškaitis 2007; Goodwin et al. 2020). In periods of scarcity, it would be expected that individuals sustain reduced body mass and hence are more likely to enter torpor. The relationship between mass and torpor changes throughout the season. Lighter individuals enter torpor from April-August though this pattern shifts in September and October when heavier individuals were more likely to be found in torpor as animals approach conditions suitable for hibernation (Juškaitis 2005). Torpor frequency later in the dormouse active season therefore appears to be a positive indicator of local conditions as it indicates that individuals have built up enough reserves to enter hibernation and survive the winter. This is further supported by my findings that adults in high torpor sites are lighter, suggesting that they are not entering winter hibernation in optimal condition.

My results give an indication of what types of site might exhibit high or low levels of torpor with regards to habitat. Dormice living on sites with more ancient woodland were more often in torpor. Perhaps counterintuitively, this could be because species composition or management practices in ancient woodland present fewer foraging opportunities to hazel dormice. Sites with greater connectivity of broadleaf habitats also had greater torpor index scores, it remains unclear why this would influence dormancy as dormice are thought to prefer high level of habitat connectivity for foraging and dispersal (Bright et al. 2006). Future research should focus on investigating how foraging opportunities vary across different habitat types and whether these variations influence the differences in torpor utilisation observed in dormouse populations at different sites. To further understand how the availability of food in different environments affects the way dormice use torpor. This will ensure positive conservation outcomes for the species, by improving habitat management decisions.

The NDMP monitoring data used for the analysis for this study comprise a lengthy series of monthly snapshots of dormouse behaviours and populations in Great Britain. Surveying takes place on one day per month at each site and no observations of torpor duration are made. To understand the dynamics of torpor and the significance of adverse conditions, information about torpor length would be useful. This would allow for more powerful analysis into the drivers of torpor. When conditions are challenging for dormice, as with other species, there is an apparent trade-off between survival and investment in productivity (Bright and Morris 1996), and as a relatively long lived species (for a small rodent), fitness is better increased by postponing breeding to subsequent years. My study highlights the links between the proximate trade-offs for daily energy budgets, and how these eventually relate to wider population dynamics. Several studies have investigated the relationships between daily torpor and breeding (McAllan and Geiser 2014). To my knowledge these mechanistic studies have not then related how these energy saving life-history manifestations affect population dynamics. Increasing our understanding of these relationships is of particular importance as many species are facing a changing climate. As climate changes, for dormice and other users of torpor, so will the frequency of their torpor, with potentially profound effects on species life history and populations.

# Chapter 3

# Climate-driven dynamics of torpor in hazel dormice (*Muscardinus avellanarius*): Implications under future climate scenarios

# Chapter 3: Climate-driven dynamics of torpor in hazel dormice (*Muscardinus avellanarius*): Implications under future climate scenarios

## *Abstract*

Climate change is predicted to become one of the biggest drivers of biodiversity decline. Understanding its effects on individuals and populations requires knowledge of the impact of climate on key life history events. Daily torpor is employed by many small mammals to save energy and is affected by variation in environmental conditions. Based on relationships between observations of torpor and variation in temperature and rainfall, and predictions of future climate, I investigated how the frequency of daily torpor in hazel dormice (*Muscardinus avellanarius)* might change in populations in Great Britain by 2080. Overall, with increasing ambient temperatures and declining rainfall in the active season, there is a predicted reduction in the frequency of daily torpor across current sites in Great Britain. However, due to inter-annual variation in weather conditions, large year to year fluctuations in daily torpor are predicted. A reduction in the use of daily torpor in isolation from other effects of climate change, such as phenology or food availability, is indicative of a possible benefit for dormice, as they will be less energetically constrained and able to invest more in breeding, which in turn should result in an increase in overall abundance. My findings indicate that in the imminent period, between 2021 and 2040, the frequency of torpor use will vary among years with a slight trend towards a reduction of torpor. This is of concern for small isolated populations and could be associated with local extinctions, due to reduced reproductive success and an inability to recover in subsequent years. My study highlights a mechanism for elements of the impact of climate change on dormouse energy budgets and ecophysiology. Such alterations in energy budgets are likely to have complex consequences that are hard to predict in full, especially for populations at the edges of their distribution, which may face heightened risk.

### *Introduction*

Between 2011 and 2020, global surface temperatures surpassed the 1850-1900 baseline by 1.1°C (IPCC 2023). Under worst case emission scenarios, this could increase to 4°C by the year 2100 (IPCC 2023). Such a temperature rise carries significant repercussions for both natural ecosystems and human well-being, affecting areas such as public health, food production, and livelihoods (IPCC 2023). Evidence suggests we are approaching a sixth mass extinction (Barnosky et al. 2011; Ceballos et al. 2015) with biodiversity declining globally across multiple taxa (Pimm et al. 1995; Ceballos and Ehrlich 2002; Schipper et al. 2008; Pereira et al. 2010). Climate change is widely acknowledged to be one of the main drivers of these declines (Pereira et al. 2010; Hoffmann and Sgrò 2011; Manes et al. 2021; Habibullah et al. 2022).

Warming ambient temperatures directly affect species physiology and behaviour, influencing population dynamics. In order to make predictions about how organisms will react to future climate change, we need to characterise how organisms experience their environments and the biological mechanisms governing their responses (Briscoe et al. 2023). Recognising that species are thermodynamically connected to their environments further underscores the importance of this ecological perspective in understanding species responses to climate change (Buckley et al. 2015; Briscoe et al. 2023). As temperatures rise, species are anticipated to modify their behaviours, including by shifting their distributions to higher latitudes and/or altitudes to reach cooler areas (Walther et al. 2002; Root et al. 2003; Hickling et al. 2005; Bradbury et al. 2011). In the global context it is predicted that species are shifting elevations at a median rate of 11 metres per decade and higher latitudes at a median rate of 16.9 kilometres per decade (Chen et al. 2011). Physiological responses to climate change have consequences for species phenology, which can cascade to population-level effects (Parmesan and Yohe 2003; Root et al. 2003; Thackeray et al. 2016; Piao et al. 2019; Iler et al. 2021; Inouye 2022).

A recent study of population extinctions across 538 plants and animals found that sites with larger and faster increases in the hottest yearly temperatures experienced the most local extinctions, these sites had significantly smaller changes in mean annual temperatures (Román-Palacios and Wiens 2020). Increased climate variability, where good years cannot compensate for the bad, adversely affects species abundance, leading to greater likelihood of localised extinctions and distributional shifts (Zimmermann et al. 2009). If it can be incorporated, studies should consider climatic variability as well as changing climatic means. Increased climatic variability, which could manifest as extreme weather events as well as greater variance around average conditions, is predicted to increase with a changing climate. Such variance can itself have distinct impacts upon biodiversity (Jentsch et al. 2007). Temporal cascades are often associated with extreme events having a delayed effect on a species physiology and development (Gutschick and BassiriRad 2003).

Endotherms maintain high and consistent body temperatures, which incurs high energetic cost, especially during periods when environmental conditions are unfavourable and foraging opportunities are limited (Geiser and Turbill 2009; Hanna and Cardillo 2014; Ruf and Geiser 2015). An endotherm life history trait that is likely to be heavily influenced by a changing climate in mammals is dormancy, with potential consequences for survival and reproduction. Hibernation, characterised by extended periods of deep torpor lasting over a week with infrequent arousals, is a seasonal response to prolonged cold and food scarcity (Geiser and Körtner 2010; Vuarin and Henry 2014). Hibernation brings advantages, such as higher survival rates (Turbill et al. 2011), but mismatches in timing could lead to resource scarcity upon emergence (Plard et al. 2014; Thackeray et al. 2016; Fuller et al. 2020). Warming winter temperatures can increase hibernation arousals, which are energetically costly and may reduce survival and individual fitness (Buck and Barnes 2000; Pretzlaff and Dausmann 2012; Wells et al. 2022; Findlay-Robinson et al. 2023). Climatic extremes, including late snowstorms and unseasonal heatwaves, can also disrupt emergence timing and subsequent breeding, impacting hibernators' population dynamics (Lane et al. 2012; Kucheravy et al. 2021).

While the predominant focus when considering mammal dormancy and climate change pertains to the timing of emergence from hibernation, limited attention has been given to the subject of daily torpor. Daily torpor, hereafter referred to simply as torpor, refers to a temporary reduction in an animal's metabolic rate

(MR) and body temperature to less than 32°C, typically lasting less than 24 hours (Wilz and Heldmaier 2000; Geiser 2020). To reduce energetic costs, daily torpor is employed by many small animals and birds (Geiser and Cooper 2023). By reducing basal body temperature (Tb) to levels closer to ambient for short periods, individuals can save considerable energy (Geiser and Cooper 2023). Maintaining high levels of metabolism and other related physiological processes also incur high energetic costs, therefore reducing MR is an effective energy saving mechanism (Wellbrock et al. 2022). On colder days, maintaining body temperature and foraging is more energetically demanding (Ruf and Geiser 2015). As ambient temperatures are predicted to rise thermoregulation should be less costly for many species, reducing the relative energetic benefits of heterothermy (Alston et al. 2022). Using temperature sensitive radio-transmitters eastern long-eared bats (*Nyctophilus bifax*) in Australia at ambient temperatures (Ta) of 18.8$^{o}$C were found to be torpid for 33.5% of the time (8.02h/day) and it is predicted that a 2$^{o}$C increase in ambient temperatures would shorten the duration of torpor to 21.8% of the time (5.23 h/day) (Stawski and Geiser 2012). Warming temperatures and a reduction in the need to utilise daily torpor may benefit bats due to earlier parturition and faster development of juveniles (Sherwin et al. 2013).Daily torpor and reproduction are, however, mutually exclusive events in many species (McAllan and Geiser 2014). Warming temperatures and reductions in the frequency of daily torpor may result in greater investment in breeding, as individuals are less constrained by cooler temperatures and associated energetic costs. Conversely, elevated temperatures, exceeding animals' thermotolerance, may increase energy expenditure, potentially reducing overall fitness by impeding reproduction and growth (Lovegrove et al. 2014). In such circumstances, the adoption of daily torpor may increase to mitigate adverse conditions. (Lovegrove et al. 2014).

Mammalian species that employ daily torpor demonstrate reduced extinction rates by effectively mitigating times of hardship and stress, a strategy anticipated to increase resilience under a changing climate (Geiser and Turbill 2009; Nowack et al. 2017). Species that are capable of daily torpor might successfully exploit a wider array of microclimates as they are able to tolerate wider ranges of temperature and humidity, which should be beneficial under climate change

(McCain and King 2014). Daily torpor allows species to have high levels of flexibility in their physiological and behavioural traits and they can adjust their energetic requirements on a day-to-day basis, which will be advantageous as climate change makes local environments more unpredictable (Vuarin et al. 2013; Blanco et al. 2018). The prevalence of daily torpor is likely to increase in order to survive such conditions (Norin and Metcalfe 2019; Fuller et al. 2020). It is therefore difficult to predict how the frequency of daily torpor might change under future climate predictions, and the subsequent effects on species population dynamics. Increasing ambient temperatures should result in a reduction in torpor bouts, however, this could be counteracted by increasing climatic variability.

The UK is predicted to have warmer, wetter winters and hotter, drier summers, with an increased likelihood of weather extremes under future climate scenarios (Kendon et al. 2020). 2022 was the warmest year since records began (Kendon et al. 2023b). There has been an increase in the number of wet extremes, in 2021 the UK experienced the second wettest May since recording began in 1836 (Kendon et al. 2022). This is of concern for biodiversity in the UK, which is already facing pressure. The hazel dormouse *Muscardinus avellanarius* (referred to henceforth simply as 'dormice') is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992) and is afforded protection in the UK, under the Habitats and Species Regulations (2017). It is categorised as Least Concern under the International Union for Conservation of Nature (IUCN) Red List and European Regional Assessment, however, there have been severe declines in the number of dormice in England and Wales; 78% since 1994-2020 (Goodwin et al. 2017; Scopes et al. 2023) and it is categorised as Vulnerable in the Great Britain Red List for mammals (Mathews and Harrower 2020).

Hazel dormice have the potential to be affected by changing climate, potentially resulting in alterations to their activity patterns. (Bright and Morris 1996; Greaves et al. 2006; Reiners et al. 2012). Hazel dormice already experience what appear to be suboptimal climatic conditions in Britain, as they are at the north-western edge of their distributional range, where the climate is marginal and more energetically demanding (Pretzlaff and Dausmann 2012). Analysis of contemporary records suggests that dormice respond to variation in temperatures, and are more abundant and produce more litters on sites with warmer, sunnier springs (Goodwin et al. 2018a). Hazel dormice utilise daily torpor when conditions are cool and wet during their active season in England and Wales (Bright et al. 2006). In comparison, dormice in Mediterranean ecosystems in Italy are thought to employ dormancy to overcome dry climatic conditions (Panchetti et al. 2004). The specific drivers of daily torpor in hazel dormice have been investigated and include intrinsic factors such as body condition and breeding status and extrinsic factors such as, ambient temperatures and rainfall (Juškaitis 2005; Pretzlaff et al. 2014). Daily torpor is also related to hazel dormouse populations; sites in Great Britain that exhibit higher frequencies of torpor have lower abundance of dormice (Chapter 2).

Warming winters appear likely to be detrimental for hibernators as a higher frequency of arousals from torpor will occur (Wells et al. 2022). Arousals are energetically costly and a lack of resources during winter months to compensate could lead to reduced survival rates. Captive hazel dormice have been shown to exhibit higher energy use and shorter bouts of torpor in warmer winters (Pretzlaff and Dausmann 2012). It is not known how a changing climate will affect the use of daily torpor in populations of hazel dormice during the active season. Frequency of torpor during the active season has been shown to be associated with variation in dormouse population dynamics in Britain, with less breeding and fewer young found on sites with higher rates of torpor. The year following high incidences of torpor, fewer adults are found on sites early (April- September) in the season, indicating poor winter survival (Chapter 2). Understanding the potential shift in the frequency of daily torpor in hazel dormouse populations in the UK during the active season under a changing climate is important, as this will have implications for their persistence, especially at sites that already have relatively low numbers.

Using a large-scale, long term dataset, the National Dormouse Monitoring Programme (NDMP), variation in torpor and its correlates and consequences has been studied and statistical models predicting the likelihood of dormice being found in torpor are available (Chapter 2). Detailed predictions of future climates have also been made for the UK and are available for minimum daily temperature and daily rainfall up to the year 2080 (Met Office Hadley Centre 2018). Hazel dormice in Britain offer an opportunity to study how the frequency of daily torpor may change in response to future climate scenarios.

I have explored how the prevalence of daily torpor might change among hazel dormice in England and Wales. My earlier analysis (Chapter 2) suggests that temperature warming during the active season would reduce rates of torpor but that any trend towards increased precipitation during the active season would drive greater rates of torpor. I predicted that torpor use among dormice populations in England and Wales will decrease under future climate scenarios as hotter, drier summers create better conditions. When focusing more specifically on populations of dormice on the very margins of their range in Britain, I expected torpor use to be higher due to rainfall intensity.

## ***Methods***

### *National Dormouse Monitoring Programme (NDMP) data*

Hazel dormice in England and Wales are monitored through the National Dormouse Monitoring Programme (NDMP). Licenced volunteers undertake surveys between April and October. Depending on the habitat and topography of a site, dormouse nest boxes are usually set up in a grid formation. The scheme was established in 1988, for a more detailed protocol see PTES (PTES 2022), and for an analysis and validation of the programme, see Goodwin et al (2017). Only observations of adult dormice were included in this analysis and data cleaning involved the removal of erroneous entries, such as negative weights. Only records from the dormouse active season (April-October) were included. Records from 1993-2018 were included in the study, data from 1988 to 1992 were excluded due to small numbers (n <30) of survey sites (Goodwin et al. 2017). Sites were included if 2 or more dormice had been found during the monitoring period. A total of 53,494 of the 77,048 observations of adult dormice, from 381 sites, were used in the analysis.

### *Statistical Analysis*

All data download and subsequent analysis was completed in R version 4.2.2 (R Core Team 2022)

### **Predictive model**

I constructed a predictive model designed to identify correlates of finding an individual dormouse in torpor during surveying. My approach entailed the development of a binomial generalized linear model (GLM) with the binary response variable representing torpid (1) and active (0) states. To accommodate the substantial proportion of zeros in the original dataset, I implemented a cloglog function (Thomas 2015). The model incorporated a suite of climatic variables, including daily minimum temperature, seasonal average minimum temperature, daily total rainfall, and total seasonal rainfall. Additionally, I included descriptors for the contents of the nest box in which the animal was located and the condition of the animal itself. An independent variable indicating breeding status (1 for breeding, 0 for non-breeding) was integrated into the model. I also factored in covariates such as body mass (in grams), sex (F for female, M for male), the number of adults sharing the nesting box, and the number of juveniles present. To capture the nuanced relationships, I introduced interaction terms between body mass and the month of observation, as well as between sex and the month of observation. The resulting model, enabled me to predict the likelihood of encountering torpid dormice in the context of prospective climate change projections.

torpor ~ month * weight + month * sex + breeding + adults + juvenile + daily minimum temperature + average season minimum temperature + month total rainfall + season total rainfall

### Future climate projections

Future climate projections were obtained from the Met Office UKCP18 data set gridded at a resolution of a 5km grid across the UK (Met Office Hadley Centre 2018). 11 different future climate projections at high emissions scenario RCP8.5 were downloaded (Met Office Hadley Centre 2018). Each projection provides an example of climate variability in a changing climate. Data for each projection, minimum daily temperature and total daily rainfall for all NDMP sites for every year available (2021-2040, 2061-2080) were downloaded. The future climate dataset assumes that there are 30 days in every month, therefore giving predicted minimum temperatures and rainfall for 210 days of the active season. The resulting dataset therefore contained 8,400 days of climate data for all 799 NDMP sites for each of the 11 projections.

To obtain minimum average temperature and total average rainfall for the seasonal climatic variables, daily data were collated and then summarised for the 90 days preceding and including the day in the active season. This was calculated for every day of the 210 of the active season to give seasonal average daily minimum temperature and total rainfall for all days in the future climate dataset. A 30-year (1990-2020) baseline for central England was then subtracted from the climate data obtained from UKCP18 data, resulting in site-level residuals from the England mean.

### Torpor predictions

Four simulated dormouse classes were considered for the analysis; 15g female, 20g female, 15g male, 20g male. These were solitary, non-breeding animals, as this is when individuals are most likely to be found torpid. Using future climate data, predictions were made on the likelihood of each of these dormice being found in torpor on each day of the active season in 2021-2040, and 2061 – 2080 across all 799 NDMP sites that I had climate data for. The predictive model was run for each of the future climate projections resulting in 840 predictions (210 for each of the simulated dormouse classes) for each of the forty years at each site. This resulted in the predicted likelihood of entering torpor for 33,600 'torpor days' at each site. For each of the simulated dormouse classes, a daily average was taken across the 11 climate projections to obtain an average likelihood of each of the dormice being found in torpor on any given day of an active season across the study period. These daily averages were then summed across years to get a total number of 'torpor days' per active season for each of the four dormouse classes. To calculate the predicted total percentage of time spent in torpor across each of the active seasons in the study the 'torpor days' for each year of each of the four dormice were averaged. I compared predicted torpor days across NDMP sites in Southeast England (Kent n=106 sites) and northeast Wales (Denbighshire, n=7 sites), to further investigate the prevalence of torpor in the core when compared to the edge of the species range in Britain.

2012 was the second wettest year on record (Kendon et al., 2015, Figure 3.1)and poor summer conditions resulted in one of two of the worst recording years for butterflies in the UK (at the time) (Fox et al. 2015). The same conditions were experienced by dormice and resulted in a poor breeding year (Ian White, *personal* *communication*). I used my predictive model to calculate the predicted time dormice spent in torpor in 2012 as a baseline for a ‘poor’ year for dormice.

### Model validation

Dormouse surveys take place once a month throughout the active season, usually on an arbitrary date when surveyors are available, providing just a snap-shot of observational data. A percentage of torpor days during the active season cannot be calculated for previous years from observational data. Therefore model validation was carried out by creating a binomial model of observed adult dormouse records from the NDMP dataset for 2021 and 2022 survey data (n=3,622) as an independent dataset, as these years have not been included in creating the predictive torpor model. Torpor was characterised as a binary response variable, dormice were either torpid (1) or not (0). For each of these observations a prediction of finding an individual in torpor was obtained using the predictive torpor model and observed climate. These torpor predictions were entered into the binomial model as a predictor variable with observed torpor as the response variable. To establish whether or not there is a relationship between observed and predicted observations of torpor to give further confidence in the results of the future torpor model.

observed torpor data ~ predicted torpor data

## ***Results***

### *Torpor predictions*

Future climate predictions from the Met Office UKCP18 dataset forecast that on average dormouse sites will get warmer during the active season (Figure 3.1). The central-England 30 year (1990-2020) average for the dormouse active season is 9.1 $^{o}$C, and all projections from 2060-2080 are predicted to be warmer than this. Under the worst case projection (12), dormouse sites are predicted to be colder than this average in eight of the twenty years from 2021 to 2040. Year to year fluctuations are also predicted for projections, for example projection 12 the average minimum temperature for the active season is 8.2 $^{o}$C (2026), 9.6 $^{o}$C (2027) and, 8.1 $^{o}$C (2028) on consecutive years.

There is a general trend toward drier conditions during the active season across dormouse sites during the active season by 2080. However, total rainfall is predicted to be changeable across years resulting in potential extremes for dormice, with major variation dependent on the projection (Figure 3.1). For example projection 15 predicts average total active season rainfall across NDMP sites at 39 cm (2031), 72 cm (2032), and 47 cm (2033) across consecutive years.

Across all NDMP sites, the predicted average number of torpor days across all sites is 29% (95% CI: 21%-37%) in 2021 reducing to 18% (95% CI: 12%-24%) by 2080 (Table 3.1). There is an overall reduction in the predicted percentage of torpor days across NDMP sites over the study period (Figure 3.2).

The mean predicted percentage of torpor days in the ‘poor’ year baseline, 2012 for dormice is 30%.

The average number of torpor days, predicted between 2021-2040 and 2061-2080 across all climate projections and NDMP sites, consistently falls below the 30% baseline, indicating improving conditions for dormice across Britain (Figure 3.3). When each projection is considered separately, the average number of ‘poor’ years across projections, across all NDMP sites, from 2021 to 2040 is 3.8 years and from 2061 to 2080 is 0.4.

When comparing a county on the edge of the dormouse distributional range in Britain (Denbighshire) and the core (Kent) there are marked differences in the predicted number of torpor days. Based on the predicted number of torpor days, conditions appear to be much more climatically favourable in Kent, with an average number of predicted torpor days of 15.5% in 2080 compared with 23.2% in Denbighshire. All average and maximum predictions in the 2021 to 2040 period are above the 30% baseline in Denbighshire, representing likely ‘poor’ years for dormice (Figure 3.4). When each projection is considered separately, the average number of ‘poor’ years in Denbighshire across projections during the period 2021 to 2040, is 14.6 years. When each projection is considered separately, the average number of ‘poor’ years in Kent across projections during the period 2021 to 2040 is 1.3 years. In Kent between 2061 and 2080, all minimum, maximum, and average projections are below the 30% threshold, suggesting improved climatic conditions for dormice by this period. When each projection is considered separately, the average number of ‘poor’ years in Denbighshire across projections during the period, 2061 to 2080, is 3.4 years.

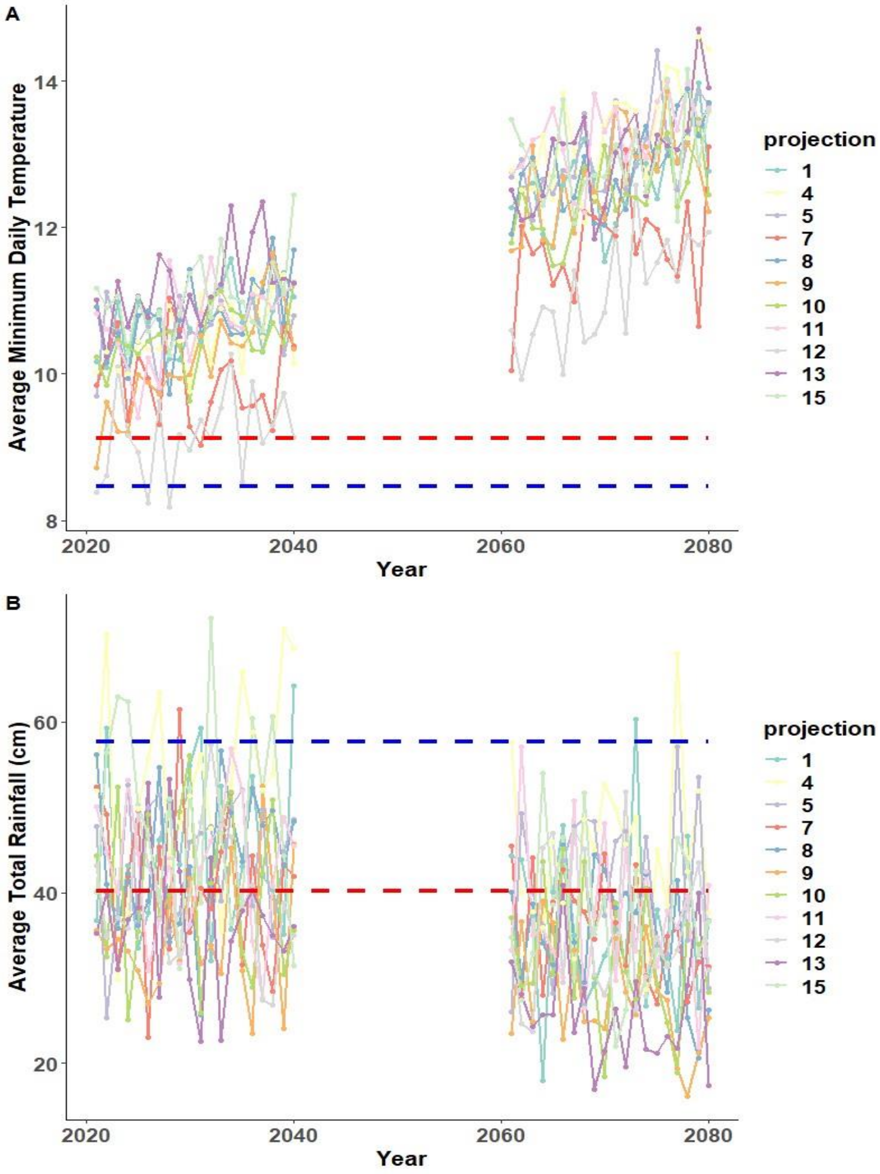


**Figure 3. 1.** *Future climate predictions for dormouse sites across the UK in the active season (April- October), as downloaded from the Met Office website. Each different coloured line represents a different climate projection. A) Minimum average temperatures. Temperatures were calculated by taking an average of daily minimum temperatures across the active season across all NDMP sites. Dotted red line denotes the Central England 30 year average (1990-2020) minimum daily temperature across the dormouse active season. Dotted blue line denotes the Central England average minimum daily temperature across the dormouse active season in 2012. B) Total Rainfall. Rainfall was calculated by taking a total rainfall for each of the 799 NDMP sites across the active season and then taking an average. Dotted red line denotes the Central England 30 year average (1990-2020) total rainfall (cm) across the dormouse active season. Dotted blue line denotes the Central England total rainfall (cm) across the dormouse active season in 2012.*

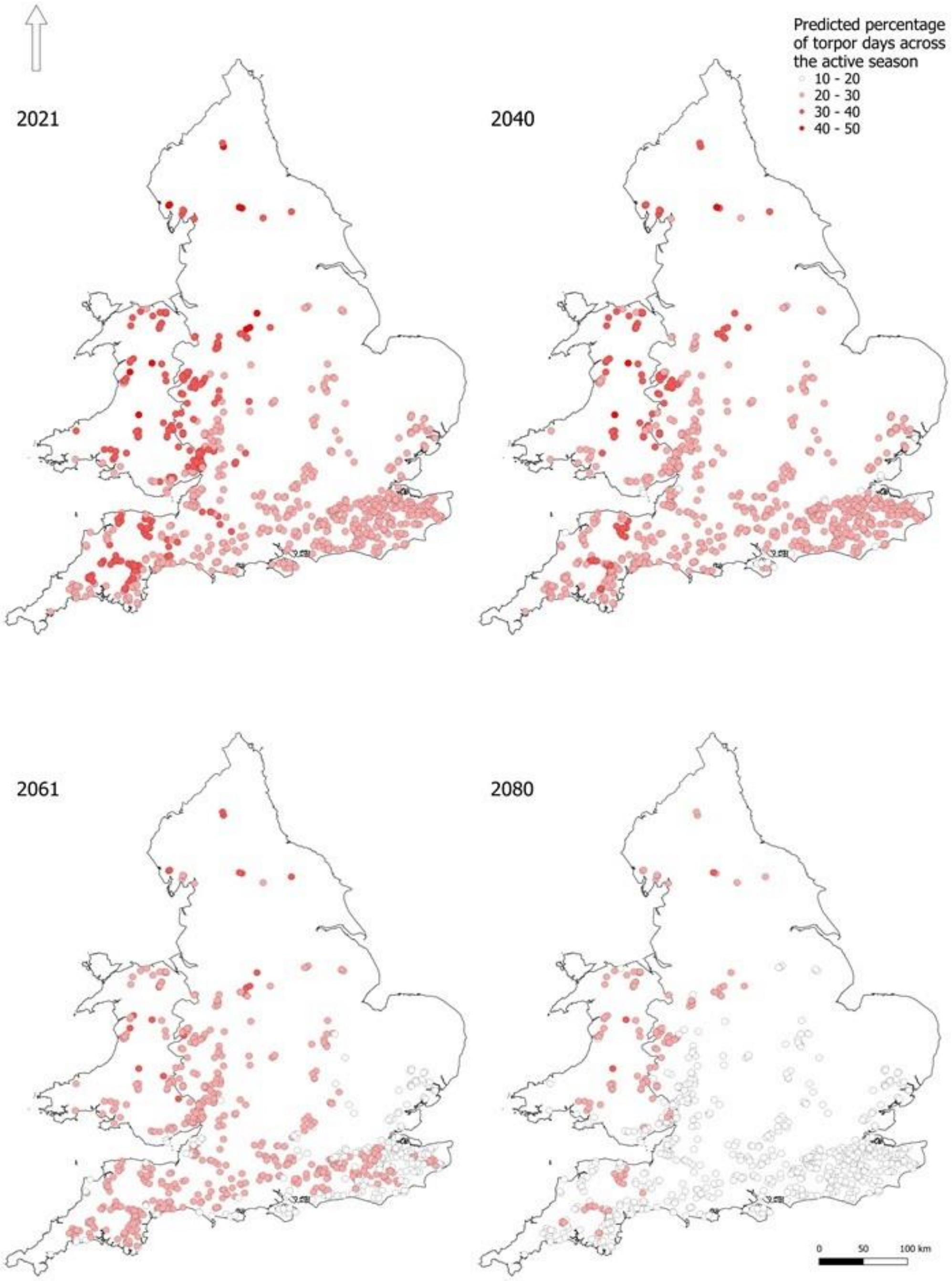


**Figure 3. 2.** *NDMP sites and their predicted percentage of torpor days across the active season using future climate change projections for 2021, 2040, 2061, and 2080. Calculated using a predictive model for intrinsic and extrinsic influencers of torpor use among dormice in the UK. The darker the site the more torpor predicted among dormice populations.*

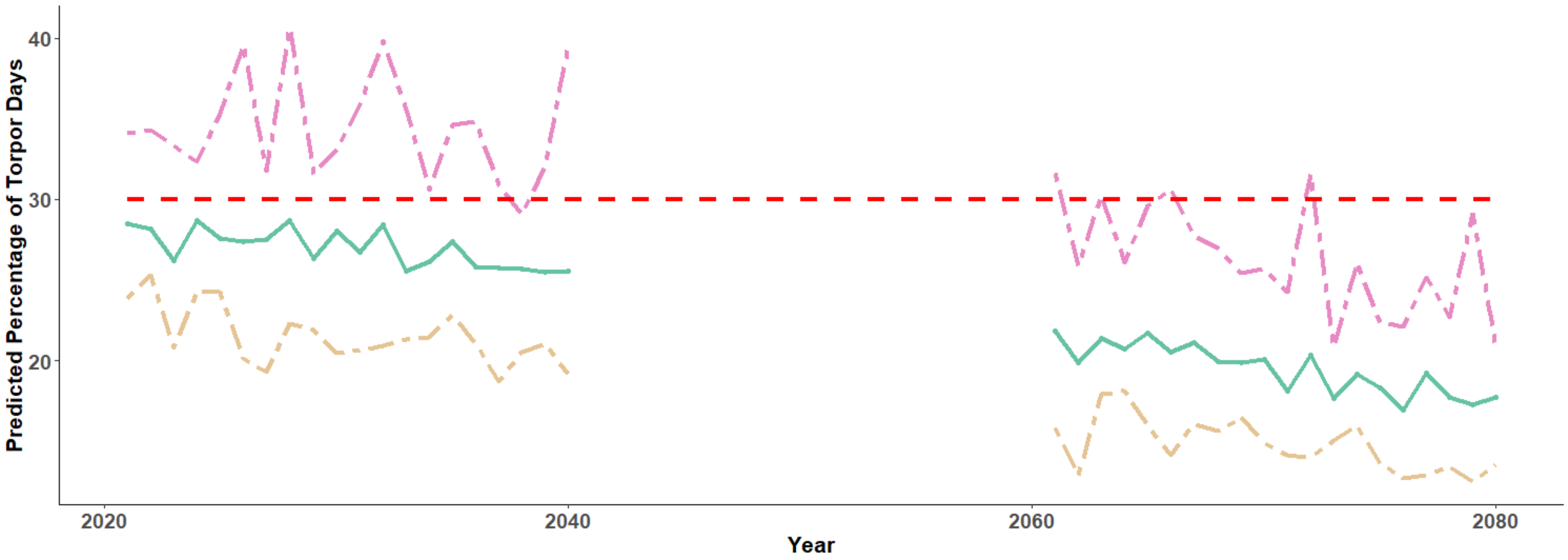


**Figure 3. 3**. *Predicted percentage of the active season (April- October) that hazel dormouse populations in England and Wales will spend torpid across different climate change projections. Calculated using a predictive model of intrinsic and extrinsic influences of torpor in dormice at the individual level. The solid green line represents the predicted percentage of torpor days across the active season averaged across all 799 NDMP sites, averaged across all future climate projections. The pink dashed line represents the maximum predicted percentage of torpor days across the active season averaged across all NDMP sites. The yellow dashed line represents the minimum predicted percentage of torpor days across the active season averaged across all NDMP sites. The red-dashed line is the baseline for a poor breeding year for dormice, based on predictions from 2012 which was a low breeding year for dormice.*

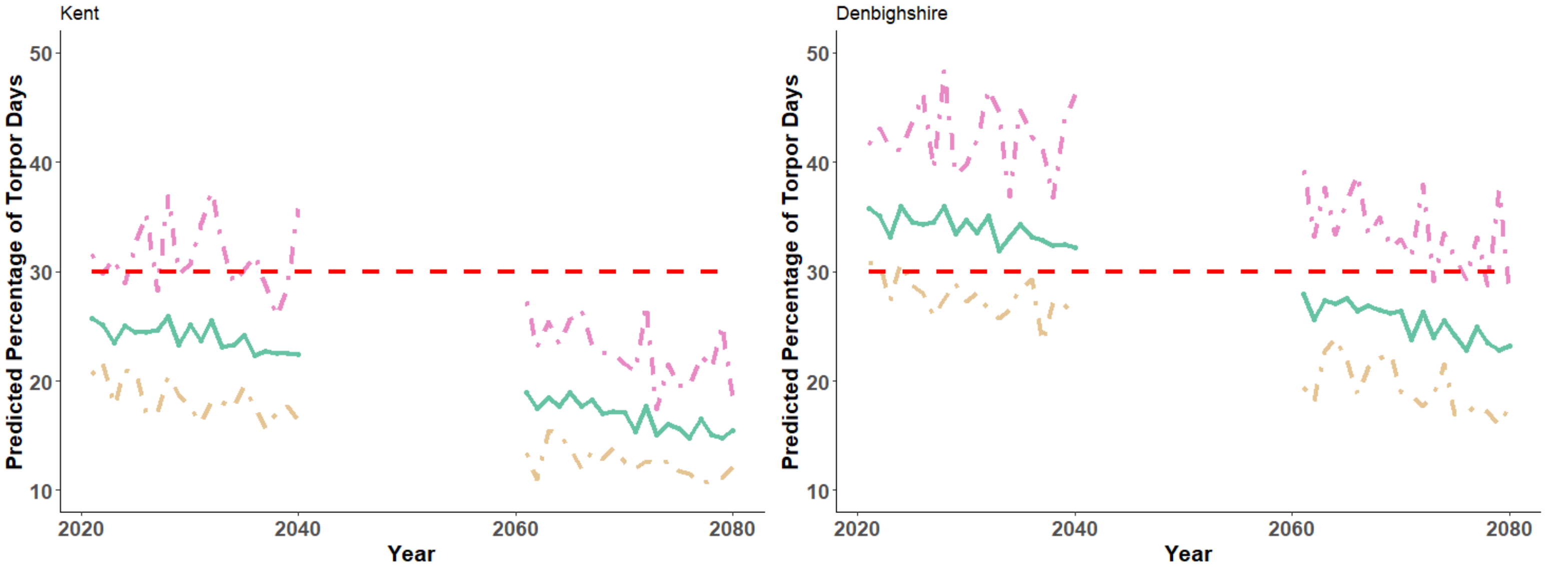


**Figure 3. 4**. *Comparison of the predicted number of torpor days that dormice will spend in torpor during their active season (April-October) across NDMP sites in Kent (a county in Southeast England) and Denbighshire (a county on the edge of their distributional range in Northeast Wales), across different climate change projections. Calculated using a predictive model of intrinsic and extrinsic influences of torpor in dormice at the individual level. The solid green line represents the predicted percentage of torpor days across the active season averaged across all 799 NDMP sites, averaged across all future climate projections. The pink dashed line represents the maximum predicted percentage of torpor days across the active season averaged across all NDMP sites. The yellow dashed line represents the minimum predicted percentage of torpor days across the active season averaged across all NDMP sites. The red-dashed line is the baseline for a poor breeding year for dormice, based on predictions from 2012 which was a low breeding year for dormice.*

| **Year** | **2021** | **2040** | **2061** | **2080** |
|---|---|---|---|---|
| Average Percentage of Torpor Days – across all NDMP sites | 29<br>(95% CI: 21-37) | 26<br>(95% CI: 19-33) | 22<br>(95% CI: 15-29) | 18<br>(95% CI: 12-24) |
| How many NDMP sites have torpor days above 2012 baseline (30%) | 225 | 101 | 19 | 3 |

**Table 3. 1**. *Summary table of results for predicted torpor days across NDMP sites. The average percentage of torpor days denotes the predicted percentage of torpor days across an active season across all 11 climate projections and all 799 NDMP sites analysed. The number of sites out of the 799 NDMP sites with a higher predicted percentage of torpor days than the 2012 'poor' breeding year baseline for dormice, are also noted.*

### *Model validation*

The GLM for observed vs predicted dormouse torpor using observations from 2021 and 2022 resulted in an ROC with an area under the curve of 0.86. K-fold cross validation had an accuracy of 0.80 (95% CI: (0.79, 0.81)). These results give confidence that the model is effectively explaining likely variation in daily torpor into the future, notwithstanding the uncertainties surrounding climate projections (Figure 3.5).

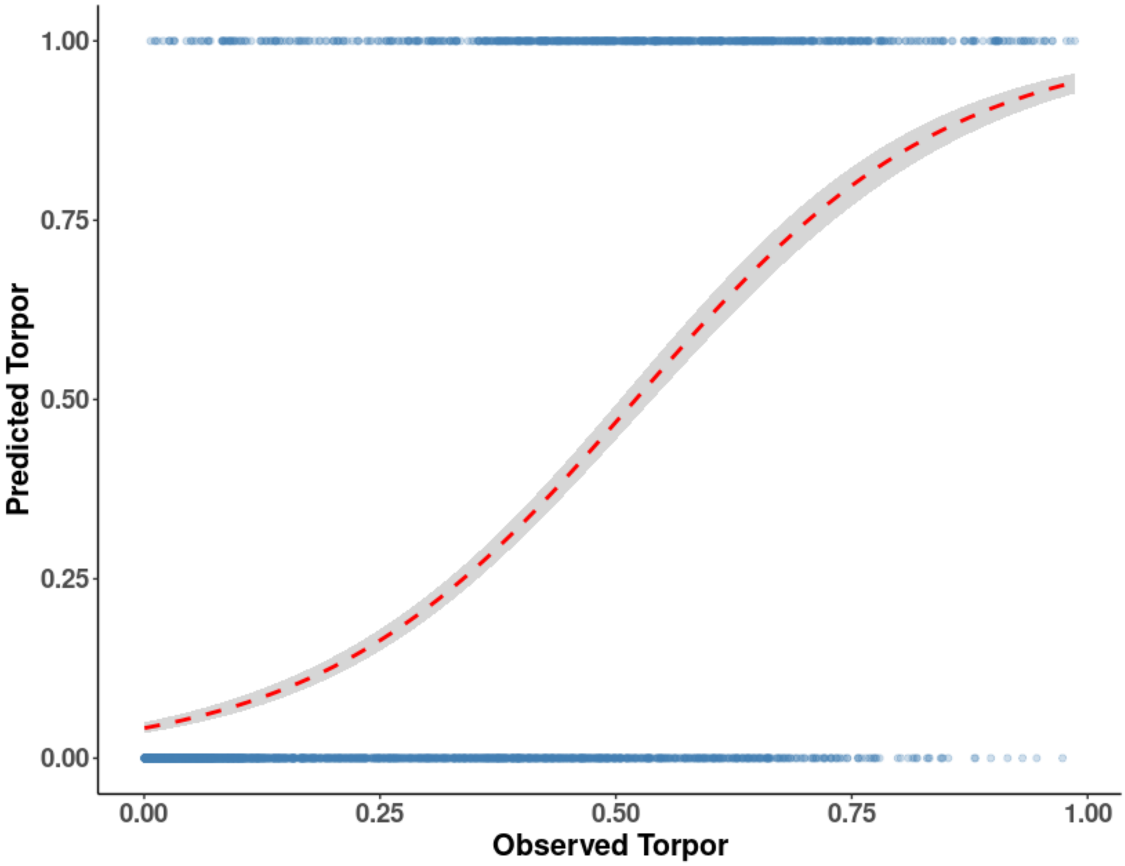


**Figure 3. 5** *The logistic regression used to test the validity of the predictions made about future daily torpor use among hazel dormice. Dormouse observations from the NDMP during 2021 and 2022 active season were obtained for the analysis. Observed torpor (yes/no) was the response variable and the predicted torpor was the explanatory variable. The x-axis: observed torpor, 0 depicts and active dormouse and 1 a torpid dormouse. The y-axis: predicted torpor for 2021/2022 records based on our predictive model. The red dashed line shows the logistic curve with shading depicting confidence intervals.*

## ***Discussion***

This study predicts a substantial decrease in the frequency of torpor among hazel dormice over time, with a projected 29% of the active season in torpor for 2021 declining to 18% by 2080 across all NDMP sites in England and Wales. This reduction is attributed to overall warmer and drier conditions anticipated during the active season in 2080, resulting in fewer predicted torpor days. The climatic changes suggest that the conditions during the active season are likely to be less energetically costly for dormice (Ruf and Geiser 2015; Geiser and Cooper 2023). Daily torpor serves as an adaptive mechanism for hazel dormice during unfavourable conditions, representing a trade-off between energy conservation and reproduction (Juškaitis 2005). Given relationships between high rates of torpor and fewer breeding events, predictions for lower incidence of torpor suggest that dormouse populations may have greater opportunities to invest in breeding. This study represents an example where climate change might be associated with some beneficial changes to the conservation status of the species.

This study focuses on how changes in extrinsic factors such as temperature and rainfall might affect change in dormouse ecology, specifically daily torpor, during the active season. However, factors other than torpor may also determine the effects of climate change on dormouse survival at the range edge. I do not directly consider foraging opportunities for dormice. Dormice are specialist feeders that are unable to digest cellulose and therefore need highly nutritional food sources such as flowers and buds in the spring and nuts and berries in the winter (Richards et al. 1984; Bright et al. 2006; Goodwin et al. 2020). The timing of biological events, crucial for a consistent food supply, is subject to change, with a growing trend toward earlier spring seasons; approximately 78% of leaf unfolding and flowering records in Europe have exhibited this advancement (Menzel et al. 2006). Phenology is predicted to change at varying degrees for different trophic levels leading to biological mismatch (Thackeray *et al.*, 2010; Thackeray, *et al.*, 2016). Consequently, the impact of phenological changes on dormouse food supplies throughout their active season remains uncertain, as these variations may indirectly affect the energetic costs and benefits of torpor.

Food availability is intrinsically tied to local conditions; heavy rains can cause fruit crops to fail and extreme drought results in reduced yields. It remains unclear whether or not dormouse food sources will be able to persist under future climate change scenarios. Composition of woodlands is predicted to change, with many areas in Britain becoming climatically unsuitable or marginal for many native trees by 2080 under worst case scenarios (Ray et al. 2010). If the species composition of dormouse habitats across Britain alter significantly, it could lead to an increase in daily torpor among individuals, because there may not be enough suitable foraging opportunities to sustain their energy budgets.

Climate change will not only affect dormice behaviour during the active season but as hibernators milder, wetter, more variable winters might also be detrimental. In response to the seasonal changes in Britain, dormice undergo an extended hibernation phase spanning from November to March, allowing them to avoid harsh climatic conditions and cope with limited food availability. Rising winter temperatures in Britain raise concerns for dormice, affecting hibernaculum locations and potentially compromising body condition due to increased arousal frequency (Pretzlaff and Dausmann 2012; Gubert et al. 2023). Additionally the premature emergence from hibernation, as a result of climate change, occurring before the availability of resources, poses a significant risk of compromising body condition just before the onset of the breeding season. Importantly, there exists a direct correlation between body condition and litter size, with lighter females tending to produce smaller litters (Naim et al. 2011). Consequently, the early emergence from hibernation carries the potential for direct consequences on breeding success and, the overall population growth of dormice. Considering such additional factors highlights the complexities involved in predicting species responses to climate change.

The thermoneutral zone of hazel dormice in Britain remains unknown. My study does not account for conditions in Britain becoming too hot or dry and individuals having to employ torpor to maintain energy budgets, another potential climate scenario. Warming temperatures have been predicted to increase the use of daily torpor in a number of small tropical mammals as a mechanism by which to avoid heat stress (Lovegrove et al. 2014). Should temperatures exceed tolerable levels for hazel dormice, a heightened occurrence of torpor may become evident as individuals seek to mitigate this stress and enhance their chances of survival. As hibernators dormice might be able to shift their active and reproductive period under warming conditions. In warmer parts of their range dormice do not hibernate at all. As winters and springs become warmer, dormice in England and Wales could shift their reproductive period to avoid the hottest parts of summer if their thermotolerance is frequently exceeded. A greater understanding of the number of different ways climate will affect species ecology, more specifically changes to active periods, is important for appropriate conservation strategies and management into the future.

Despite the overarching trend pointing towards a decline in the use of daily torpor, fluctuations in the prevalence of daily torpor are expected to continue year after year (Figure 3.3), this is especially important for populations on the very edge of their distributional range, as in Britain. These variations imply that hazel dormice, particularly those dwelling at the fringe of their distributional range, will continue to experience 'good' and 'poor' years in response to climatic variability, which may include extreme conditions. This can be seen when comparing predicted torpor use in Kent, the range core, and Denbighshire, on the margins (Figure 3.4). Torpor use is predicted to be much more prevalent at the edge of the range and particularly between 2021 and 2040. A succession of too many 'poor' years could potentially culminate in local extinctions, as these populations may struggle to rebound from declines in previous years (Pereira et al. 2010; Hoffmann and Sgrò 2011; Manes et al. 2021; Habibullah et al. 2022). When individuals are predicted to spend over a third of the active season in a state of daily torpor, it suggests a preference for energy conservation over breeding. Dormouse populations on the edge of the range will remain at risk from poor weather conditions during the active season for decades, despite a steady trend towards improving conditions.

My investigation suggests that there is likely to be a lessening requirement for daily torpor across Britain by 2080, this is of particular importance for populations at the edge of their range especially those in northern areas in England and

Wales. At these cooler and wetter margins, a reduction in the frequency of daily torpor could be a factor that allows the expansion of local populations and/or the spread of dormice further north in England, if appropriate habitat is available. However careful consideration is needed of the risk of climatic extremes at the site level, especially before 2040. Areas where dormice currently subsist in low numbers, especially marginal, range edge sites; such as those at high elevations, and at northern and western margins are at particular risk of local extinctions as a result of repeated climatic extremes and subsequent high torpor use.

# Chapter 4

## Chapter 4: Challenges in predicting distribution at the edge: A case study with hazel dormice (*Muscardinus avellanarius*) in Britain

# Chapter 4: Challenges in predicting distribution at the edge: A case study with hazel dormice (*Muscardinus avellanarius*) in Britain

## *Abstract*

Species at the edge of their range are often associated with low habitat suitability and increased exposure to extreme climatic events, which requires specific conservation considerations. These peripheral populations exhibit geographic isolation and face distinct threats compared to core populations, resulting in lower abundance and increased vulnerability to local extinctions. The distribution of rare and cryptic species at the edge of their range is often poorly understood, but such knowledge could aid in their conservation. This study investigates whether the distribution of hazel dormice (*Muscardinus avellanarius)* can be accurately predicted at the edge of their range in Britain in non-typical habitats. Using current information to build species distribution models (SDMs), a regional, 100m resolution, SDM is compared to an existing national SDM at a coarser 1km resolution. The accuracy of the SDMs were tested by conducting an independent survey of dormouse presence in the field. Both SDMs failed to accurately predict dormouse distribution at the edge of the species range in North Wales, in a non-typical habitat. The survey found dormice present in Clocaenog forest, a coniferous plantation habitat, but no dormice were detected in other similar conifer habitats in the region. My findings suggest that SDM predictions based on typical habitat characteristics may fail to predict presence of species at the edge of their range. My study underscores the complexity of modelling species distributions, particularly in non-typical habitats at the periphery of a species range.

## *Introduction*

Species at the edge of their range exist in areas that are often associated with declining suitability and abundance of habitat (Caissy et al. 2020) and have a higher severity and frequency of extreme climatic events when compared with the core (Rehm et al. 2015). At the edge of the range populations often exist in geographic isolation and experience different threats from those in the core (Thakur et al. 2018). These populations are often associated with lower overall abundance than those at the core and are therefore susceptible to local extinctions (Lawton 1993; Fisher 2011; Fristoe et al. 2023). For example when investigating declines in Galliform species, local extinctions were more frequent at the edge of the range in the Palearctic (Boakes et al. 2018). Populations at the edge of a species range should be included in conservation planning, to effectively mitigate overall population declines.

The conservation value of species at the edge of their range has been debated as small isolated populations are susceptible to inbreeding and genetic drift (Ellstrand and Elam 1993; Lesica and Allendorf 1995; Brown et al. 1996; Caissy et al. 2020). Edge populations can therefore be harder to conserve and have been argued to be less important for overall species persistence (Bunnell et al. 2004). However these peripheral populations often comprise genetic variants as they are locally adapted to unusual conditions and are often genetically different from core populations (Lesica and Allendorf 1995; Rehm et al. 2015). There is evidence of adaptive differentiation of populations at the edge of their range (Angert et al. 2020), which includes; behaviour change (Hudina et al. 2014; Liebl and Martin 2014; Gruber et al. 2017; Johnston and Smith 2018), morphological differences (Hudson et al. 2016), and population dynamics (Aikens and Roach 2014; Chuang and Peterson 2016). The preservation of these adaptations is particularly important under a changing climate as edge populations might be better adapted to rapid changes in the environment (Rehm et al. 2015).

In the context of climate change, range margin populations also assume heightened conservation significance due to their susceptibility to amplified, non-linear fluctuations in response to small changes in environmental conditions (Thomas et al. 1994; Westerbom et al. 2019). These populations are likely to be the first to go extinct under deteriorating conditions but could also be on the front line of species expansion if conditions improve for a species (Kanda et al. 2009; Furrer and Pasinelli 2016; Goel and Keitt 2022). Populations residing at the edge of a species' range frequently serve as early indicators of the species' response to climate change (Wiens 2016; Fogarty et al. 2017). We often lack appropriate data to achieve positive conservation outcomes for populations at the edge of their range because of their sparse distribution and propensity for unusual habitats (Sexton et al. 2009). Traditional survey methods to collect the necessary distribution data requires extensive time and resource (Anderson et al. 2002). To predict where efforts should be placed, conservation planning requires models that incorporate habitat and species range.

Hazel dormice *Muscardinus avellanarius* (referred to henceforth simply as ‘dormice’) are an arboreal mammal considered to have an optimal habitat in Britain of broadleaf coppice and favour woodland with an understory which is dense and diverse, they also favour dense species rich hedgerows (Bright and Morris 1990; Bright and Morris 1993; Bright and Morris 1996; Bright et al. 2006; Juškaitis 2008b; Juškaitis and Augutė 2008; Hutterer et al. 2021). Dormice are believed to prefer these habitats due to their inability to digest cellulose. They rely on a variety of plant resources at different life stages throughout the season, such as buds and pollen in the spring and tree seeds later in the year (Richards et al. 1984). However more recent work suggests dormice's opportunistic nature, adapting to local-scale resource availability, including invertebrates when plant resources are scarce (Goodwin et al. 2020). Habitat preferences of hazel dormice vary across Europe but a diversity of fruiting shrub species appear to be vital for their continued persistence (Wuttke et al. 2012; Ramakers et al. 2014; Sozio et al. 2016; Goodwin et al. 2018a; Goodwin et al. 2018a; Mortensen et al. 2022). This dense vegetation structure not only provides a source of food but nesting opportunities and predator avoidance.

Dormice reach the north western edge of their range in Britain, where climatic conditions are likely to be suboptimal and therefore more demanding (Pretzlaff and Dausmann 2012). Despite this dormice seem able to persist in low numbers in sometimes unfavourable conditions (Bright 1995). Dormice have attracted substantial conservation attention and intervention in England and Wales, yet continue to decline - populations have fallen by 78% between 1994- 2020 (Goodwin et al. 2017; Scopes et al. 2023). The hazel dormouse is protected under the UK Habitats Regulations (1994) and is a European Protected Species, listed under Annex IV of the European Habitats Directive (1992). It is of Least Concern under the International Union for Conservation of Nature (IUCN) Red List and European Regional Assessment, however this assessment does state that in parts of its northern range, there is cause for concern (Hutterer et al., 2021). Dormice have become extinct in half of their range in England and Wales over the last half century (Hurrell and McIntosh, 1984), and are listed as Vulnerable in Britain (Mathews and Harrower 2020).

Dormice are a cryptic species and can be hard to locate. They are thought to be rare and sparsely distributed on the edge of their range, with evidence that they can occupy non-typical habitats including spruce plantations, deciduous edges in conifer plantations and high canopy deciduous forests with no understory (Bright 1995; Wuttke et al. 2012; Mortensen et al. 2022). Dormice in these areas are often under-recorded and their distribution in non-typical habitats is poorly understood. Forest management is known to affect the richness and composition of mammal communities (Fisher and Wilkinson 2005; Paillet et al. 2010; Bogdziewicz and Zwolak 2014). Conservation initiatives for dormice predominantly target 'conventional' habitats, yet research on populations within conifer plantations has revealed their susceptibility to intensive thinning operations (Zapponi et al. 2013; Trout et al. 2018). Dormice, as an arboreal species, are particularly susceptible to timber harvesting practices, resulting in a loss of nesting sites and habitat which can affect abundance and reproductive success (Blumstein 2010; Raad et al. 2021).

Managing productive forests for wildlife has implications on cost and time when compared to traditional clear felling methods (Tsushima et al. 2023). Foresters are legally obligated to manage their plantations for particular protected species in Britain which can lead to conflicts (Niemelä et al. 2005; Borrass 2014). Forest managers have to navigate complex legislation with regards to the protection status of species and habitats with often incomplete information (Ray and Broome 2007; Borrass 2014). Applying for appropriate licences and the restrictions these impose, can slow forest operations even further (Borrass 2014). Dormice are afforded legal protection and their presence at sites impacts forestry practice (Mortensen et al. 2022).  Surveys for dormice in non-typical habitats have typically been absent, and even when conducted, the available information is often incomplete. Traditional ecological survey methods are time-consuming, resource-intensive, and may fall short in detecting species or accurately mapping their full range within a site (Raad et al., 2021).

Species distribution models (SDMs) are widely used as a conservation tool (Guisan and Thuiller 2005). SDMs use the concept of the ‘ecological niche’ described by Hutchinson (1957) and aim to define specific variables within the environment that have a relationship with species and estimate the corresponding distribution (Peterson and Soberón 2012; Gobeyn et al. 2019). These models provide insights into the subset of conditions conducive to a species' survival and reproduction (Warren 2012). SDMs require environmental data to predict likely species occurrence across a defined geographical area and usually incorporate habitat and climatic variables (Guisan and Thuiller 2005; Miller 2010; Warren 2012; Noce et al. 2020). SDMs then use available species data to estimate species occurrence based on these environmental predictors (Gobeyn et al. 2019). SDMs have gained popularity in recent years, as gridded environmental (climate and land cover), and occurrence data is much more readily available in digitised form (Araújo and Guisan 2006; Olivier and Wotherspoon 2006; Tole 2006; Araújo et al. 2019). They can be used to predict the movement of invasive species (Sung et al. 2018; Lake et al. 2020), disease risk (Murray et al. 2011; Lippi et al. 2021), wildfire mangement (Bosso et al. 2018), and species response to climate change (Peterson et al. 2018; Diengdoh et al. 2022). SDMs can incorporate modern or historical data to estimate distributions and are especially useful when there is a lack of suitable information to accurately guide conservation measures (Raxworthy et al. 2003; Warren 2012).

SDMs are useful tools for poorly sampled, rare, and cryptic species, and can provide first-pass hypotheses when no other information is available, increasing the proportion of species that can be studied using these methods (Peterson 2001; Anderson et al. 2002; Pearson et al. 2006). By guiding field surveys this modelling approach has been successful and led to the discovery of new populations of highly endangered species (Engler et al. 2004; Groff et al. 2014;

McCune 2016; Rhoden et al. 2017). However SDMs should be used with caution as there are associated challenges with their application and use. There are a number reasons why SDMs fail to accurately predict where species occur and this is described extensively in the literature (Araújo and Guisan 2006; Rathore and Sharma 2023). SDMs can be limited by available species occurrence data and sampling bias (Peterson 2001; Reddy and Dávalos 2003; Elith et al. 2006), the creation of pseudo-absences in the wrong place (Engler et al. 2004; Phillips et al. 2009), coarse explanatory variables (Lee-Yaw et al. 2022), and how their predictive power is tested (Vaughan and Ormerod 2005; Elith and Graham 2009).

The environmental requirements of any given species can vary across its geographic range (Fernández et al. 2015). Using SDMs for peripheral populations presents challenges due to the heightened risk of extinction brought about by demographic stochasticity and sometime sub-optimal conditions at the range's edge. This can lead to sporadic colonisations and extinctions across habitat patches, impacting metapopulations (Holt and Keitt 2000; Anderson et al. 2009). Differing species-habitat relationships, biotic interactions and demographic processes often occur at the margins of species ranges when compared with the core and are usually not successfully incorporated into SDMs (Braunisch et al. 2008; Zurell et al. 2009; Radomski et al. 2022). This is particularly evident when species occurrence data from their core range is employed in model development. For instance, the use of core-range data to construct models for butterfly species in Donana National Park proved ineffective in accurately predicting the distribution of individuals at the periphery (Fernández et al. 2015). National and regional datasets produce very different results, highlighting the importance of spatial scale when building SDMs (Razgour et al. 2011). For example when modelling distributions of the grey long eared bat *(Plecotus austriacus)* in the UK, models using national data found that climatic variables described the distribution of individuals best whereas more fine-scale modelling found habitat to be a better predictor (Razgour et al. 2011).

Although accompanied by limitations, the development of an effective SDM using existing data could offer a valuable resource. Such a model would aid in the identification of areas where dormice may potentially inhabit non-typical habitats, facilitating targeted survey and mitigation efforts where they might otherwise remain undetected. Dormice offer an excellent opportunity for testing this, particularly at the edge of their range where we have some records in non-typical habitats, and the effectiveness of SDMs for this species in marginal areas remains unexplored. Given their pronounced declines, and the unique genetic assemblages of dormice at the edge of the range (Naim et al. 2012; Combe et al. 2016), which need preservation, gaining a deeper insight into their distribution within marginal landscapes has the potential to significantly enhance dormice conservation efforts.

My study was conducted in the Welsh counties of Conwy and Denbighshire, situated at the northern edge of dormice distribution in Britain. There is evidence of dormice occupying conifer plantation across the region, but this has previously been under recorded (Bright 1995). This landscape was chosen because it contains an area where dormice are known to inhabit an 80-year old conifer plantation, Clocaenog Forest, this site was the inspiration for my study. Dormice were only discovered at Clocaenog in 2009 when mitigation works were carried out during the construction of a wind turbine site. Extensive dormouse monitoring in specific areas of the site has continued since. Historically, inappropriate survey techniques have been used to detect dormice presence in the region, for example using gnawed hazel *(Corylus avellana)* nuts when there is a lack of this tree species in non-typical habitat (Jermyn et al. 2001).

This study aimed to investigate if the distribution of dormice in non-typical habitats at the edge of their range could be accurately predicted by SDMs using existing records. By building a regional and comparing to an existing national SDM for dormice I aimed to counteract some of the challenges of studying rare species at the edge of their range. The national model was commissioned by Natural Resources Wales as a strategic support tool for planning decisions and infrastructure. I hypothesised that the regional SDM being of a higher resolution would capture spatial heterogeneity and hence identify small patches of suitable habitat, in a way the national model would not, because it incorporates observations from peripheral populations, which are more relevant to the edge of the species' range. This study investigates the use of SDMs as a conservation tool for dormice which have sparse distributions and limited data at the range's periphery, in the context of conifer plantations. The results of this research may offer valuable insights for both dormice conservation efforts and forest management.

## ***Methods***

All analysis was completed using QGIS version 3.14 (QGIS 2022) and R version 4.2.2 (R Core Team 2022).

### *Species distribution model (SDM)*

I obtained the results of a pre-existing national SDM with a 1km resolution covering the entire UK (van der Waal et al. 2021). Dormouse records for this SDM were obtained from the NBN atlas and Wales Local Environment Records Centres.

### *Regional species distribution model*

I built a regional SDM at a 100m resolution and where possible variables were obtained at this resolution. A 7km buffer was added around Conwy and Denbighshire to be included in the analysis resulting in 300,261 100m grid squares. 100m grid squares containing British grid references for the study area were obtained using the OSGR tool produced by the Field Studies Council in QGIS.

#### **Species presence/absence**

Dormouse records for the regional model, were obtained from the Local Environmental Records Centre for North Wales- ‘Cofnod’, similarly to the national model. 1,530 dormouse observations were located in Conwy and Denbighshire (Cofnod, 2022, accessed June 2022). I designated a 100m grid square a presence square if it contained one or more dormouse records. This resulted in 261 presence squares. Records that were not biologically meaningful, for example from beaches, were removed, resulting in 257 presence squares.

Dormouse absence is difficult to prove and not routinely recorded (Bright et al. 2006). I therefore created pseudo-absences for my analysis. From my 100m resolution grid all presence squares were removed, to ensure my pseudo-absences would not overlap with dormouse presence. With the remaining squares 250 random points were generated in QGIS. Climate data is not available for grid squares that contain over 50% water, such as coasts and river banks, therefore squares where climate data were not available were removed resulting in 242 pseudo absences.

Using pseudo-absences introduces the risk of erroneously designating an absence in an area where a species is actually present (Engler et al. 2004). This is particularly pronounced in the regional model due to the relatively low sample size, and selecting an absence inappropriately can significantly compromise model quality (Engler et al. 2004; Barbet-Massin et al. 2012). This is especially true as the pseudo-absence data is distributed randomly across the region contrasting with the sampling bias present in observational data for dormice (Phillips et al. 2009). However, regression techniques demonstrate that randomly selected pseudo-absences contribute to the most reliable distribution models (Barbet-Massin et al. 2012).

### Terrain

Topographic data was included in the regional SDM as a proxy for microclimate. Microclimate may affect the presence of dormice directly through solar radiation or indirectly through vegetation composition. Elevation raster for the UK was obtained from Ordnance Survey OS Terrain 50 (Ordnance Survey 2022). Using zonal stats tool in QGIS the minimum, maximum, and mean slope for each 100m grid square was calculated. Slope was calculated as a percentage. Aspect was calculated as two variables NS and WE the values of which range from -1 to 1. These represent how much a slope faces north (NS=1), south (NS=-1), east (WE=1), or west (WE=-1) (Deng et al. 2007).

### Forest cover

I used two data sources to derive forest cover: the UKCEH Land Cover Map (LCM) and the National Forest Inventory (NFI) (Rowland et al. 2017; Morton et al. 2020c; Morton et al. 2020b; Morton et al. 2020a; Rowland et al. 2020; Forestry Commission 2022). I obtained LCM data from 1990, 2015, 2017, 2018, and 2019 and calculated the percentage cover of each grid square of 'Deciduous woodland' and 'Coniferous woodland' for each of these years. Percentage cover in 2011 and 2019 was calculated for the following NFI classes; 'Mixed mainly conifer,' 'Mixed mainly broadleaved,' 'Broadleaved,' and 'Conifer.' The percentage cover of these vegetation types were calculated using the QGIS tools 'dissolve' and 'intersect' to overlay the 100m grid square onto the different land cover types.

'Mixed mainly broadleaf' cover occurred in 14 of 509 grid squares and 'mixed mainly conifer' in 12 of 509 grid squares. These variables were therefore added to broadleaf and conifer variables in the NFI respectively. An average of LCM percentage cover for each grid square was calculated across all the years obtained, and absolute change was calculated between 1990 and 2015 as this is when the data is comparable (van der Waal et al. 2021). An average of NFI percentage cover for each grid squares was calculated, and absolute change between the two years.

The average for each forest type (broadleaf and conifer) as measured by the NFI and LCM was used as variables for the SDM. The absolute change that was greater for either LCM or NFI for each grid square for broadleaf and conifer were used as variables for the SDM.

### Climate data

Climate data from 5 years prior to each dormouse observation were used to establish climatic variables for the SDM (van der Waal et al. 2021). I assigned a year to pseudo-absences at the same frequency as dormouse records so climate variables could also be calculated for these grid squares. Climate data were obtained from the HadUK-Grid dataset with 1 km grid resolution, published in 2020 (Met Office et al. 2021). The data consisted of the total rainfall (mm), minimum, and maximum daily air temperatures (°C) for each month.

As climatic variables are likely to be highly correlated I checked for correlations above 0.7, as multicollinearity can affect model performance (Zuur et al. 2010; Dormann et al. 2012). Multicollinearity arises in regression models when two or more independent variables exhibit a strong correlation with each other, leading to challenges in isolating the specific impact of each independent variable on the dependent variable. Where two variables were highly correlated the one with the greater explanatory power based on AUC was chosen (Table 4.1). Maximum summer temperature and summer rainfall are highly correlated and temperature had a higher AUC than rainfall. However recent work regarding dormice and torpor highlights the importance of rainfall on dormouse life history events (Chapter 2). Therefore the Variance Inflation Factor (VIF) was tested for the two variables and returned a low score (1.71) I therefore decided to keep both maximum summer temperature and summer total rainfall in subsequent analysis.

### Building the species distribution model

I constructed the SDM using 90% of the dormouse presence/absence records, randomly selected as the training data. The response variable was dormouse presence/absence and the environmental variables were the predictor variables. I estimated relationships using binomial generalised linear models (GLMs). A GLM was chosen as they have similar performance to more complex models, can deal with different types of predictors, and have been shown to have success at higher resolutions (Engler et al. 2004; Andersen et al. 2017; Seidle et al. 2020). Using backward elimination I identified the most informative model using the Akaike Information Criterion (AIC). The model's predictive power was tested with the remaining 10% of the dormouse presence/absence records.

When the SDM was built, it was used to predict dormouse presence likelihood across all 100m grid cells in Conwy and Denbighshire, with a 7km buffer, providing a landscape suitability assessment. For these squares climatic variables were averaged from 2015-2020.

*Model validation- in the field*

Independent validation data was collected, this provides the most reliable evaluation metrics for the SDMs (Vaughan and Ormerod 2005; Roberts et al. 2017; Fourcade et al. 2018). Presence/absence data was collected using dormouse footprint tunnels across the landscape (Mills et al. 2016). Dormouse footprint tunnels were selected due to their practical and straightforward construction in the field and are likely to achieve positive results within shorter timescales when compared to traditional methods using nest boxes (PTES 2022). 525 tunnels were erected across 7 coniferous plantations (sites) in the landscape during September and October 2022 (Figure 4.1). Each site had between 2 and 6 lines consisting of 25 tunnels placed 10m apart. The study had 21 lines in total. It is considered that there is a 94.5% chance of dormouse detection in high canopy woodland over 2 months with this length of line (PTES, *unpublished data*). The locations of lines were selected according to the output of the SDM; ‘low’ (<0.5), ‘medium’ (0.5-0.75), or ‘high’ (>0.75) suitability areas for dormice. Site selection was carried out with a preliminary model run. Due to difficulties establishing accurate location in the field near grid square boundaries and subsequent model refinement some tunnels were selected to be within one category but subsequently found to be in a grid square classified in another category (n=17 tunnels). All lines were on the Natural Resource Wales (NRW) estate and appropriate permissions for the survey were obtained from the North West and North East teams. All work was undertaken with ethical approval from the FESE Cornwall Ethics Committee at the University of Exeter (Application ID 517107).

Tunnels were placed in the first week of September 2022 and were checked every 2 weeks and re-set. Some lines contained scrubby edges, defined as early successional woodland dominated by goat willow (*Salix caprea*), in these instances tunnels were placed alternatively between scrub and coniferous habitat to determine if dormice exhibited a preference. Tunnels were checked until November 2022 (the end of the dormouse active season) and then taken down. Each tunnel was checked four times during this period, when any dormouse footprints were found the check number, tunnel number, and location was noted.

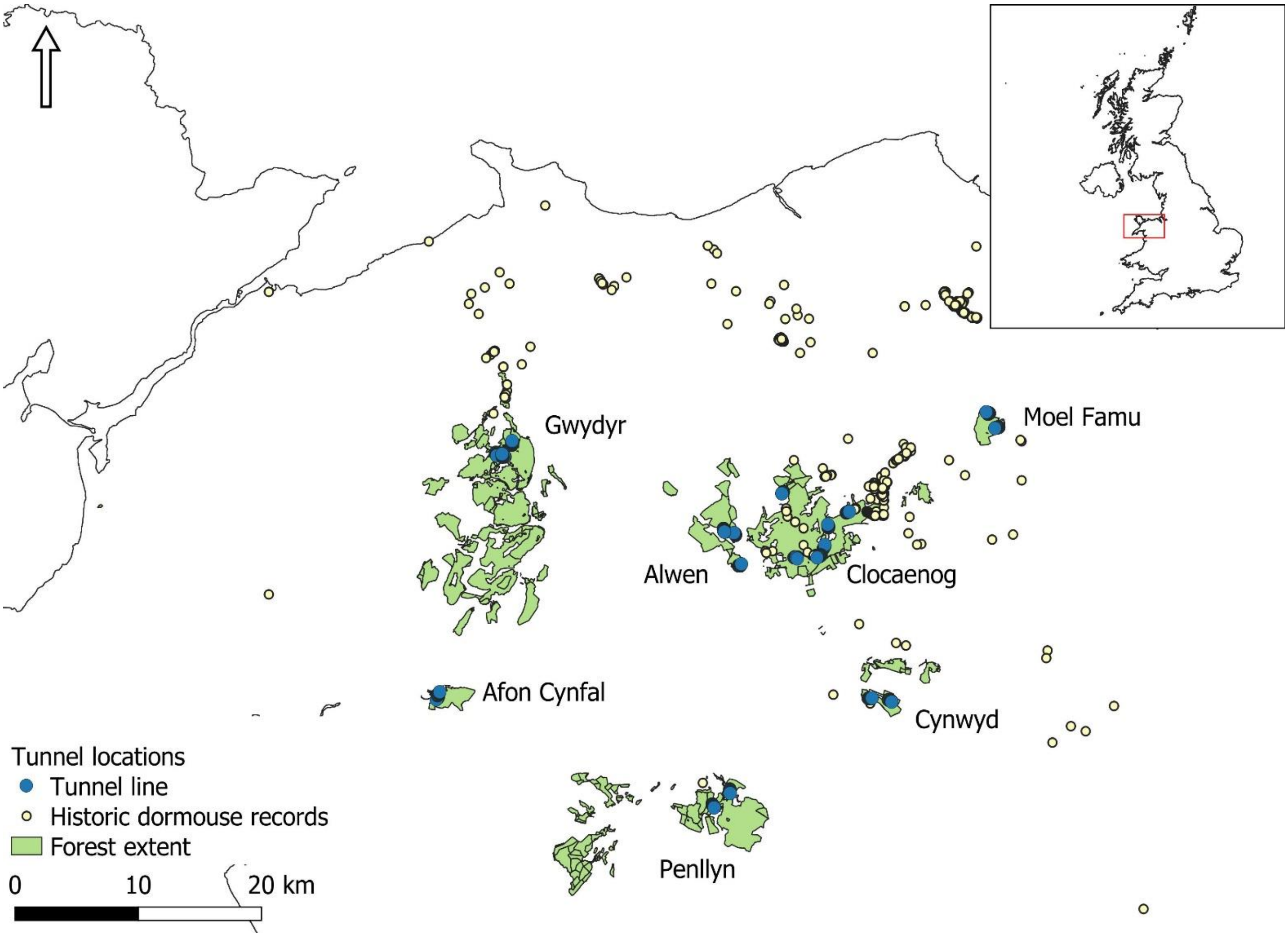


**Figure 4. 1.** *Forest extents (green areas) of the sites chosen for dormouse tunnel construction based on the results from the regional species distribution model (SDM). The regional SDM was built from existing dormouse records, in Denbighshire and Conwy, obtained from North Wales Environmental Information Service (Cofnod). The regional SDM was built to predict the likely distribution of dormice across conifer plantations in the region. From the results dormice footprint tunnels were placed across the landscape to test the SDM outcomes, as an independent dataset for the presence/absence of dormice. Blue circles denote where tunnels were placed. Yellow circles denote historic dormouse records, supplied by Cofnod, and used to build the regional SDM.*

### *SDM performance and dormouse tunnel preferences*

Variables that may determine occupancy were collected at the tunnel level which included, plant species within 1 metre of a tunnel, diameter and height of the tree that the tunnel was placed in, and the habitat type the tunnel was placed in (scrub or conifer). Variables collected at the line level included dominant vegetation in the area, information regarding adjacent land use, and management practices (Appendix 2).

Analysis at both tunnel and line levels was undertaken to determine dormouse habitat preferences at different spatial scales. Mixed models with a binomial error structure were built using the results from the tunnel survey with dormouse footprint presence (1) and no footprints recorded/absence (0) as a binary response variable, to determine if there were any habitat preferences amongst dormice presences found during the study. The cloglog link function was used to account for there being many more absences (0) than presences (1) (Thomas, 2015). The site and check number were entered into models as random effects to account for pseudo replication. To reduce the number of variables, first mixed models were built and tested separately for all variables, those with $P > 0.5$ were removed from further analysis (Ramakers et al. 2014). The prediction from the SDM for the tunnel location was entered into all individual models as an explanatory variable to help them converge.

Dormouse presence/absence ~ variable + prediction from SDM + (1|Site) + (1|Check)

All variables that were significant on their own were entered into a mixed model together and the dredge function in R package MuMIn used to select for the best model based on AIC (Bartoń 2023).

Line level analysis was conducted using a GLM with a quasi-binomial structure and the proportion of tunnels with dormice detected on a line across all tunnel checks was entered as the response variable. Variables were tested separately and those with P>0.5 were removed from further analysis. The average prediction from the SDM along the line was entered into all individual models as an explanatory variable to help them converge.

Proportion of dormouse along line ~ variable + prediction from SDM

All variables that were significant on their own were entered into a GLM with a quasi-binomial structure and the Dredge function used to select for the best model based on AIC (Bartoń 2023).

The predictive power of the regional and national model were tested by calculating the Area Under the Curve (AUC), True Skill Statistic (TSS), and the Kappa score with the tunnel survey results (Allouche et al. 2006; Elith and Graham 2009). The sensitivity (true positives) and specificity (true negatives) were also calculated for each of the models.

## ***Results***

### *SDM variables*

The regional SDM predicted that dormice were more likely to be found in areas with a high percentage of conifer cover, a high percentage of broadleaf cover, and areas with less change in conifer cover (Figure 4.2 & 4.3). Dormice were predicted to be in areas with higher minimum winter temperatures and greater winter temperature ranges (Table 4.2). Dormice were predicted to be less likely in areas with higher summer rainfall. There was an interacting relationship with north south aspect and maximum summer temperature; dormice were predicted to be found in areas with lower summer temperatures on south facing slopes and with higher summer temperatures on north facing slopes. This suggests that there is an optimal summer temperature for dormice which is consistent with other work that dormice are more abundant on warmer, sunnier, and dryer sites (Goodwin et al. 2018a).

The national model had different explanatory climatic and habitat preferences for hazel dormice (Figure 4.2 & Table 4.2). Variables included in the national model were; broadleaf cover, conifer cover, felled cover, autumn rainfall, max autumn temperature, minimum winter temperature (van der Waal et al. 2021). See supplementary information for the relationships between these variables and the suitability for dormice (Appendix 3).

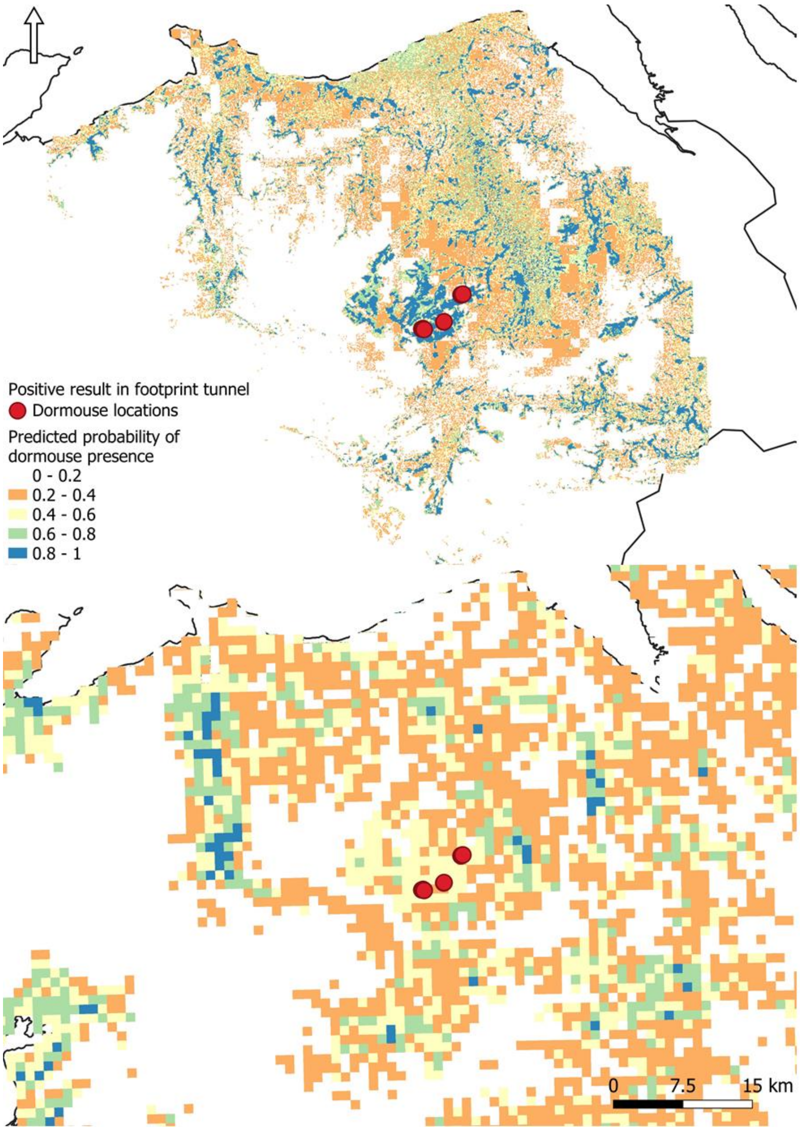


**Figure 4. 2**. R*esults of the regional at 100m resolution and national dormouse species distribution model (SDM) at 1km resolution. The top map illustrates the predicted dormouse distribution in North Wales as predicted by the regional SDM. The regional SDM was built from existing dormouse records, in Denbighshire and Conwy, obtained from North Wales Environmental Information Service (Cofnod). The bottom map shows the predicted dormouse distribution in North Wales as predicted by the national SDM. Results of the national SDM were obtained from Early (unpublished) this model covered the whole of the UK. A higher predicted probability of dormouse presence denote more suitable areas for dormice. Red dots denote positive dormouse records from independent field validation.*

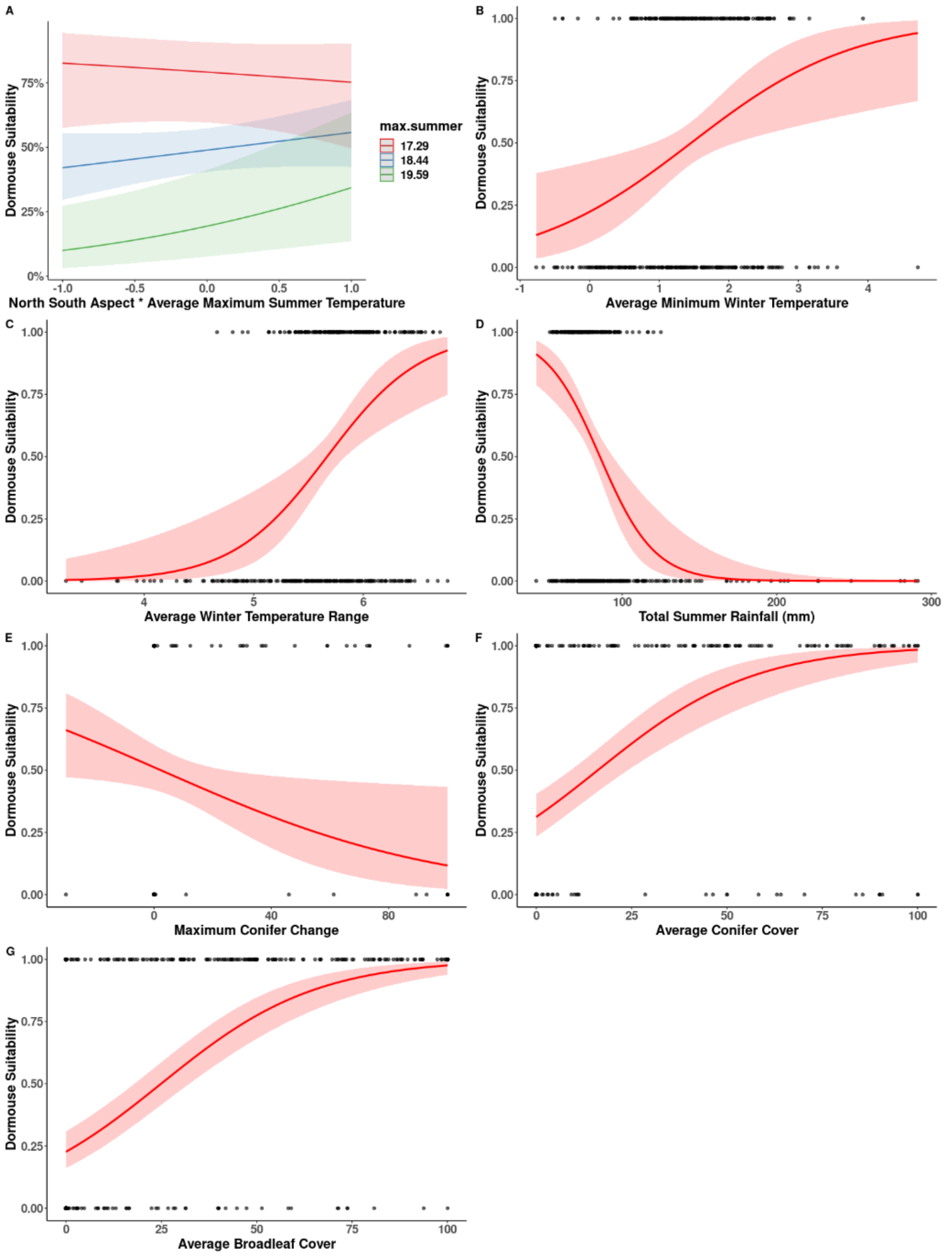


**Figure 4. 3**. *Climatic and habitat variables that were significant in the regional dormouse species distribution model (SDM). Plots show the relationship between the explanatory variable and dormouse habitat suitability. A) Interacting relationship of NS Aspect and average maximum summer temperature- the blue line shows the relationship at the mean average maximum summer temperature, the red line less one standard deviation, and the greed line plus one standard deviation. B) average minimum winter temperature. C) average winter temperature range. D) total summer rainfall. E) maximum average conifer change. F) average conifer cover. G) average broadleaf cover.*

| **Group 1** | **Climate Variables** | **Spearman correlation** | **Variable to be entered into the model and AUC** |
|---|---|---|---|
| 1 | Range winter + max spring | 0.8 | Max Spring 0.72 |
|  | Range winter + max summer | 0.75 |  |
| 2 | Max spring + max autumn | 0.95 | Max Spring 0.72 |
|  | Max spring + max summer | 0.94 |  |
|  | Max summer + max autumn | 0.93 |  |
| 3 | Rain spring + rain autumn | 0.9 | Rain summer 0.67 |
|  | Rain summer + rain autumn | 0.87 |  |
|  | Rain spring + rain summer | 0.81 |  |
| 4 | Max summer + rainfall summer | -0.71 | Max summer 0.70 |

**Table 4. 1**. *Climatic variables considered for the regional dormouse species distribution model (SDM). Spearman correlation tests were conducted and climatic variables that were highly correlated were tested independently in the model. Where two variables were highly correlated the one with the greater explanatory power based on AUC was chosen. The table summarises which climatic variables were correlated and which one was then selected. The resulting climatic variables were then used to build a regional SDM for habitat suitability for dormice in North Wales. 'Rain' denotes total rainfall, 'max', 'min', and 'range' all relate to temperature.*

| Regional SDM | Relationship | National SDM | Relationship |
|---|---|---|---|
| Percentage Conifer Cover | Positive | Conifer Cover | Hump-shaped |
| Percentage of Broadleaf Cover | Positive | Broadleaf Cover | Hump-shaped |
| Change in Conifer Cover | Negative | Felled Cover | Negative |
| Minimum Winter Temperature | Positive | Autumn Rainfall | Hump-shaped |
| Winter Temperature Range | Positive | Maximum Autumn Temperature | Positive |
| Summer Rainfall | Negative | Minimum Winter Temperature | Hump-shaped |
| North South Aspect * Maximum Summer Temperature | Dormice were more likely to be found in areas with lower summer temperatures on south facing slopes and with higher summer temperatures on north facing slopes | Felled coverage * autumn rainfall | Any coverage of felled forests are less suitable for dormice in areas with less autumn rainfall |
|  |  | Coniferous forest * autumn rainfall | Any coverage of coniferous forest are less suitable for dormice in areas with less autumn rainfall |
|  |  | Broadleaved forest * minimum winter temperature | Intermediate coverages of broadleaved forests are less suitable for dormice in areas with warmer winters |
|  |  | Broadleaved forest * autumn rainfall | Intermediate coverages of broadleaved forests are less suitable for dormice in areas with less autumn rainfall |

**Table 4. 2**. *Significant variables included in the final regional and national species distribution model (SDM). The table details which explanatory variables were entered into each model and if an interaction term was included, denoted with an asterisk. The relationship between each explanatory variable and the habitat suitability for dormice is also detailed.*

### *SDM performance before independent data collection*

When using the 10% testing data the regional model performed well with an AUC of 0.86 and TSS of 0.57; this shows good predictive power. When a threshold of 0.5 is set the model had sensitivity of 0.74 and specificity of 0.83, false negatives were spot checked and included observations of dormice in hedgerows which fail to be captured by the model with the habitat variables available.

The national SDM had an AUC of 0.83, tested on randomly-selected, semi-independent validation data which consisted of 30% of the presence/pseudo-absence locations, retained as training data, from across England and Wales (van der Waal et al. 2021).

### *Independent data collection*

2,100 tunnel checks were conducted (525 tunnels each checked 4 times). Data was collected from 7 sites with between 2 and 6 lines of 25 tunnels in each. I had low detection rates of dormice with 27 incidences of presence, all from one site, from the 2,100 checks. All dormice footprints were exclusively found in Clocaenog forest across three different lines. These lines had high, medium, and low suitability for dormice with regards to the regional SDM. I noted the presence of other mammal footprints on 1,150 of the tunnel checks indicating that the methodology is adequate for detecting small mammals, at human height.

### *Dormice habitat preferences*

Significant variables from the tunnel level analysis (Table 4.3), were incorporated into a larger model and the top performing model was chosen. The best performing model shows that dormice are more likely to be found in tunnels where bramble, service and, fir are within 1m of the tunnel (Table 4.4, Figure 4.4). Dormice are less likely to be found in tunnels that have Sitka spruce within 1m of the tunnel location and in areas that the regional SDM predicted to be highly suitable for dormice (Table 4.4, Figure 4.4). This model is run using a limited number of observations, and therefore the relationships with species may potentially be artefacts, coincidences that these particular species were present at the sites where dormouse presence was detected.

At the line level, two variables—distance to the nearest known dormouse population and the proportion of service within 1m of tunnels on the line—demonstrated a significant relationship with dormouse presence. When tested the top performing model was the null model (Table 4.5).

| **Variable** | **Estimate** | **P value** |
|---|---|---|
| Bramble *(Rubus fruticosus)* | 1.20 | 0.024 |
| Sitka *(Picea sitchensis)* | -1.42 | 0.0009 |
| Service *(Sorbus domestica)* | 1.67 | 0.025 |
| Rhododendron *(Ericaceae)* | -3482.74 | <0.0001 |
| Fir *(Abies)* | 4.83 | 0.0022 |
| Ash *(Fraxinus excelsior)* | -779.34 | <0.0001 |
| Larch *(Larix decidua)* | -1333.87 | <0.0001 |
| Gorse *(Ulex)* | 1.63 | 0.046 |
| Alder *(Alnus glutinosa)* | -1495.34 | 0.012 |
| Hazel *(Corylus avellana)* | -1522.03 | <0.0001 |

**Table 4. 3**. *Tunnel level analysis investigating the habitat preferences for hazel dormice at this spatial scale. Using habitat variables collected when conducting a footprint tunnel survey to collect independent data to test species distribution model (SDM) performance. The table denotes significant variables when tested separately, containing the effect size (estimate) of the variable and the p value. Mixed models were built and tested separately for all variables, those with P >0.5 were removed from further analysis. Each variable corresponds to a different plant species which was either present (1) or absent (0) within 1m of a dormouse footprint tunnel.*

| Intercept | Alder | Ash | Bramble | Fir | Gorse | Hazel | Larch | Prediction | Rhododendron | Service | Sitka | df | logLik | AICc | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| -15.89 | NA | NA | + | + | NA | NA | NA | -2.33 | NA | + | + | 8 | -73.66 | 163.4 | 0 | 0.095 |
| -22.61 | NA | NA | + | + | NA | + | NA | -2.34 | NA | + | + | 9 | -73.48 | 165.1 | 1.67 | 0.041 |
| -15.86 | NA | NA | + | + | NA | NA | + | -2.30 | NA | + | + | 9 | -73.52 | 165.1 | 1.74 | 0.040 |
| -18.28 | NA | NA | + | + | + | NA | NA | -2.29 | NA | + | + | 9 | -73.59 | 165.3 | 1.88 | 0.037 |

**Table 4. 4**. *Results of model selection for dormouse presence and any relationship with tunnel level variables. Habitat preferences for hazel dormice, using habitat variables collected when conducting a footprint tunnel survey to collect independent data to test species distribution model (SDM) performance. All significant variables were run with the Dredge function in R to determine a top model set. The top model set is presented and includes all models within 2 AIC of top performing model. Results show the intercept of each model, coefficient of each variable within the model, degrees of freedom (df), logLik, AIC score, Delta, and Weight.*

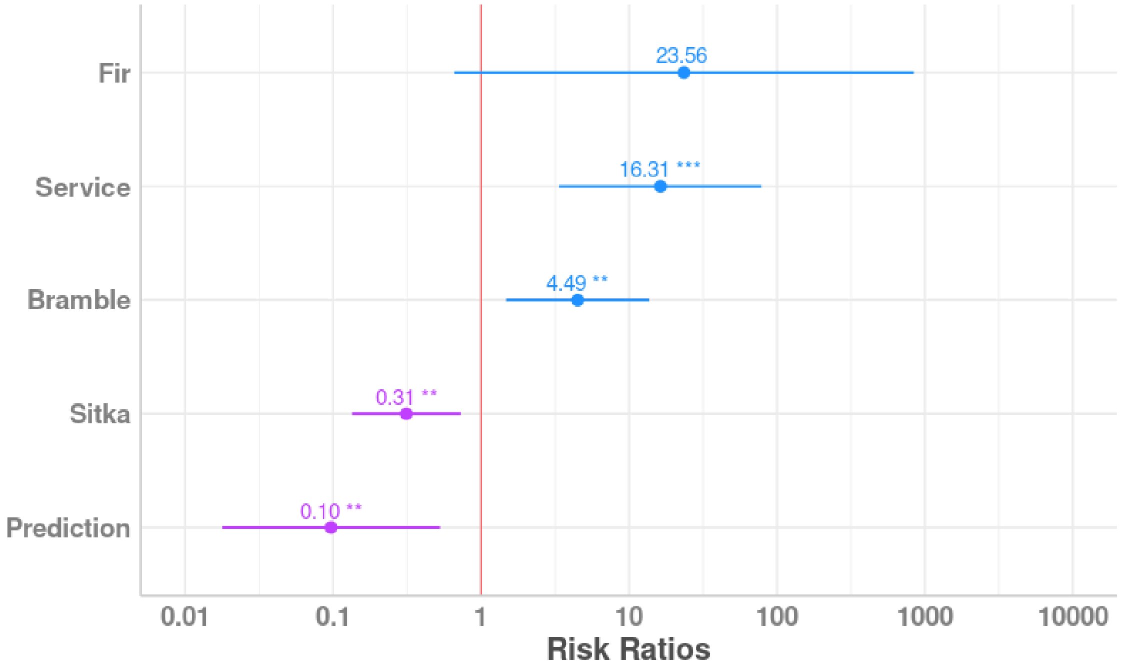


**Figure 4. 4**. *Results of the top performing model from GLMM testing for a relationship between dormouse presence and tree species found within 1 metre of a dormouse footprint tunnel (used to detect dormice). Prediction of dormouse suitability based on the results from the regional dormouse species distribution model (SDM) was also included in the model as an explanatory variable. Blue points denote a positive effect on the presence of dormice, purple points denote a negative effect on dormouse presence, and confidence intervals for each variable are included.*

| Intercept | Distance to dormouse | Service | df | logLik | AICc | delta | weight |
|---|---|---|---|---|---|---|---|
| -4.3409 | NA | NA | 2 | 0.7282 | 3.2102 | 0 | 0.6428 |
| -1.8479 | -0.00292 | NA | 3 | 0.7208 | 5.9702 | 2.7600 | 0.1617 |
| -5.1100 | NA | 42.1922 | 3 | 0.7171 | 5.9775 | 2.7674 | 0.1611 |
| -2.7876 | -0.00173 | 16.2126 | 4 | 0.7158 | 9.0685 | 5.8589 | 0.0344 |

**Table 4. 5**. *Results of model selection for dormouse presence and any relationship with line level variables. Habitat preferences for hazel dormice, using habitat variables collected when conducting a footprint tunnel survey to collect independent data to test species distribution model (SDM) performance. Significant explanatory variables included; distance from nearest dormouse population and proportion of service tree found along the line. The top model set is presented and includes all models within 2 AIC of top performing model. Results show the intercept of each model, coefficient of each variable within the model, degrees of freedom (df), logLik, AIC score, Delta, and Weight.*

### *SDM performance with independent data set*

The lack of dormice records during surveying coupled with their presence in areas of varying suitability, indicates that the regional model did not accurately predict dormouse distribution. Testing the regional model with the independent data from the tunnel results produced an AUC score of 0.46, a Kappa score of -0.005, and a TSS of -0.14. These results signify poor predictive accuracy, as an AUC score of 0.5 would represent random chance. The national model exhibited slightly better performance with an AUC of 0.61. However, a low Kappa score of -0.003 and TSS of -0.027 still suggest that the model's ability to distinguish between dormouse presence and absence is quite poor. The regional model contained false positives (1437 of 2073 negative checks*);* dormice were predicted to be in climatically favourable conifer plantations across the study area (Figure 4.2). Conversely the national model contained false negatives (22 of 27 positive checks*)*, as in this model conifer plantation was largely predicted to be poor habitat for dormice across the whole region (Figure 4.2).

## ***Discussion***

Independent data collection using dormouse footprint tunnels revealed that dormice were present in previously un-surveyed areas of Clocaenog forest. I did not find evidence of dormice in other conifer habitats across the study region. Clocaenog forest seems to represent an anomaly within the landscape, and it remains unclear why dormice populations are able to subsist in this conifer plantation and were not detected in others in the region. At the periphery of their range, dormice populations may exhibit different behaviours than their counterparts in the core, and consequently habitat would not be expected to be the biggest predictor of dormouse presence. Using current knowledge and data, the distribution of dormice in non-typical habitats at the edge of their range cannot be accurately predicted by SDMs in North Wales.

My footprint tunnel survey indicated a relationship between dormouse presence and the proximity of bramble, service, and fir trees to the tunnels. High fruiting species of trees and shrubs are an important habitat feature for hazel dormice (Wuttke et al. 2012; Ramakers et al. 2014; Sozio et al. 2016; Mortensen et al. 2022). Dormice were less likely to be found in tunnels that were in close proximity to Sitka spruce, this is likely due to the dense planting and lack of understory associated with this species. When investigating habitat characteristics of the whole line my null model performed best. These results suggest that habitat quality might not be the best predictor of dormouse presence. The field sampling produced a relatively small number of positive records (n=27), therefore conclusions based on the site characteristics of presences should be treated with caution.

When testing the regional SDM, instances occurred where dormouse absences were predicted inaccurately, with presences located within a line of 'low' suitability (15 of 27 positive records across four 100m grid squares). This indicates that the environmental conditions that enable dormice to subsist at Clocaenog forest but not in other similar habitats in the area were not correctly identified by the model. Clocaenog has a high altitude (501m at the highest point) and dormice have been found at high altitude conifer sites in Europe (511m mean altitude of sites, n=30) , but seem unable to colonise conifer sites at lower altitudes, the reasons behind this remain unknown (Juškaitis 2008b; Juškaitis and Augutė 2008; Wuttke et al. 2012). While the regional SDM may accurately predict habitat quality, this might be a poor predictor of dormouse occupancy at the range margin. Possible explanations include interspecific interactions, limited colonisation ability or local extinctions (Peterson 2001). Similar findings have arisen in the context of predicting the distribution of the Cape Sable seaside sparrow (*Ammodramus maritimus mirabilis*) using SDMs, where birds are absent in some patches of predicted suitable habitat (Jenkins et al. 2003). A notable limitation in the application of SDMs is their inability to account for biotic factors or species population dynamics especially at the range edge, a constraint that may influence model performance in my study (Anderson et al. 2002; Araújo and Pearson 2005).

My study does not account for metapopulation dynamics, a key aspect at the range edge due to factors such as small population sizes, different species compositions, and dispersal capabilities, which all define the continued persistence of a species (Holt and Keitt 2000; Anderson et al. 2009). Metapopulations, defined as collections of local populations capable of enduring even if individual components (local populations) face extinction risks (Hanski and Thomas 1994). The broadleaf habitat surrounding Clocaenog is known to have a high abundance of dormice (Goodwin et al. 2017). Clocaenog maintains continuous woodland connections to these sites, suggesting potential immigration sources from broadleaf habitats, possibly indicative of source-sink dynamics (Amarasekare and Nisbet 2001). Dormice are known to subsist in very small habitat patches (Büchner 2008) and site level extinction events are driven by connectivity and not patch size (Iannarilli et al. 2017). Future research should focus on what factors determine dormouse presence beyond abiotic factors, such as; connectivity, dispersal capabilities, species interactions and other biotic factors (Pearson and Dawson 2003; Zurell et al. 2009; Sinclair et al. 2010). My study highlights the importance of collecting independent test data when building SDMs especially on the edge of species range where stochastic processes involving biotic factors are more likely to have a greater influence than on core populations (Angert et al. 2020). My results indicate that SDMs are of limited use in guiding surveys for dormice at range edges where there is limited occurrence data for training the model and their use should be treated with caution.

The regional SDM could be poorly constrained at range margins because I haven't included variables relevant to determine habitat quality within conifer sites. A limitation of SDMs is the resolution of environmental variables that are available to build models (Gogol-Prokurat 2011; Sillero and Barbosa 2021). Coarse explanatory variables are used to predict species distribution at a much finer scale leading to inaccuracies in model predictions (Gogol-Prokurat 2011; Sillero and Barbosa 2021; Lee-Yaw et al. 2022). For both models if environmental variables at a finer spatial scale were available greater intricacies in dormice habitat might be incorporated, for example the presence of forest edges and glades. Due to the available data both the regional and national SDM failed to incorporate habitats outside of woodland, such as hedges, that are known to be important for dormice (Bright et al. 2006; Juškaitis 2008b). If such data was available then measures of the landscape connectivity of habitat patches could be incorporated into the models.

Due to time constraints my independent survey could only be undertaken across one survey season, although I did do repeated tunnel checks. It is difficult to accurately verify whether or not absences during surveys were true absences and repeating the tunnel survey across multiple seasons would allow more confidence in my results (Lee-Yaw et al. 2022). To my knowledge this is the first survey that has used dormouse footprint tunnels in conifer plantation, there is the possibility that this survey method is not reliable at conifer sites, at human height. Forestry staff in the local area have observed the occurrence of dormice at elevated levels within conifer plantations throughout the region, often detected during canopy-related work (Natural Resources Wales staff, *personal communication*). Alternative developing survey methods for dormice such as eDNA (Priestley et al. 2021) and bioacoustics (Ancillotto et al. 2014; MacIsaac

2022) should be considered and tested in conifer plantations, to account for dormice presence in the canopy, to verify absence in this habitat.

The regional and the national SDM in this study both failed to accurately predict where dormice are found on the edge of their distributional range in North Wales, where they are sparsely distributed (Bright 1995). This is reflected in the dormice presence records used to build the regional SDM. This has resulted in the regional model over fitting the data and incorrectly predicting suitable dormouse habitat. The regional SDM could be poorly constrained because I don't have enough observations from marginal habitats, I therefore don't have the observations to establish how the species responds to the relevant variables. The GLM used for this study is particularly sensitive to outliers due to the patchy nature and relatively low sample size of the dormice observation data obtained for this study (Wisz et al. 2008; Rathore and Sharma 2023). The national model built with a large sample size, has not incorporated stochastic processes at the edge of the range and conifer habitat is not predicted as suitable habitat.

SDMs performance is also susceptible to sampling bias, as species occurrence data are more likely to be recorded in accessible areas, such as along roads and rivers, or close to research camps (Reddy and Dávalos 2003; Boria et al. 2014). Dormice, being easier to detect along forest edges and rides than further into taller forests with a less developed understory, are also affected by this bias (Dietz et al. 2018). Sampling bias will affect the performance of the regional and national SDMs and should be considered when evaluating the usefulness of this technique. This highlights the importance of the original dataset used to build models. Different motivations for searching for species, can led to discoveries in previously unexplored territories (Lissovsky et al. 2021). The detection of dormice at Clocaenog, facilitated by the construction of a wind turbine farm, exemplifies how populations may remain undetected without targeted efforts. However, this heightened monitoring, especially during wind farm construction, has introduced sampling bias at Clocaenog, when compared with other populations, across all habitat types in the area. This has affected the regional model performance with all conifer plantations with optimal climate, predicted to be suitable for dormice.

My study has determined that current dormouse data from the area is insufficient for building an effective SDM. My results highlight the limitations of SDMs, urging a cautious approach in their application, particularly at the range edge.

## Chapter 5

# Dietary variation in hazel dormice (*Muscardinus avellanarius)* among woodland habitats

# Chapter 5: Dietary variation in hazel dormice (*Muscardinus avellanarius)* among woodland habitats

## *Abstract*

Specialist species often face a greater risk of decline and extinction than generalists in the face of habitat degradation and environmental change. Hazel dormice (*Muscardinus avellanarius*) in Great Britain have experienced significant population declines, despite extensive conservation efforts. These efforts focus on their perceived reliance on broadleaf woodlands with specific plant species, in part because of perceptions of their specialised diets. This study aims to investigate dietary variation in hazel dormice by comparing their diets in broadleaf and conifer woodland habitats, using stable isotope analysis (SIA). Dormice were found to utilise a variety of food sources, including invertebrates, tree seeds and berries, with their dietary composition varying between sites and seasons. My analysis shows that dormice in both conifer and broadleaf habitats exploited a range of 'non-typical' food sources, depending on local availability, and challenging notions that they are solely dependent on specific plant species. These findings indicate that dormice can adapt to local conditions and exploit available resources, contributing to their persistence in a range of habitats. The study highlights the importance of broadening the focus of dormouse management and conservation efforts to include a wider range of habitats, rather than attributing conservation value solely, or primarily, on the presence of specific plant species.

## *Introduction*

Evidence that specialised species are declining more rapidly than generalist species is prevalent across diverse taxa, spanning butterflies (Thomas 2016), mammals (Fisher et al. 2003), birds (Norris and Harper 2004) and coral reefs (Munday 2004). Specialist species, with their specific habitat requirements, face heightened vulnerability amid habitat loss and degradation, limiting the availability of their unique niches (Owens and Bennett 2000; Marvier et al. 2004; Cousins and Vanhoenacker 2011; Hilpold et al. 2018; Watts et al. 2020). In the face of anthropogenic environmental change, generalist species appear to have a distinct advantage, by exploiting a broader range of environments, ultimately leading to the replacement of specialists by generalists and fostering a homogenised ecosystem of functionally similar species and communities (Marvier et al. 2004; Rooney et al. 2004; Clavel et al. 2011; Denelle et al. 2020). While the provision of protected areas and habitat creation is often seen as a solution for conservation (Godet and Devictor 2018), their effectiveness is reliant on accounting for the specific needs of specialist species to prevent inadvertently favouring generalists and promoting biotic homogenisation (Filippi-Codaccioni et al. 2010).

The conservation of ostensibly specialist species, like hazel dormice *Muscardinus avellanarius* (referred to henceforth simply as ‘dormice’), often requires an in-depth knowledge of their ecology so specific aspects of their ecological niche that are essential for their survival can be incorporated into management or restoration efforts (Adams-Hosking et al. 2015; Avotins et al. 2022; Phukuntsi et al. 2022). Dormice are undergoing chronic declines in Great Britain and populations have fallen by 78% between 1994-2020, despite considerable conservation intervention and investment (Goodwin et al. 2017; Scopes et al. 2023). Dormice are considered highly specialised in Britain, with an ideal habitat of broadleaf woodlands and coppices with a dense and diverse understorey (Bright and Morris 1990; Bright 1993; Bright and Morris 1996; Juškaitis 2008b; Juškaitis and Augutė 2008; Hutterer et al. 2021). Dormice are thought to favour these habitats as they are specialist feeders unable to digest cellulose so require nutritional food sources such as flowers, fruit and insects

(Richards et al. 1984; Bright and Morris 1993; Bright and Morris 1996). In particular the presence of honeysuckle (*Lonicera periclymenum*), bramble (*Rubus fruticosus*), and hazel (*Corylus avellana*) are seen as indicator species for suitable dormouse habitat (Bright and Morris 1990; Bright and Morris 1990; Bright and Morris 1992). Habitat loss and the decline in traditional woodland management techniques, such as coppicing, are associated with the decline of dormice (Bright and Morris 1996; Bright et al. 2006).

Conservation approaches, guided by perceptions of dormice as specialists, have focused on traditional habitats, relying on indicators like gnawed hazel nuts and nest boxes in broadleaf woodlands (Bright et al. 1996a; Jermyn et al. 2001; Bright et al. 2006; PTES 2022). Such sites are also the focus of a re-introduction programme that aims to restore the species' range (Bright and Morris, 1994; Mitchell-Jones and White, 2009; White, 2019, 2012) and are selected on the basis of broadleaf woodland habitat; management that promotes a diverse understory, and woodland area greater than 20ha (Bright and Morris 1994; Cartledge et al. 2021). Despite such measures, current conservation practice is failing to halt the decline of the species. Dormice are recently being found more often in habitats other than those perceived to be ideal, including: scrub (Chanin and Woods, 2003; Scopes, *unpublished*) and conifer plantation (Trout et al. 2012; Trout et al. 2018). European research challenges the perception of dormice as habitat specialists (Fedyń et al. 2021), and suggests they are able to adapt to various environments, including high altitude conifer plantations (Wuttke et al. 2012), tall forest stands (Fedyń et al. 2021), roadside habitats (Kelm et al. 2015), young spruce stands, and mixed forests (Juškaitis 2008b). When investigating dormouse habitats in continental Europe, the presence of plant species offering sustenance, such as fruiting shrubs, emerges as a key determinant, rather than the presence of any one particular species, such as hazel (Wuttke et al. 2012; Ramakers et al. 2014; Sozio et al. 2016; Mortensen et al. 2022). Dormice are able to subsist in continental landscapes in habitat patches much smaller than 20ha, which might suggest that, given an ample food supply, the size of the habitat patch becomes a less constraining factor for their persistence (Büchner 2008; Iannarilli et al. 2017).

My investigation seeks to determine how dormice are able to subsist in marginal habitat. Through the application of stable isotope analysis (SIA), we compared the dietary patterns of dormice in what is perceived as 'optimal' (broadleaf) habitat with those in conifer plantations. My work builds on that of Goodwin et al (2020) who showed, contrary to prior assumptions, dormice were highly opportunistic feeders, demonstrating a reliance on invertebrates (Chanin et al. 2015). Additionally, dormice will predate on bird eggs early in the season when necessary (Sarà and Sarà 2007; Adamík and Král 2008). Examining dormouse diets in German spruce and beech forests, which are characterised by a lack of understorey, revealed that inflorescences, seeds, and invertebrates comprised the primary food sources, with a notable absence of soft mast in their diets (Büchner et al. 2018). Through the analysis of faecal samples, dormice's versatile foraging habits have been revealed, encompassing a range of invertebrates, including spiders (*Araneae*), harvesters (*Opiliones*), and centipedes (*Chilopoda*) (Büchner et al. 2018). Additionally, dormice can forage silver birch (*Betula pendula*) seeds in the absence of other food sources, a dietary element previously overlooked (Juškaitis et al. 2016).

Stable isotope analysis is a tool used to investigate animal dietary variation and foraging ecology (Inger et al. 2006; Inger and Bearhop 2008; Ben-David and Flaherty 2012; Fink et al. 2012; Layman and Allgeier 2012), among other ecological studies. Fundamentally, SIA is based on assessment of variation in ratios of heavy to light stable isotopes in a consumer’s tissues, which reflect those in their food sources in a predictable way (Kelly 2000; Crawford et al. 2008; Inger and Bearhop 2008). SIA as a method for dietary analysis complements other methods, such as faecal or gut analysis. While these methods provide a specific snap shot of an individual’s diet, these approaches can lead to an over representation of food sources that are more readily identified and less easily digested (Araújo et al. 2007; Crawford et al. 2008; Phillips et al. 2014). SIA can provide a broader picture of feeding habits as consumer tissues integrate their source proteins over an extended period, that varies among tissue types, and hence reflect different timeframes of food intake (Araújo et al. 2007). For example; whisker and claw samples reflect a much longer time period than blood plasma (Bearhop et al. 2002; Bearhop et al. 2004). SIA has allowed the quantification of trophic niches across animal populations and the investigation of dietary composition and variation (Fink et al. 2012; Phillips 2012).

To conduct SIA of hazel dormice the Carbon and Nitrogen ($\delta^{13}C$ and $\delta^{15}N$) ratios in fur was analysed. Hair is metabolically inert and therefore provides dietary information from when it is grown; during moult and regrowth of the pelage (Goodwin et al. 2020). I conducted a dietary assessment of the dormouse population, across conifer and broadleaf habitats, estimating the proportional contribution of each putative food group. To investigate whether dormice are surviving in small numbers on the broadleaf edge of conifer plantations, or whether they have the capacity to forage in the conifer habitat itself.

My investigation extended to examining the effect of site on the trophic characteristics of populations. I predicted the dormice found in conifer plantations would be able to exploit a range of ‘non-typical’ food sources. Notably, honeysuckle and hazel, deemed necessary for dormouse sustenance (Bright and Morris 1991; Bright and Morris 1992; Bright and Morris 1993; Bright and Morris 1996; Bright et al. 2006) were completely absent from one conifer site. Furthermore I hypothesised that dormice in broadleaf habitats would have access to a wider range of plant foods and consequently populations would have a larger isotopic niche area, generally indicative of a more varied diet. Through this assessment of diets of dormice in distinct habitats, I aim to enhance understanding of how dormice subsist in non-typical habitats.

## ***Methods***

All work was undertaken with ethical approval from the CLES Cornwall Ethics Committee at the University of Exeter (Application ID 517107), and under dormouse licence (Natural England 2022-10734-CL10B-DOR and Natural Resource Wales S091137/2).

### *Sample collection and processing*

I sampled dormice at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer - Fingle; Figure 5.1). Dormice were captured during nest box surveys in late spring (June), spring sampling, and autumn (September and October), autumn sampling, of 2022. This was to determine if there were variations in dormice diets throughout their active season.

To obtain samples for SIA, hair samples were cut from the upper right hind leg of animals that were independent from their mother (>10g). One fur sample was taken from each dormouse. Late spring and autumn sampling periods were chosen in line with Goodwin et al., (2020), as dormice are thought to have a moulting period in spring and late summer (Juškaitis and Büchner 2013). Samples obtained in June are expected to have grown during the spring season, thus representing the spring diet. Conversely, hair samples taken in the autumn will consist of hair that has grown in the summer, reflecting the summer diet.

In order to ascertain the local availability of potential plant and invertebrate foods, surveys were conducted within a 50 m radius of a designated ‘dormouse area’ at each site. This area was defined as the area along the length of pre-existing dormouse next boxes, approximating feasible nightly distances travelled by dormice from their nest sites (Bright and Morris 1992; Goodwin et al. 2018b). Four, three, two and one ‘dormouse areas’ were sampled at Clocaenog, Bontuchel, Fingle, and Okehampton respectively based on the number of nest boxes at each site. All flowering and fruiting trees, shrubs, and terrestrial plant species above 0.5 m within a ‘dormouse area’ were recorded and samples collected. Specific parts of plant species that had been identified as being potentially important in dormouse diet in the literature were also collected (Appendix 4; Bright and Morris, 1993; Juškaitis et al., 2016; Juškaitis and Baltrūnaitė, 2013; Richards et al., 1984; Sarà and Sarà, 2007). In the two conifer sites, all species of conifer and broadleaf trees were sampled to investigate whether dormice could utilise conifer vegetation (Appendix 4).

Invertebrate samples were obtained by beating trees along the ‘dormouse area’ until a large enough sample for analysis of invertebrates in the area had been collected (n>40). I could only collect samples in the day time, and samples could only be collected to head height. In the two conifer sites, broadleaf and conifer invertebrates were collected separately by beating differing tree species, this was to test whether invertebrates found in the two separate habitat types were isotopically distinguishable and therefore making potentially distinctive contributions to dormouse diets. In broadleaf sites, just one group of invertebrates were collected. Samples were frozen at -20$^{o}$C before being identified to Order and counted (Appendix 4).

Other non-plant and invertebrate food sources such as fungi and bird eggs were not collected due to practical and ethical reasons. Some of the fungi at sites available to dormice was above human height, and therefore could not be sampled.

**Figure 5. 1**. *Sites sampled for dormouse diet analysis; investigating the variation in dormouse diets across different habitat types. Sites at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle). Green sites denote broadleaf habitat and orange sites are conifer plantations.*

### *Stable isotope analysis*

Plant and invertebrate samples were processed by freeze-drying for 24 hours and 72 hours respectively to ensure all water content had been removed. Samples were then homogenised with a pestle and mortar. Dormouse fur was rinsed in distilled water to remove surface contaminants and left to air-dry. 1.5 mg ± 10% (plants) and 0.8 mg ± (invertebrates) of dried and homogenised sample was weighed into tin capsules. 0.8 mg ± of dormouse hair sample was weighed directly into tin capsules. A sub-sample of plant and invertebrates that were collected were analysed, sample sizes were based on between-sample variation previously established (Goodwin et al. 2020), and only samples distinct in isotopic space were analysed.

Stable isotope analysis was conducted using a Sercon INTEGRA2 elemental analyser-isotope ratio mass spectrometer at the University of Exeter. Stable isotope ratios were expressed as delta (δ) values in ‰, using international standards for each element Vienna Pee Dee Belemnite (VPBD) ($\delta^{13}C$) and atmospheric N2 ($\delta^{15}N$). A laboratory QC material (bovine liver standard for animal samples and wheat flour for plant samples) run within sample batches. Standards USGS40 and USGS41 (Glutamic acid) were used to scale-correct samples for both elements. Based on these standards, average precision was 0.05‰ ± 0.008 and 0.09‰ ± 0.02 (1 standard deviation ± standard error) for $\delta^{13}C$ and $\delta^{15}N$ respectively.

### *Statistical analysis*

R version 4.3.0 (R Core Team 2022) was used for all analyses.

#### Stable isotope dietary composition

Bayesian stable isotope mixing models (BSIMMs) were used to estimate diet composition on the four sites. Before running BSIMMs I plotted the data to ensure that consumer isotopic values at each site fell within the diet sources (Figure 5.2

& 5.3), and that all sites that were included in the analysis for spring and autumn sampling were within the ‘mixing space.’ This is a requirement of the geometric arrangement of the data to allow models to find diet solutions for diet composition of consumer values (Phillips et al. 2014).

For all sites, stable isotope analysis was conducted for potential food sources to reliably quantify variation among sources (Phillips 2012). Variation in food sources at the different sites meant that food groups differed across sites (Appendix 5). Food groups were created that were both isotopically and biologically meaningful, while capturing variation amongst potential sources (Phillips and Gregg 2001). The R package SIMMR was used to assess the contribution of the different food groups to dormouse diets (Parnell and Govan 2019). SIMMR is an R package designed to solve mixing equations for stable isotopic data within a Bayesian framework (Parnell and Govan 2019). This is achieved through the application of isotopic mixing models, which transform isotopic data into estimations of food source contributions from the various components of an animal’s diet (Phillips 2012).

Trophic Discrimination Factors (TDFs) were used to account for the enrichment of heavy isotopes in the consumer’s (dormouse) hair. TDFs were chosen based on previous studies of dormouse diets and were 3.49 (SD 1.54) for $\delta^{15}N$ and 2.67 (SD 1.91) for $\delta^{13}C$ (Goodwin et al. 2020) and had been derived using the R package SIDER (Healy et al. 2018). TDFs are created using habitat, diet-type, and phylogenetic information of the study species (Healy et al. 2018; Swan et al. 2020).

### Population trophic analysis

I estimated isotopic (trophic) niche areas to establish whether or not dormice have different niche characteristics across habitat types and seasons. Bayesian standard ellipses ($SEA_B$) corrected for a small sample size ($SEA_C$) were calculated using $\delta^{13}C$ and $\delta^{15}N$ data from dormouse fur samples using the R package SIBER (Jackson et al. 2011). This calculates range of ellipses that could explain the data, with a concentration near the most probable solution. The depiction of a mean, median, or modal $SEA_C$ is not possible. Instead I calculated each one of the ellipses' areas, from which I derive summary statistics (Jackson et al. 2011). These summaries allow for comparison of $SEA_C$ across sites and seasons.

### ***Results***

Isotope values from 50 dormice from 4 sites were analysed (16 in spring and 34 in autumn). A total of 222 plant and invertebrate samples were analysed across all sites during both sampling periods, comprising 121 plants and 101 invertebrates (Table 5.1). Notably, samples from Okehampton (Southwest England -broadleaf) in the spring collection were not analysed due to the absence of dormice. Of the 4 sites sampled adequate dormouse samples (n>2) were collected for the sites in North Wales in June, and all sites had sufficient samples for analysis of the autumn samples (Table 5.2).

| **Site** | **Season** | |
|---|---|---|
| | Spring | Autumn |
| Clocaenog | | |
| Plant Samples | 38 | 14 |
| Invertebrate Samples | 16 | 29 |
| Bontuchel | | |
| Plant Samples | 15 | 15 |
| Invertebrate Samples | 5 | 8 |
| Fingle | | |
| Plant Samples | 21 | 11 |
| Invertebrate Samples | 17 | 16 |
| Okehampton | | |
| Plant Samples | 0 | 7 |
| Invertebrate Samples | 0 | 10 |

**Table 5. 1**. *The number of samples analysed using Sercon INTEGRA2 elemental analyser-isotope ratio mass spectrometer. Plant and invertebrate samples were collected at paired broadleaf and conifer woodlands in North Wales (broadleaf - Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle). Samples were collected for use in SIA to establish diets of dormice in different habitat types.*

| **Site** | **Season** | |
|---|---|---|
| | Spring | Autumn |
| Clocaenog | 6 | 10 |
| Bontuchel | 7 | 11 |
| Fingle | 2 | 8 |
| Okehampton | 0 | 4 |

**Table 5. 2**. *The number of dormice sampled at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle). Fur was collected for use in SIA to establish diets of dormice in different habitat types.*

*Stable isotope dietary composition*

Plots of dormice fur samples with sample food sources illustrate the generalist nature of their diet, as dormouse signatures fall within food groups (Figures 5.2 & 5.3). A comparison of spring diets at Clocaenog and Bontuchel underscores the distinct isotopic space of food sources at Bontuchel (Figure 5.2). Invertebrates in conifer and broadleaf habitats at Clocaenog were indistinguishable isotopically during spring so were classed as one food source; ‘inverts’ (Appendix 5, Figure 5.2). Spring sampling at Clocaenog indicates a mixed diet, whereas Bontuchel highlights seeds as a predominant component, constituting 80% (beech *(Fagus sylvatica)* nuts and flowers, birch *(Betula)* seeds, and sycamore *(Acer pseudoplatanus)* seeds, 66-92%) of the diet.

Differences in dormouse diets between Clocaenog and Bontuchel are evident in autumn sampling, with tree seeds 40% (7%, 63%) and conifer invertebrates 39% (4%, 75%) dominating at Clocaenog, while berries 70% predominate at Bontuchel (50%, 88%) (Figure 5.3).

Similarly, Fingle exhibits isotopically indistinguishable invertebrates during autumn sampling, which were therefore consolidated as one food source for analysis, labelled 'inverts' (Appendix 5, Figure 5.3). Invertebrates represent the primary dietary source at the two Southwest England sites during autumn sampling, constituting 82% (69%, 93%) at Fingle and 59% at Okehampton (45%, 79%) (Figure 5.3).

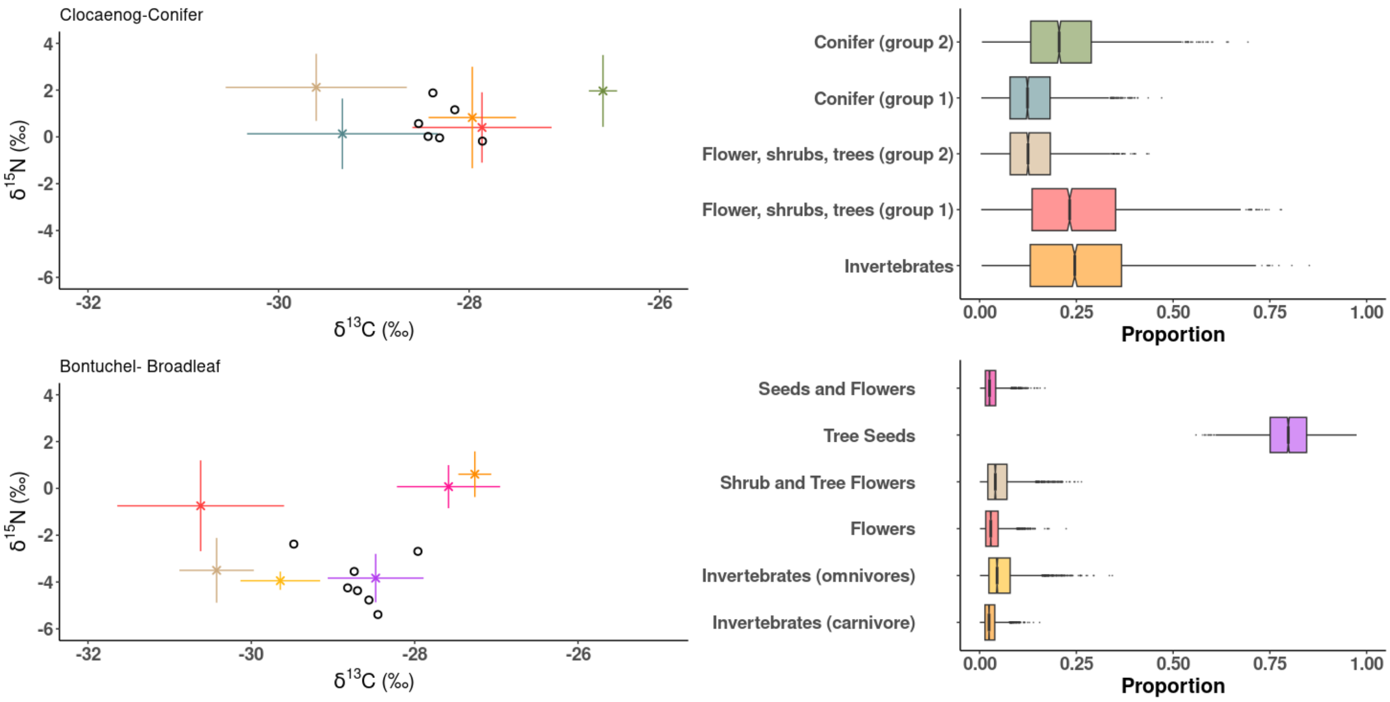


**Figure 5. 2**. *Diet composition of dormice and their potential food groups from spring sampling in North Wales at Clocaenog- conifer and Bontuchel- broadleaf. Dormice are shown as black circles, food groups are shown as mean* $\delta^{13}$*C and* $\delta^{15}$*N ± standard deviation error bars. Trophic discrimination factors have been applied to adjust dormice isotopic positions downwards for both* $\delta^{13}$*C and* $\delta^{15}$*N. Estimates of the proportional contributions of potential food groups to the diets of dormice during spring sampling, calculated using Bayesian mixing models in SIMMR.*

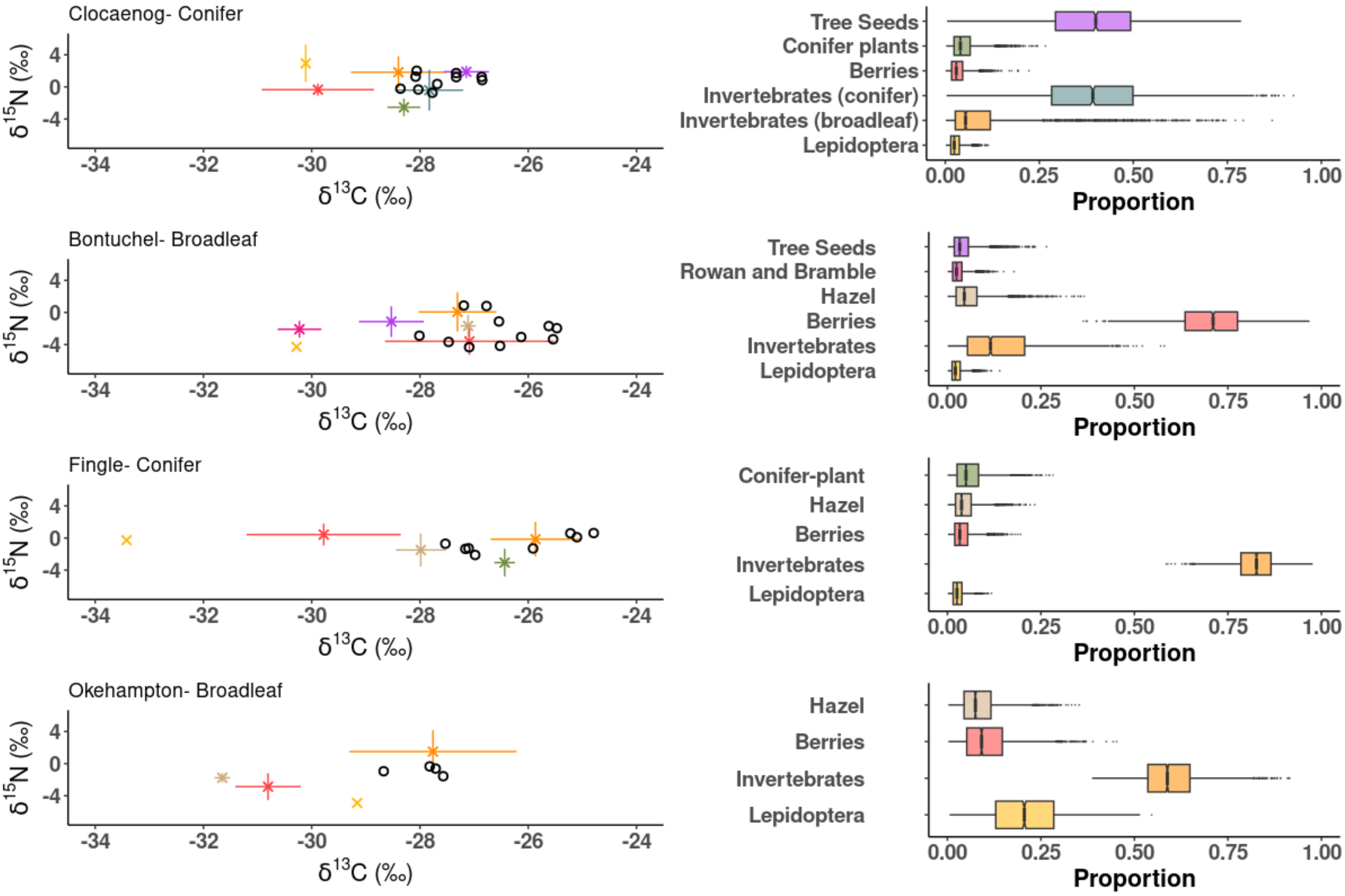


**Figure 5. 3**. *Diet composition of dormice and their potential food groups for autumn sampling in North Wales at Clocaenog- conifer and Bontuchel- broadleaf and Southwest England at Fingle- conifer and Okehampton- broadleaf. Dormice are shown as black circles, food groups are shown as mean $\delta^{13}$C and $\delta^{15}$N ± standard deviation error bars. Trophic discrimination factors have been applied to adjust dormice isotopic positions downwards for both $\delta^{13}$C and $\delta^{15}$N. Estimates of the proportional contributions of potential food groups to the diets of dormice during autumn sampling, calculated using Bayesian mixing models in SIMMR.*

*Population trophic characteristics*

In spring, SEAc were larger in broadleaf habitat compared to conifer plantation in North Wales, 94% of probability distribution comparisons were larger in Bontuchel than Clocaenog (Figure 5.4). The modal SEAc in spring was 0.50 (95% CI: 0.23, 1.39) and 1.35 (95% CI: 0.63, 3.32) for Clocaenog and Bontuchel, respectively (Figure 5.5). Bontuchel maintained a larger trophic niche area in autumn sampling as well, with 99% of probability distribution comparisons larger for Bontuchel than Clocaenog. The modal SEAc in autumn was 1.36 (95% CI: 0.66, 2.74) for Clocaenog and 4.13 (95% CI: 2.48, 8.61) for Bontuchel (Figure 5.5). These results consistently indicate that dormice in broadleaf habitats have larger trophic niches than those in conifer plantations, both in spring and autumn. When comparing SEAc within the same site across the two sampling periods, the proportion of overlap between autumn and spring at Clocaenog was 0.39, and at Bontuchel was 0.05.

Dormice sampled in the Southwest of England in conifer habitat (Fingle) in autumn exhibited larger SEAc than those found in Okehampton (broadleaf habitat); 96% of probability distribution comparisons were larger (Figure 5.4). For autumn sampling, the modal SEAc was 0.63 (95% CI: 0.24, 2.36) and 2.34 (95% CI: 1.01, 5.16) respectively for Okehampton and Fingle (Figure 5.5).

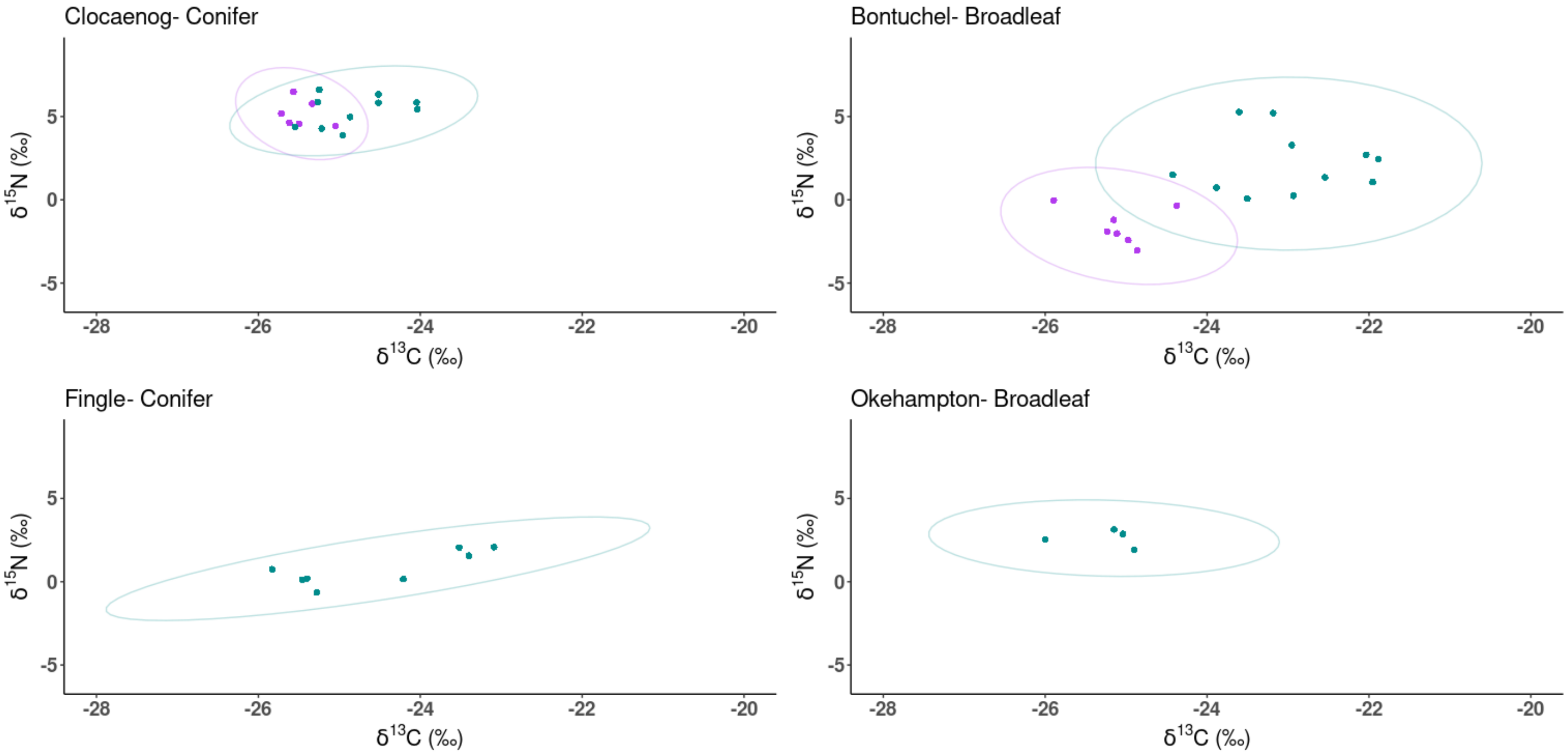


**Figure 5. 4**. *Bayesian standard ellipses ($SEA_B$) corrected for a small sample size ($SEA_C$) calculated using $\delta^{13}$C and $\delta^{15}$N data from dormouse fur samples. To estimate isotopic trophic niche areas at each site in each sample period isotopic trophic niche areas were calculated to establish whether or not dormice have different niche characteristics across habitat types. Sites at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle) are shown in the plots, purple points denotes isotopic signatures of dormice from spring sampling and blue points denote isotopic signatures of dormice from autumn sampling.*

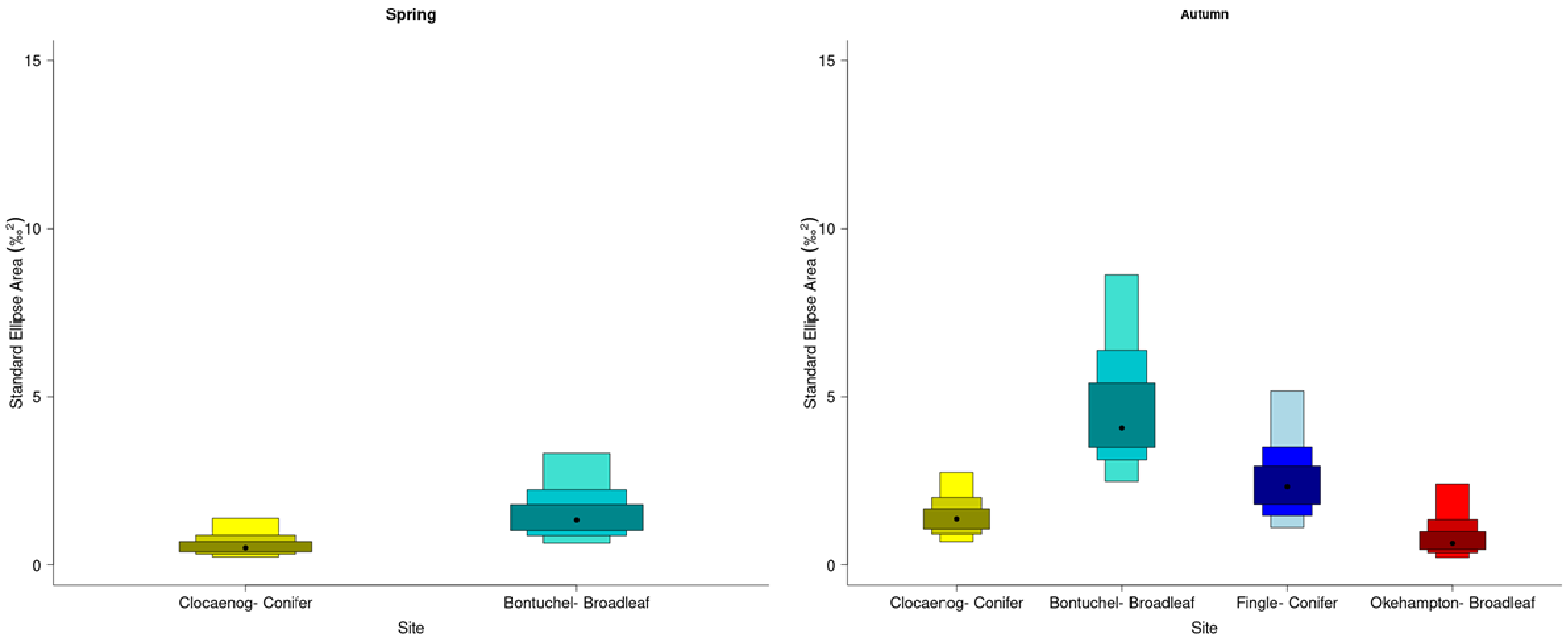


**Figure 5. 5**. *The area of Bayesian standard ellipses (SEA$_B$) corrected for a small sample size (SEA$_C$) calculated using $\delta^{13}$C and $\delta^{15}$N data from dormouse fur samples. To estimate isotopic trophic niche areas at each site in each sample period isotopic trophic niche areas were calculated to establish whether or not dormice have different niche characteristics across habitat types. Sites at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle) are shown in the plots..*

### ***Discussion***

The outcomes derived from mixing models underscore the distinctive dietary patterns exhibited by dormice at each of the surveyed sites. The models reveal that during the spring season, dormice at Clocaenog exhibit a versatile foraging behaviour, utilising all available food sources, including those within the conifer plantation. This aligns with findings in Europe suggesting dormice are able to subsist beyond the broadleaf edges (Wuttke et al. 2012; Büchner et al. 2018; Fedyń et al. 2021). In contrast, at Bontuchel in spring, tree seeds constitute a significant portion of dormice diets. This includes seeds from tree species not traditionally associated with dormouse diets, such as birch, sycamore, and beech. A similar pattern has been observed in Lithuanian dormouse populations, where birch seeds feature prominently (Juškaitis et al. 2016).

These findings underscore the ability of dormice to feed on ‘non-typical’ food sources, particularly with a high reliance on invertebrates during autumn sampling. While prior studies in Britain have emphasised the importance of invertebrates, typically Lepidoptera larvae and adults (Richards et al. 1984; Chanin et al. 2015), my research reveals a broader spectrum of invertebrate consumption, though resolution of finer taxonomies remains low. This suggests dormice forage opportunistically on a diverse range of invertebrate species, aligning with work by Büchner et al. (2018). The extreme drought in the summer of 2022, the hottest on record (Kendon et al. 2023b), may have influenced dormouse foraging behaviours and my results. Potentially diminished yields from soft and hard mast trees that could have prompted dormice to increase their reliance on invertebrates. If this is the case this response underscores dormice's ability to adapt to local conditions and exploit available resources. If the drought did influence foraging opportunities for dormice, leading to prolonged fasting periods, this would exert an influence on the dormouse $\delta^{15}N$ and $\delta^{13}C$ values, impacting the outcomes derived from mixing models (Doi et al. 2017). Considering potential effects on isotopic values, I suggest a multi-season repetition of this study to investigate the impact of local weather on dormouse diets.

Surprisingly, hazel nuts were not a primary component of dormouse diets during autumn sampling, even at sites where hazel was present. This discrepancy may stem from the dormouse fur sampled in autumn growing in the summer before hazel ripened (Goodwin et al. 2020). Hazel has been thought to be a key component in dormice diets (Richards et al. 1984; Bright and Morris 1993; Bright and Morris 1996), my findings from Clocaenog suggest that, in the absence of hazel, dormice utilise various 'non-typical' food sources.

The need to create more distinctive food groups for mixing models and that many of the source groups overlapped isotopically, means that some finer scale resolution of dormouse diets could be obtained by complementing with additional methods of diet investigation, such as molecular analysis of faeces (Inger and Bearhop 2008). The strength of my approach however is that dormouse faeces can be difficult to find in the field and my results represent diet composition over a much longer time-frame and is not sensitive to short-term changes in diet (Richards et al. 1984; Juškaitis et al. 2016; Büchner et al. 2018). My mixing models could not, however, build a detailed picture of the specific plant and invertebrate foods being consumed by dormice (Araújo et al. 2007). Such information would be useful for future dormouse management but direct observations of their diet is extremely difficult, as they are rarely observed foraging in the wild.

My food sampling was subject to some practical constraints, I was unable to sample bird eggs and fungi, though these have previously been found to be consumed by dormice (Bright and Morris 1993; Sarà and Sarà 2007; Adamík and Král 2008). I was also unable to sample aphids, a reportedly important food source for dormice, because of their low biomass (Juškaitis 2007). Although I was able to catch a range of different taxa using tree-beating methods, it is likely that there are some species that were missed such as night-flying and ground-dwelling invertebrates. However these omissions are unlikely to have substantially altered my conclusions given that food species were grouped broadly, and sampling methods were uniform across sites (Goodwin et al. 2020).

Hair sampled in Clocaenog (conifer) overlaps in isotopic space between spring and autumn, whereas at Bontuchel (broadleaf) the niche in autumn moves into a completely new isotopic space when compared with spring. This suggests that dormice at Bontuchel are able to shift their diet over the season as different food sources become available, such as insects, berries, and nuts (Bright and Morris 1993; Juškaitis and Baltrūnaitė 2013; Goodwin et al. 2020). My results indicate that dormice at Clocaenog are consistent in their selection of particular sources throughout the season (Figure 5.4). The smaller SEAc at Clocaenog indicate the population has a smaller trophic niche, which is indicative of a more restricted diet. My study challenges existing paradigms by demonstrating dormice's capacity to subsist in sites with low plant diversity. Only 4 broadleaf tree species were found at Clocaenog, contrary to evidence emphasising the species' need for highly diverse successional woodland (Bright and Morris 1993; Bright and Morris 1996; Bright et al. 2006). My study indicates that dormice are able to subsist in marginal habitats, relying on a restricted but presumably nutrient-rich diet, aligning with other studies highlighting their flexible and adaptive feeding strategies (Adamík and Král 2008; Juškaitis et al. 2016; Büchner et al. 2018; Goodwin et al. 2020).

Expanding on previous work, my study illuminates the hazel dormouse's dietary plasticity, capable of adapting to local conditions and exploiting a diverse range of food sources based on spatial and temporal availability (Chanin and Woods 2003; Trout et al. 2012; Wuttke et al. 2012; Büchner et al. 2018; Goodwin et al. 2020; Fedyń et al. 2021). Notably, my findings suggest dormouse diets closely reflect the availability of local plants and invertebrates at the site level (Juškaitis et al. 2016; Goodwin et al. 2020). My study does not find evidence of dormice relying heavily on specific plant species, with varying species found at each site (Appendix 4). Consequently, my results have practical implications for dormouse management, suggesting potential measures that emphasise the creation and maintenance of diverse habitats along pathways and in clearings, rich in plant species and invertebrates. Preserving large trees with abundant flowers, distributed throughout a site, is also recommended. Given the opportunistic feeding habits of dormice, management plans need not be overly prescriptive. I advocate for broader survey methods beyond hazel-rich sites. Innovations like footprint tunnels, which do not require a license holder and enable swift detection rates, offer an alternative across a range of habitat types (Mills et al. 2016). To ensure efficient protection, survey and monitoring protocols should encompass a wider range of habitats, avoiding an exclusive focus on any particular plant species.

# Chapter 6

# Discussion

# Chapter 6: Discussion

## *Overview*

In this thesis I aimed to i) investigate the drivers and consequences of daily torpor during the dormouse active season; ii) understand how daily torpor use among dormice populations in Britain might change under future climate scenarios; iii) evaluate whether current knowledge bases are adequate for dormouse conservation at the edge of their range in Britain; iv) assess dormouse diets in non-typical habitat.

In this chapter I will review how I have addressed each of these research objectives, and how the findings of this thesis contribute to our knowledge of dormice life-history strategy, ecology and conservation. I will then set the work in the wider context of energetics, life-history strategy and climate change and the preservation of species at the edge of their range in marginal habitats.

In **Chapter 2**, I revealed spatial and temporal variations in torpor use among dormouse populations in Britain. Factors influencing torpor include site location, elevation, woodland type, weather conditions, breeding status, body mass, and sex. I demonstrated a link between torpor rates and abundance at a site level with potential implications for population dynamics. Using these findings, in **Chapter 3**, I have projected a decline in the frequency of daily torpor in hazel dormice in Great Britain by 2080 due to increasing temperatures and declining rainfall. While overall reductions suggest potential benefits for breeding, the inter-annual weather variations may lead to fluctuations, posing a concern for small populations with potential implications for local extinctions. In **Chapter 4** I found species distribution models (SDMs) built using available data sources failed to accurately predict dormouse presence in North Wales. This research highlights the challenges of modelling species distributions, especially in non-typical habitats at the periphery of a species range. In **Chapter 5** dormice were found to exploit a variety of 'non-typical' food sources, suggesting their ability to adapt to local conditions**.**

### ***Hazel dormice and life history strategies***

My findings on the drivers of daily torpor among dormice support established theories regarding energy budgets in this species but also provides new insights **(Chapter 2)**. I identified previously unrecognised factors influencing torpor use, most notably the impact of rainfall. Additionally, I have investigated the short (daily), medium (weekly), long (monthly) and, very long (seasonal) effects of climate on the propensity for individual dormice to be found in torpor, which has not been attempted in other studies. Daily and seasonal minimum temperature and rainfall were important drivers of torpor use, with more torpid animals found on colder and wetter sites. Weekly and monthly climatic variables were not significant in my study indicating that intrinsic factors such as mass, sex, breeding condition and how many animals are inhabiting a box are more important in determining torpor use. My findings that torpor use in hazel dormice occurs at colder ambient temperatures, and in lighter, non-breeding individuals has been echoed in other studies (Juškaitis 2005; Pretzlaff et al. 2014).

The spatial extent of the National Dormouse Monitoring Programme (NDMP) data has allowed for new insights into site-level characteristics that drive torpor use among dormouse populations **(Chapter 2)**. While there have been many studies regarding dormouse habitat requirements in Britain and Europe (Bright and Morris 1990; Juškaitis 2008b; Wuttke et al. 2012; Sozio et al. 2016; Goodwin et al. 2018b; Mortensen et al. 2022), there has been no work providing this in the context of daily torpor and energy budgets. Daily torpor is a mechanism by which to save energy among dormice, therefore variables that are connected with high rates of torpor use might be indicative of the quality of a site for dormice. I have found that dormice are more likely to be found in torpor at sites with a higher proportion of ancient woodland and more broadleaf connectivity. The proportion of broadleaf woodland in a NDMP site was not found to have a relationship with torpor use which is in contradiction that this as optimal habitat for dormice (Bright and Morris 1990; Bright and Morris 1996). Proxies for climate at the site level were also found to influence torpor use, with greater incidences of torpor at sites in the west of Britain and at sites with higher elevations. Environmental conditions of a site have been shown to affect other aspects of dormouse ecology with higher abundance and breeding rates at sites with warmer spring and summer temperatures (Goodwin et al. 2018a).

I provide new insights into the trade-offs involved in daily torpor use in hazel dormice and its potential influence on dormice population dynamics. The use of daily torpor is associated with a requirement for energy saving to avoid harsh environmental conditions and times of hardship (Ruf and Geiser 2015; Geiser and Cooper 2023). Torpor and reproduction in mammals and birds are often mutually exclusive events because of opposing energetic demands (McAllan and Geiser 2014). My findings suggest this is the case in hazel dormice with lower counts of adults and young in years where sites exhibit high rates of torpor. High rates of torpor in both sexes appear to drive a lower number of breed events but only high rates of torpor in males is associated with smaller litter sizes **(Chapter 2)**. My findings are in agreement with studies conducted on edible dormice (*Glis glis);* males are the energetic constraint for breeding. The quantity of males producing testosterone directly correlates with the number of litters produced, and males refrain from entering torpor during testosterone production (Fietz et al. 2004; Fietz et al. 2010).

### *Hazel dormice and life history strategies under future climate*

Limited knowledge exists regarding the strategies employed by dormice to reduce energy expenditure during their active season (Pretzlaff et al. 2014). In **Chapter 2** I provided evidence that torpor use among dormice populations in England and Wales is highly influenced by daily and seasonal climate. Predictions suggest that British summers are anticipated to become drier and hotter, with an elevated likelihood of weather extremes (Kendon et al. 2022). Consequently, the energy requirements of hazel dormice during summer are expected to change, thereby impacting other life history events such as breeding and survival.

Torpor is an efficient response to balancing energy budgets in times of environmental stress it however compromises annual fecundity **(Chapter 2)**, which echoes other anecdotal evidence of dormice (Bright and Morris 1996). In **Chapter 3** I was able to predict that under future climate scenarios that the requirement for dormice to enter torpor in England and Wales should decrease. This indicates that conditions in Britain are likely to become more favourable for dormice during the active season. Consequently, breeding rates for dormice populations in Britain are anticipated to increase by 2080, potentially leading to population growth. As dormice are more prevalent on sites with lower torpor rates **(Chapter 2)**, a decrease in torpor rates across England and Wales is expected to coincide with an increase in population abundance across sites. Conversely as hibernators dormice are at a disadvantage as winters warm; as increased arousals are energetically costly (Pretzlaff and Dausmann 2012). Dormice benefit from consistently cold weather over the winter (Goodwin et al. 2018a; Combe et al. 2023). However recent evidence suggests they do exhibit a high degree of plasticity during hibernation; with the ability to forage during periods of arousal during warmer winters (Pretzlaff et al. 2021).

Under worst case climate scenarios high fluctuations in weather patterns are expected across summers (Kendon et al. 2023a). In years characterised by unfavourable climatic conditions, torpor rates above 30% (baseline for a poor year) are expected among dormice (**Chapter 3**). Coupled with evidence indicating lower survival rates due to warmer, wetter winters and density-dependent breeding limiting reproduction as habitats become more degraded, dormice populations may struggle to recover amid ongoing climatic variability (Combe et al. 2023). This represents a significant risk to dormice populations especially those in small populations, in marginal habitats at the edge of their distributional range in Britain. While the reduced frequency of torpor in England and Wales by 2080 appears advantageous for dormice, hibernation under future climate scenarios poses a potential risk. Further investigation into dormancy patterns among dormice into the future is essential to fully understand the implications of these two adaptive strategies on population dynamics.

### ***Using the National Dormouse Monitoring Programme to study torpor***

In **Chapter 2 and 3** using NDMP data, I was able to assess the drivers and consequences of daily torpor among dormouse populations in England and Wales and use this to make predictions about the prevalence of torpor into the future that would not have been possible without citizen scientists. The length of time, the spatial extent and the amount of data have allowed me to quantify more fully the intrinsic and extrinsic influences of daily torpor use during the active season and the subsequent implications for dormouse population dynamics. This moves beyond the site-level approach applied in other studies (Juškaitis 2005; Pretzlaff et al. 2014).

Monitoring data from NDMP sites were also included in the data used to create national and regional SDMs for **Chapter 4.** The selection and use of sites with known dormouse populations for **Chapter 5** were made possible through information provided by volunteers from the NDMP. The programme can therefore act as a starting point and information resource for more detailed research on dormice in England and Wales.

A major strength of this work is the use of the NDMP; a large-scale monitoring data set collected by citizen scientists. The Programme provides a wealth of data spatially across England and Wales and temporally, originating in 1988. There are inherent challenges of survey design and implementation in all citizen science schemes (Kallimanis et al. 2017; Tiago et al. 2017). This dataset has already been validated in previous work on dormice populations and therefore provided a robust method for studying other aspects of dormouse ecology (Goodwin et al. 2017; Goodwin et al. 2018a; Scopes et al. 2023).

### *Hazel dormice subsistence in marginal habitats*

In **Chapter 5** I found evidence to support the generalist and opportunistic nature of dormouse diets. My results indicate that dormouse diets exhibit strong site specificity rather than being strictly dictated by habitat type. Previously, dormice have been thought to have highly specialised habitat requirements because of their specific diets and inability to digest cellulose (Richards et al. 1984; Bright and Morris 1993; Bright and Morris 1996). However, recent findings suggest that dormice can exploit a diverse array of food sources within their local environment (Sarà and Sarà 2007; Adamík and Král 2008; Juškaitis et al. 2016; Büchner et al. 2018; Goodwin et al. 2020).

There is growing evidence that dormice are subsisting in non-typical habitats in England and Wales, including conifer plantation and coastal scrub (Chanin and Woods 2003; Bright et al. 2006; Trout et al. 2012; Trout et al. 2018). European dormouse populations are able to exploit a diverse range of habitat types including; high conifer plantations, road-side habitat, tall forest stands and spruce stands with mixed forests (Juškaitis 2008b; Wuttke et al. 2012; Kelm et al. 2015; Fedyń et al. 2021). Enhancing our comprehension of dormouse populations subsisting in non-typical habitat will prove instrumental in their future conservation and management. The findings from **Chapter 4** underscore the significance of specific flora, such as bramble, for dormouse presence in conifer plantations. This aligns with European studies emphasizing the importance of habitats that offer adequate feeding opportunities rather than adhering to a singular habitat type (Wuttke et al. 2012; Ramakers et al. 2014; Sozio et al. 2016; Mortensen et al. 2022). **Chapter 5** further supports these observations, suggesting that dormice can subsist on a limited diet even in non-typical habitats, presumably due to the availability of key foods. My work supports the idea that dormice exhibit greater adaptability than previously thought and possess the capacity to exploit resources across diverse habitat types. Recent evidence even suggests that they are most generalist of all dormouse species in Europe (Fedyń et al. 2021).

### ***Conservation of dormice at the edge of their range***

Dormice populations experience sub-optimal environmental conditions in England and Wales, situated at the edge of their European range. The insights gained from **Chapters 2 and 3**, where I established the drivers of torpor use in dormice and their consequential impacts on life history events, provide potential reasons for the national decline of dormouse populations. While spring and summer temperatures have risen in the UK, precipitation and the occurrence of extreme precipitation events has increased (Hoffmann et al. 2010). This poses a particular concern for dormice populations at the very edges of their range in England and Wales, where the occurrence and intensity of climatic extremes may be more pronounced (Rehm et al. 2015). The propensity for non-typical habitats at the edge of their range contributes to the low numbers of dormice as site carrying capacity and density-dependent breeding restrict the abundance of animals (Combe et al. 2023). Due to poor environmental conditions and high energy requirements dormice torpor use is predicted to remain relatively high at the range margins when compared to the core **(Chapter 3)**, consequently reducing the overall fecundity of these populations **(Chapter 2)**. Animals at the edge of their distributional ranges may struggle to maintain positive energy budgets as they have already reached their physiological limits (Pretzlaff et al. 2021). To enhance the resilience of dormouse populations in Britain, conservation efforts and mitigation strategies are imperative, particularly in the range margins.

The reliance of dormice on a small number of key foods identified in **Chapter 4 and 5** suggests that resources should be evenly distributed throughout a site in order to increase its dormouse population density. Increased foraging opportunities might also negate the requirement for daily torpor and increase dormouse abundance at marginal sites. **Chapter 4** highlighted significant knowledge gaps with regards to dormice populations at the edge of their range in marginal habitats, as national and regional SDMs failed to accurately predict distributions. To inform effective conservation of dormice in England and Wales at the very margins of their range a more comprehensive understanding of the factors enabling subsistence in non-typical habitat is imperative. To ensure continued persistence of dormice populations at the edge of their range in Britain, especially in marginal habitat, conservation priorities for the species must focus on a wider range of habitat types.

### ***Dormice populations under future climate change and conservation implications***

Daily torpor serves as a life history strategy enabling species to persist in sub-optimal conditions. Therefore, as weather variability increases in Britain during the dormice active season, they may exhibit greater resilience to these changes. However the ability to avoid unfavourable environments comes at the cost of breeding **(Chapter 2)**. By 2080 conditions during the reproductive period are expected to improve for dormice in England and Wales, especially those at the core **(Chapter 3)**. Monitoring incidences of daily torpor among dormice populations is crucial for determining whether local conditions are deteriorating or improving. Active management may be necessary at sites with persistently high torpor rates to ensure continued reproductive success.

To ensure the preservation of existing dormice populations in Britain, that have already undergone significant declines, effective conservation mitigation is needed. Forest management can improve nesting and foraging opportunities by affecting habitat complexity and in turn increase animal abundance (Chaudhary et al. 2016). Recognised for its substantial impact on dormouse populations, forest management has the potential to enhance local abundance (Juškaitis 2008a; Sozio et al. 2016; Goodwin et al. 2018b). This will be particularly important under a changing climate to ensure resilience in British woodlands and maintain habitats with ample food sources for dormice. Dormice are notably sensitive to fragmentation and changes in habitat quality, as survival requires high energy resources (Fedyń et al. 2021). Efforts should be made to increase foraging opportunities at sites, which may include tree felling and coppicing, to allow the regeneration of key food sources **(Chapter 4 and 5)**. My results from **Chapter 5** contribute to a growing body of evidence that dormice are more adaptable than previously thought, and under certain conditions can subsist in habitats that are often considered to be marginal for this species **(Chapter 4)**. Management for dormice, therefore, does not need to be overly prescriptive, but enhancing diversity and understory in woodlands will benefit dormice by allowing opportunistic feeding across a site.

### *Species conservation at the edge of range*

There is often a limited understanding of species at the edge of their distributional range and their use of marginal habitats within these landscapes. The ability to adapt to marginal habitats, especially on the edge of their range, plays a crucial role in the evolution of ecological niches and species ranges (Kawecki 2008). Survival and reproduction in these habitats are usually initially poor and extinction risk is high (Böhme et al. 2007; Boakes et al. 2018; Thakur et al. 2018; Britnell et al. 2023). These populations hold significant ecological importance, contributing to resilience, especially when the conservation objective is to reverse declines. Populations at the edge of the range in marginal habitats have demonstrated distinct behaviours, morphology, and life history traits compared to counterparts in the core (Latron et al. 2023; Tranquillo et al. 2023). An increased understanding of habitat requirements, diets, and environmental influences in marginal habitats at the edge of species ranges is needed for a wide range of taxa to enable positive conservation outcomes.

The conservation of populations at range margins is especially important under future climate change scenarios. Edge populations often experience higher climate variability than those in the core which can manifest as climatic extremes (Thomas et al. 1994; Rehm et al. 2015; Westerbom et al. 2019). Extreme climatic events are predicted to become increasingly important in defining species' distributions, emphasising the need to preserve any local adaptations within populations at the edge of the range (Rehm et al. 2015). Marginal populations are prone to extinction under deteriorating conditions but are also at the forefront of expansion under improving conditions (Kanda et al. 2009; Furrer and Pasinelli 2016; Goel and Keitt 2022). Populations at the edge of the range can act as early indicators for an overall species response to climate change but present a conservation challenge because of their sparse distribution and propensity for marginal habitats (Sexton et al. 2009; Wiens 2016; Fogarty et al. 2017). Local management is often needed for the preservation of species on the edge of their range because of their unique requirements and local adaptations (Lawson et al. 2012; Kosanic et al. 2018; Shay et al. 2021). Understanding the drivers of local colonisation and extinctions events of populations in marginal habitats at the edge of their range is vital to halt further declines.

### ***Concluding remarks***

Effective conservation of a species requires knowledge of its life-history strategies, requirements, distribution, and the influence of changing environmental conditions. This is particularly useful under human induced change, when conservation must preserve species in often rapidly changing environments. In this thesis I have quantified the frequency of daily torpor use in populations of dormice across England and Wales, through the use of citizen science data. Further use of this data has allowed for the assessment of intrinsic and extrinsic factors that determine torpor use at large temporal and spatial scales. I have also examined torpor use at multiple scales, highlighting the drivers of torpor at an individual level and across sites. Using these findings I have been able to predict how torpor frequency might change under future climate scenarios in Britain, and what the impacts on dormouse population dynamics might be. I have then focused on dormice in marginal habitat, at the north-west edge of their distributional range in Britain to better understand their habitat and dietary requirements in these landscapes. The outcomes of the research in this thesis illustrate that significant knowledge gaps remain for the effective conservation of dormice in marginal, edge of range habitats in England and Wales, but that positive steps can be achieved that benefit dormice. This research provides practical recommendations for the preservation of dormice at their range margins, while also placing this work in the importance of understanding species energy budgets. I recommend expanding the scope of dormouse conservation initiatives beyond conventional habitats, closely monitoring rates of daily torpor, and adopting proactive habitat management practices. This involves evenly distributing resources throughout a site, enhancing habitat complexity, and increasing foraging opportunities for dormice. Dormouse declines are symptomatic of wider management and environmental changes that are affecting mammal species across Britain. By focusing on the conservation of this species in marginal habitats at the edge of their range, population declines and local extinctions can be reduced building resilience especially in the face of climate change.

# Appendices

**Appendix 1***: Summary of different models ran to test for relationships between population dynamics and yearly dormouse torpor scores (Chapter 2)*

| | **Measure** | **Model Type** | **Error Structure** | **Off-set** | **Years Tested** | **Age Classes Included** | **Additional information** |
|---|---|---|---|---|---|---|---|
| **1.** | Counts of Adult Dormice- across the whole season<br>(72,000 observations, 614 NDMP sites) | GLM | Poisson | Number of boxes checked in the survey season | Year T and Year T + 1 | Adults | |
| **2.** | Counts of Young Dormice- across the whole season<br>(39,985 observations, 548 NDMP sites) | GLM | Poisson | Number of boxes checked in the survey season | Year T and Year T + 1 | Pinks, Greys Eyes Closed, Eyes Open, Juveniles | |
| **3.** | Counts of Adult Dormice- early and late in the season<br>(72,000 observations 614 NDMP sites) | GLM | Poisson | Number of boxes checked in the survey season | Year T + 1 | Adults | |
| **4.** | Counts of Young Dormice- early and late in the season<br>(39,985 observations, 548 NDMP sites) | GLM | Poisson | Number of boxes checked in the survey season | Year T and Year T + 1 | Pinks, Greys Eyes Closed, Eyes Open, Juveniles | Counts of young in Year T were tested using early and late torpor scores. Tests for Year T + 1 used the torpor score in Year T for the entire season. |

| | **Measure** | **Model Type** | **Error Structure** | **Off-set** | **Years Tested** | **Age Classes Included** | **Additional information** |
|---|---|---|---|---|---|---|---|
| **5.** | Breed Events<br>(28,082 surveys where breeding was monitored across 800 NDMP sites) | GLM | Binomial | | Year T and Year T + 1 | Pinks, Greys Eyes Closed, Eyes Open | A breed event was determined as any time pink, greys eyes closed, or eyes open dormice were found in a box the young are dependent on the mother therefore certain that the individuals were born during the current active season. |
| **6.** | Litter Size<br>(6,860 potential litters) | Mixed GLM using the package ‘lme4’ (Bates et al. 2015) | Poisson | | Year T and Year T + 1 | Pinks, Greys Eyes Closed, Eyes Open | Mixed models were chosen to account for pseudo-replication within the model as yearly torpor score was repeated for each litter found within a site during any given survey year. |
| **7.** | Average Mass of Adult Dormice (g) – proxy for individual fitness<br>(72,000 observations, 614 NDMP sites) | GLM | Gaussian | | Year T and Year T + 1 | Adults (only respective sex in relation to Yearly Torpor Score). | |

| | Measure | Model Type | Error Structure | Off-set | Years Tested | Age Classes Included | Additional Information |
|---|---|---|---|---|---|---|---|
| **8.** | Average Mass of Young Dormice (g) – proxy for individual fitness<br>(10,525 observations, 348 NDMP sites) | GLM | Gaussian | | Year T and Year T + 1 | Eyes Open | Eyes open was chosen as these are the most commonly encountered age class during surveys so allowed for the most data to be included into the subsequent models. |

**Appendix 2:** *Tunnel and site level variables collected during independent data collection to test dormouse habitat preferences (Chapter 4)*

### Tunnel level variables collected

Dominant plant species within 1m of the tunnel location (up to 5 species collected)

Diameter of tree tunnel placed in (cm)

Height of tree tunnel placed in (m)

Habitat type tunnel placed in- edge-scrub or conifer

### Line level variables collected

*Tunnels in the edge habitat:*

Is there connection between mid-storey shrubs/trees?

Number of paths wider than 1m

Average height (m) of the shrub portion of the edge

Dense, medium or encroaching scrub

Is there any evidence of management/cutting of the edges of the patch?

Is there any evidence of management within the patch?

Number of emergent trees

Dominant species <0.5m: Ground cover

Dominant species 0.5-2m: Mid storey

Dominant species >2m: Upper storey

*Tunnels in the conifer habitat:*

Is there ground cover?

Average height (m) of the conifer

Dense, medium, young plantation

Is there any evidence of management/felling on the edge of the patch?

Is there any evidence of management within the patch?

Are there any emergent broadleaf trees?

Dominant species <0.5m: Ground cover

Dominant species 0.5-2m: Mid storey

Dominant species >2m: Upper storey

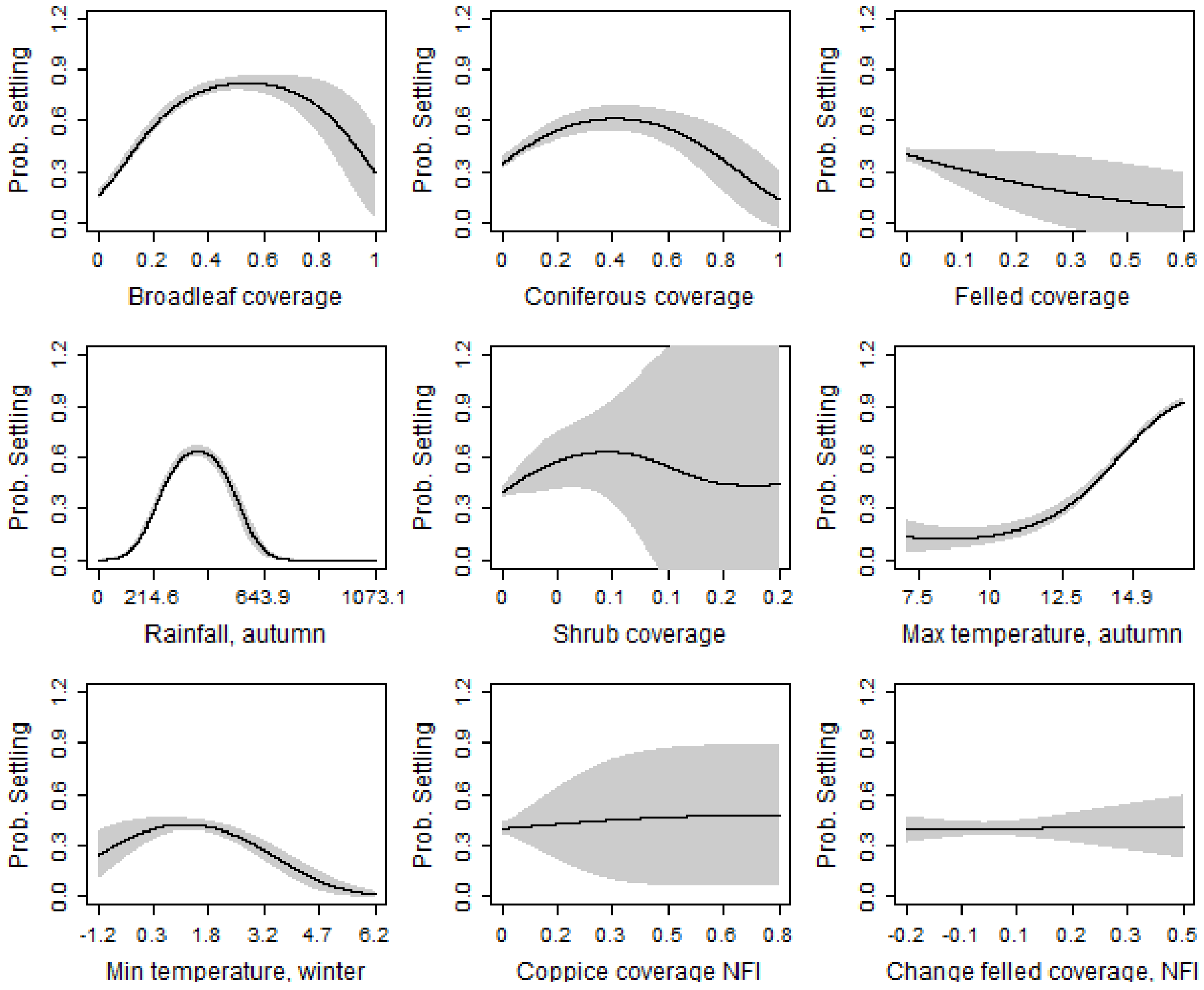
*Across the whole line:*

Is there edge habitat within the line?

Adjacent land use (%) - arable, water, road/route, pasture/grass, woodland

DAFOR (Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent) – hazel, willow species, sycamore, birch species, yew, conifer species, honeysuckle, bramble.

## **Appendix 3:** *graphical representation of significant variables from the national Species Distribution Model (Chapter 4)*



**Appendix 4:** *Plant and Invertebrate food sources sampled across all sites in the spring and autumn sampling periods. Sites are at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle) Fingle includes food sources sampled in spring that were not included in further analysis. Okehampton only includes autumn sampling as no dormice were found during spring sampling. N denotes the number of tree species or invertebrate orders collected at each site (Chapter 5).*

| **Site** | **Sample Type** | **Species** | |
|---|---|---|---|
| **Clocaenog** | **Broadleaf** | Beech (*Fagus sylvatica)* | |
| | | Bilberry (*Vaccinium myrtillus*) | |
| | | Bluebell (*Hyacinthoides non-scripta*) | |
| | | Bramble (*Rubus fruticosus)* | |
| | | Red Clover (*Trifolium pratense*) | |
| | | Elder (*Sambucus nigra*) | |
| | | Gorse (*Ulex)* | |
| | | Hawthorn (*Crataegus monogyna*) | |
| | | Rhododendron (*Ericaceae)* | |
| | | Rowan (*Sorbus aucuparia)* | |
| | | Sycamore (*Acer pseudoplatanus)* | |
| | | Willow (*Salix caprea)* | n=12 |
| | **Conifer** | Larch (*Larix decidua*) | |
| | | Scots Pine *(Pinus sylvestris)* | |
| | | Sitka Spruce (*Picea sitchensis)* | |
| | | Western Hemlock (*Tsuga heterophylla)* | n=4 |
| **Clocaenog** | **Invertebrates-broadleaf** | Aranaea | |

| Site | Sample Type | Species |  |
|---|---|---|---|
|  |  | Coleoptera |  |
|  |  | Dermaptera |  |
|  |  | Diptera |  |
|  |  | Hemiptera |  |
|  |  | Hymenoptera |  |
|  |  | Julida |  |
|  |  | Lepidoptera |  |
|  |  | Neuroptera |  |
|  |  | Opiliones |  |
|  |  | Plecoptera |  |
|  |  | Psocoptera | n=12 |
|  | **Invertebrates-conifer** | Aranaea |  |
|  |  | Coleoptera |  |
|  |  | Collembola |  |
|  |  | Dermaptera |  |
|  |  | Diptera |  |
|  |  | Hemiptera |  |
|  |  | Hymenoptera |  |
|  |  | Isopod |  |
|  |  | Julida |  |
|  |  | Lepidoptera |  |
|  |  | Lithobiomorpha |  |
|  |  | Neuroptera |  |
|  |  | Opiliones |  |
|  |  | Orthoptera |  |
|  |  | Psocoptera | n=15 |
| **Bontuchel** | **Plant** | Ash (*Fraxinus excelsior)* |  |
|  |  | Beech (*Fagus sylvatica)* |  |
|  |  | Birch *(Betula)* |  |
|  |  | Blackthorn *(Prunus spinose)* |  |
|  |  | Bluebell (*Hyacinthoides non-scripta*) |  |
|  |  | Bramble (*Rubus fruticosus)* |  |
|  |  | Common Broom (*Cytisus scoparius)* |  |
|  |  | Dog Rose (*Rosa canina)* |  |
|  |  | Elder (*Sambucus nigra*) |  |
|  |  | Gorse (*Ulex)* |  |

| **Site** | **Sample Type** | **Species** | |
|---|---|---|---|
| | | Hawthorn (*Crataegus monogyna*) | |
| | | Hazel (*Corylus avellana)* | |
| | | Holly (*Ilex aquifolium)* | |
| | | Honey Suckle *(Lonicera periclymenum)* | |
| | | Oak (*Quercus robur)* | |
| | | Rowan (*Sorbus aucuparia*) | |
| | | Sycamore (*Acer pseudoplatanus)* | |
| | | Wild Garlic (*Allium ursinum)* | |
| | | Wych Elm *(Ulmus glabra)* | n=19 |
| | **Invertebrates** | Aranaea | |
| | | Coleoptera | |
| | | Hemiptera | |
| | | Julida | |
| | | Lepidoptera | |
| | | Neuroptera | |
| | | Opiliones | n=7 |
| **Fingle** | **Broadleaf** | Ash (*Fraxinus excelsior)* | |
| | | Birch *(Betula)* | |
| | | Bluebell (*Hyacinthoides non-scripta*) | |
| | | Bramble (*Rubus fruticosus)* | |
| | | Common Broom (*Cytisus scoparius)* | |
| | | Dog Rose (*Rosa canina)* | |
| | | Elder (*Sambucus nigra*) | |
| | | Gorse (*Ulex)* | |
| | | Hawthorn (*Crataegus monogyna*) | |
| | | Hazel (*Corylus avellana)* | |

| **Site** | **Sample Type** | **Species** | |
|---|---|---|---|
| | | Holly (*Ilex aquifolium)* | |
| | | Honey Suckle *(Lonicera periclymenum)* | |
| | | Ivy (*Hedera helix)* | |
| | | Rowan (*Sorbus aucuparia*) | n= 14 |
| | **Conifer** | Douglas Fir (*Pseudotsuga menziesii)* | |
| | | Sitka Spruce *(Picea sitchensis)* | |
| | | Western Hemlock (*Tsuga heterophylla)* | n=3 |
| | **Invertebrates-broadleaf** | Aranaea | |
| | | Coleoptera | |
| | | Diptera | |
| | | Entomobryomorpha | |
| | | Hemiptera | |
| | | Hymenoptera | |
| | | Isopod | |
| | | Julida | |
| | | Lepidoptera | |
| | | Neuroptera | |
| | | Opillones | n=11 |
| | **Invertebrates-conifer** | Aranaea | |
| | | Coleoptera | |
| | | Hemiptera | |
| | | Hymenoptera | |
| | | Isopod | |
| | | Julida | |
| | | Lepidoptera | |
| | | Opillones | |
| | | Orthoptera | |
| | | Psocoptera | n=10 |
| **Okehampton** | **Plant** | Bramble *(Rubus fruticosus)* | |
| | | Elder (*Sambucus nigra*) | |
| | | Hawthorn (*Crataegus monogyna*) | |

| **Site** | **Sample Type** | **Species** | |
|---|---|---|---|
| | | Hazel (*Corylus avellana)* | |
| | | Holly (*Ilex aquifolium)* | |
| | | Rowan (*Sorbus aucuparia*) | n=6 |
| | **Invertebrates** | Aranaea | |
| | | Coleoptera | |
| | | Dermaptera | |
| | | Diptera | |
| | | Hemiptera | |
| | | Isopod | |
| | | Julida | |
| | | Lepidoptera | |
| | | Neuroptera | |
| | | Opiliones | n=10 |

**Appendix 5:** Source food groupings for Bayesian Stable Isotope Mixing Models (BSIMMs) - *diet composition analysis. Samples were collected at paired broadleaf and conifer woodlands in North Wales (broadleaf -Bontuchel, conifer - Clocaenog) and Southwest England (broadleaf - Okehampton, conifer – Fingle). Source food groupings were created that were both isotopically and biologically meaningful while capturing variation amongst potential sources (Chapter 5)*

| **Site** | **Sampling Period** | **Food Group** | **Food Sources** |
|---|---|---|---|
| Clocaenog | Spring | Conifer (group 1) | Larch (pollen cones) |
| | | | Western Hemlock (ovulate cones) |
| | | Conifer (group 2) | Larch (ovulate cones) |
| | | | Larch (leaf buds) |
| | | | Scots Pine (pollen cones) |
| | | | Sitka Spruce (pollen cones) |
| | | | Sitka Spruce (leaf buds) |
| | | | Western Hemlock (leaf buds) |
| | | | Western Hemlock (pollen cones) |
| | | Flower, shrub, trees (group 1) | Bilberry (petals) |
| | | | Clover (flower) |
| | | | Gorse (flower) |
| | | | Gorse (seeds) |
| | | | Rhododendron (flower) |
| | | | Sycamore (flowers) |
| | | Flower, shrub, trees (group 2) | Bluebell (flowers) |
| | | | Bramble (flowers) |
| | | | Elder (flower) |
| | | | Hawthorn (flowers) |
| | | | Rowan (flower) |
| | | | Willow (seeds) |
| | | Invertebrates | Aranaea |
| | | | Coleoptera |
| | | | Dermaptera |
| | | | Diptera |
| | | | Hemiptera |

| **Site** | **Sampling Period** | **Food Group** | **Food Sources** |
|---|---|---|---|
| | | | Lepidoptera |
| | | | Opiliones |
| | | | Psocoptera |
| Clocaenog | Autumn | Tree Seeds | Beech (nut) |
| | | | Hawthorn (berry) |
| | | | Sycamore (seeds) |
| | | Conifer- plants | Hemlock (ovulate cone) |
| | | | Scots Pine (pollen cone) |
| | | | Sitka (ovulate cone) |
| | | | Sitka (pollen cone) |
| | | Berries | Bilberry (berry) |
| | | | Bramble (berry) |
| | | | Gorse (flower) |
| | | | Rowan (berry) |
| | | Invertebrates (Conifer) | Aranaea |
| | | | Coleoptera |
| | | | Collembola |
| | | | Diptera- adult |
| | | | Diptera- larvae |
| | | | Hemiptera |
| | | | Hymenoptera |
| | | | Isopod |
| | | | Julida |
| | | | Lithobiomorpha |
| | | | Opiliones |
| | | | Orthoptera |
| | | Invertebrates (broadleaf) | Aranaea |
| | | | Coleoptera |
| | | | Coleoptera- larvae |
| | | | Dermaptera |
| | | | Diptera |
| | | | Hemiptera |
| | | | Hymenoptera |
| | | | Lepidoptera |
| | | | Neuroptera- adult |
| | | | Neuroptera- larvae |
| | | | Opiliones |
| | | | Plecoptera |
| | | Lepidoptera | Lepidoptera- adult (conifer) |
| | | | Lepidoptera- larvae (conifer) |

| **Site** | **Sampling Period** | **Food Group** | **Food Sources** |
|---|---|---|---|
| Bontuchel | Spring | Seeds and flowers | Bramble (flower) |
| | | | Rowan (flower) |
| | | | Hazel (nut) |
| | | | Elm (key) |
| | | Tree seeds | Beech (flower) |
| | | | Beech (nut) |
| | | | Birch (seed) |
| | | | Sycamore (seed) |
| | | Shrub and tree flowers | Dog rose (flower) |
| | | | Hawthorn (flower) |
| | | | Hazel (flower) |
| | | | Honey suckle (flower) |
| | | Flowers | Bluebell (flower) |
| | | | Common Broom (flower) |
| | | | Wild garlic (flower) |
| | | Invertebrates (omnivores) | Hemiptera |
| | | | Lepidoptera- larvae |
| | | Invertebrates (carnivore) | Aranaea |
| | | | Coleoptera |
| | | | Opiliones |
| Bontuchel | Autumn | Tree seeds | Ash (seed) |
| | | | Beech (nut) |
| | | | Dog Rose (hips) |
| | | | Gorse (flowers) |
| | | | Oak (acorn) |
| | | | Sycamore (seed) |
| | | Rowan and Bramble | Bramble (berry) |
| | | | Rowan (berry) |
| | | Hazel | Hazel (nut) |
| | | | Hazel (catkin) |
| | | Berries | Blackthorn (berry) |
| | | | Elder (berry) |
| | | | Hawthorn (berry) |
| | | | Holly (berry) |
| | | | Honey Suckle (berry) |
| | | Invertebrates | Aranaea |
| | | | Coleptera |
| | | | Hemiptera |
| | | | Neuroptera- adults |

| **Site** | **Sampling Period** | **Food Group** | **Food Sources** |
|---|---|---|---|
| | | | Neuroptera- larvae |
| | | | Opiliones |
| | | Lepidoptera | Lepidoptera- larvae |
| Fingle | Autumn | Conifer- plants | Sitka spruce (ovulate cone) |
| | | | Sitka spruce (pollen cone) |
| | | Hazel | Hazel (catkin) |
| | | | Hazel (nut) |
| | | Berries | Bramble (berry) |
| | | | Dog rose (hip) |
| | | | Elder (berry) |
| | | | Gorse (flowers) |
| | | | Hawthorn (berry) |
| | | | Holly (berry) |
| | | | Rowan (berry) |
| | | Invertebrates | Aranaea |
| | | | Coleoptera |
| | | | Entomobryomorpha |
| | | | Hemiptera |
| | | | Hymenoptera |
| | | | Isopod |
| | | | Julida |
| | | | Neuroptera |
| | | | Opiliones |
| | | Lepidoptera | Lepidoptera- larvae |
| Okehampton | Autumn | Hazel | Hazel (catkin) |
| | | | Hazel (nut) |
| | | Berries | Bramble (berry) |
| | | | Elder (berry) |
| | | | Hawthorn (berry) |
| | | | Holly (berry) |
| | | | Rowan (berry) |
| | | Invertebrates | Aranaea |
| | | | Coleoptera |
| | | | Dermaptera |
| | | | Diptera |
| | | | Hemiptera |
| | | | Isopod |
| | | | Julida |
| | | | Opiliones |
| | | | Neuroptera |
| | | Lepidoptera | Lepidoptera- larvae |

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