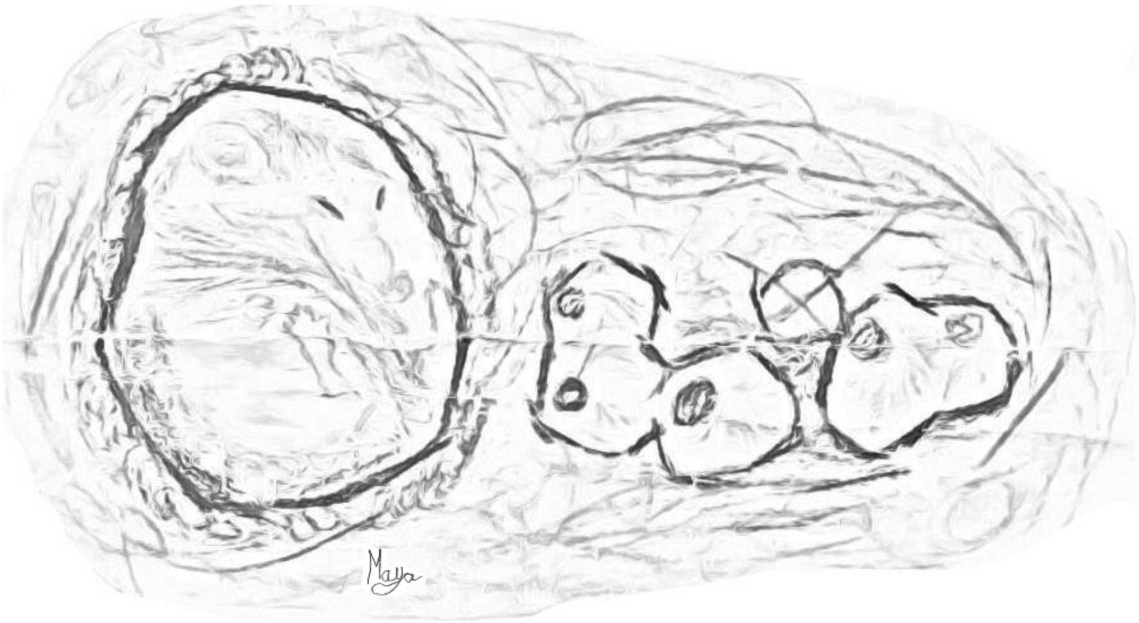
Hibernation ecology and population biology of the hazel dormouse



Submitted by Leonardo Gubert to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences,

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Abstract

Detailed knowledge of the ecology and environmental conditions suitable for individual species across the landscape is vital for effective conservation measures. Similarly, understanding demographic factors that influence the structure of animal populations is crucial for understanding species trends.

In this thesis, I explore one of the most interesting aspects that distinguishes the hazel dormouse (*Muscardinus avellanarius*) from other woodland small mammals - its ability to hibernate. Hibernation is a complex strategy with marked trade-offs that shapes the demography and structure of hazel dormouse populations and yet it is one of the least studied facets of their life cycle. Firstly, I introduce relevant background to the thesis. I evaluate different methods to locate hibernacula, investigate dormouse movements before hibernation, their behaviour as they prepare to face months of low activity at low temperatures and fewer foraging opportunities, to the point where they find a suitable place to build a nest to hibernate on the ground. I then examine population structure and estimate overwinter survival of different hazel dormouse populations.

Using telemetry, I found that hazel dormice select hibernation sites within their autumnal home range. I investigate the impact of hibernation on body weight of hazel dormice and quantify rates of weight loss in wild animals. With the use of high-resolution airborne LiDAR derived canopy structure and topography, I develop novel models to characterise hazel dormouse hibernaculum locations and predict suitable locations across the landscape. I demonstrate that topography, sky view and canopy height can influence hibernaculum location selection. At the hibernaculum location, I demonstrate how hazel dormouse hibernation nests are built in a similar fashion to their summer nests and that they utilise a range of materials that are available in the immediate vicinity of the selected hibernation site. I quantify hazel dormouse overwinter survival of different populations and find that on average 0.36 (0.29 - 0.44, 95% Confidence Intervals (CI) of the population survives.

My findings, based on the existing literature and evidence I collected in the field, suggests that hazel dormice are resourceful, able to cope with diverse habitat characteristics and resources. Conservation efforts should therefore focus on creating, managing and/or enhancing diversity within their habitat by promoting a varied canopy

structure that is well connected and made up of assorted tree and shrub species of value to the hazel dormice in order to increase nesting and foraging opportunities through the seasons.

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Tables and figures

Acknowledgements

One of the main reasons that led me to embark on my PhD is the incredible ability that the hazel dormouse has to attract interest and bring people together. Consequently, I have inevitably and gratefully, many, many individuals to thank for. This research has been an enjoyable journey and has certainly been so because of those that have been involved in some way or another as it would have been extremely challenging to reach this point by myself.

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To you.

Author’s declaration for co-authored manuscripts

Chapters 2, 3, 4 and 5 have been published or written for publication as co-authored academic papers. I developed the direction and research design for chapter 2 in conjunction with Jon Bennie (JB) and Fiona Mathews (FM), chapter 3 with JB, FM, Rob Wilson (RW) and Robbie McDonald (RM), chapter 4 with JB, FM, RW and RM and chapter 5 with JB and RM.

For chapter 2, I carried out the radio tracking exercise with the occasional assistance from volunteers. Radio collar tests were carried out at Paignton Zoo with assistance from the keepers and at Exeter University Streatham Campus with support from post graduate students. I carried out the systematic searches with contribution of five hibernaculum locations shared by licenced ecologists. FM and Katharine Evans carried out the dog searches led by chocolate Labrador Charlie Brown. I analysed the data with assistance from JB and RM.

For chapter 3, I designed the fieldwork in the UK with assistance from FM and conducted with assistance from helpers and volunteers. Data originated from the Netherlands was associated with an independent project planned by Pim Lemmers (PL), Maurice La Haye (MLH) and Ruud P. B. Foppen (RF) where fieldwork was carried out by PL and RF. Data was analysed by LG, with advice from FM, JB, RM and RW. Photographs in Figure 3.3a is credited to PL and Figure 3.3f to Lorna Griffiths.

For Chapter 4, I planned the fieldwork with Paul Chanin (PC), FM and RW and conducted it with the occasional assistance of volunteers. I analysed the data with advice from FM, JB and RW.

For chapter 5, I designed and conducted the field work with occasional assistance of trainees, volunteers, and co-workers. I analysed the data with assistance of JB and RM.

I wrote all 4 manuscripts and revised them in response to comments, suggestions and advice from JB, FM, RW, RM and other co-authors PC, PL, and RF.

Chapter 1

General Introduction

Chapter 1: General Introduction

The following chapters describe research on specific elements of the ecology and population biology of the hazel dormouse *Muscardinus avellanarius* and provide practical recommendations on habitat management and conservation of the species. The hazel dormouse is one of the most elusive mammals in the United Kingdom that has been identified as a species of conservation concern within most of its range. In the UK, the hazel dormouse is considered a charismatic species drawing attention from the general public and researchers as well as professional ecologists and amateur naturalists.

Before describing the contents of this research in detail I will address some broader concepts surrounding the core of this investigation that lead to the chapters of my thesis. Specifically, aspects of animal physiology and thermoregulation; dormancy as a strategy for energy saving; habitat selection in animals; the use of remote sensing for ecological studies, population biology and the impact that climate change can have on species and ecosystems.

Aspects of animal physiology and thermoregulation

Organisms depend on their biotic and/or abiotic environments for energy to survive, grow and reproduce. The processes controlling the uptake and use of food, nutrients and light by organisms and their use for maintenance, growth, maturation, and propagation are still not entirely understood and are a matter of much debate amongst scientists (Kooijman & Kooijman 2010). However, it is generally accepted that physiological processes involved in the uptake of resources are optimised within a narrow range of body temperatures. Vertebrates have two different strategies to maintain body temperatures within this range: endothermy and ectothermy.

Endothermy is the maintenance of a high and constant body temperature by metabolic means. It is considered an adaptation of great significance and a key transition in vertebrate evolution (Bennett & Ruben 1979, Grigg et al. 2004). The ability to maintain constant body temperature around 37 ^{o}C even at rest, provide tachymetabolic endotherms (birds and mammals) with an advantage over ectothermic species, such as fishes, reptiles and amphibians whose regulation of body temperature depends on external sources, to consistently function at optimal physical performance over a wide range of ambient temperatures. Ectotherms are susceptible to ambient temperatures often outside their optimal body temperature and rely on external sources of heat such as sunlight or a heated rock surface, to achieve their operational body temperature or to cool down, which can result in restrictions in performance and/or activity levels during different times of the day. In terrestrial ectotherms in particular, the reliance on external sources leads to geographical restrictions since most species live in tropical or desert areas, where thermoregulatory priorities are keeping cool rather than staying warm (Kearney et al. 2009).

Many models have been developed to explore different aspects in thermoregulation in vertebrates such as body mass growth (Werner et al. 2018), metabolic rate (White et al. 2005), feeding rate and offspring development (Węgrzyn 2013) but as suggested by Buckley et al (2012), it is likely that differences in thermal physiology affect how organisms interact with and are constrained by their environment.

The advantage of endothermy over ectothermy is particularly evident at low temperatures, where animals can enhance their rate of heat production in proportion to the rate of heat loss to maintain body temperature at a desired level (Heldmaier et al. 2004) enabling them to extend daily activities into the night, increase capacity for sustained activity, sustain higher digestion rates (Grigg et al. 2004) and improved parental care (Farmer 2000).

However, endothermy is a high-cost strategy that requires continuous maintenance of internal body temperature by metabolic processes that is only possible by constant food intake (Clarke & Pörtner 2010). By assessing the metabolic capacity for energy production in liver, heart, brain, and kidney in both lizard and mouse, Else and Hulbert (1981) suggested that endotherms (mouse) require about eight times as much energy as ectotherms when compared at the same body size and temperature.

Bennett & Ruben (1979) suggested that the fact that the evolution of endothermy required substantial restructuring of many systems of the vertebrate body indicates that selective factors must have been great to result in such discrepancy in the physiology and behaviour of two groups of vertebrates.

Dormancy as an energy saving strategy

To minimise the amount of energy spent in thermoregulation, some endotherms are able to suspend the maintenance of high body temperature by allowing it to drop considerably during unfavourable biotic conditions such as drought, cold weather and food shortage. The high thermoregulatory cost has been suggested as being one of the reasons why not all mammals and birds are permanently homeothermic (i.e. constantly maintaining high body temperatures (T_b)), but during low ambient temperatures (T_a) at certain times of the day or the year enter a state of torpor (Lyman 2013, Boyer & Barnes 1999). This energy saving approach, as suggested by (Schmidt-Nielsen 1997), offers an alternative solution to animals that are not able to escape harsh environmental conditions by migration and is used by many birds and mammals that employ hypometabolism, i.e. periods of profoundly reduced metabolic rate (MR) and T_b. Such periods of low metabolic rate are known as dormancy and have been observed in a wide range of taxa from plants to insects and to microbial organisms to phytoplankton (Lennon & Jones 2011, Bewley 1997, Lyman 2013). In mammals, three major forms of dormancy have been classified: torpor, hibernation and estivation (or aestivation).

Several authors have attempted to differentiate hibernation, daily torpor and estivation based on ecological and physiological parameters and it is widely recognised by most that they are in fact different distinct strategies of dormancy (Ruf & Geiser 2015, Lyman 2013, Geiser 2004) as opposed to only minor differences of the same strategy (Wang 1978, Bartholomew & MacMillen 1961).

Hibernation or deep torpor and (daily) torpor share similarities but have been treated as different patterns of heterothermia. Torpor in heterothermic endotherms is characterized by a controlled reduction of T_b, MR, and other physiological functions. The T_b during torpor falls from high normothermic values of around 32°C to 42°C to values between −3°C to <30°C, and the minimum torpid metabolic rate (TMR) is on average reduced to 5–30% of the basal metabolic rate (BMR, Ruf & Geiser 2015, Barnes 1989). In some species, entering torpor can lead to a TMR of less than 1% of the normothermic resting metabolic rate (RMR) at low T_a, highlighting the effectiveness of torpor in reducing MR (Geiser 2004).

Daily torpor in endotherms is limited to a duration of less than 24 hours and is normally followed by continued foraging. Hibernation, on the other hand, is characterised by reduced MR and T_b near T_a over prolonged times under low temperatures. During this state, animals enter a state of deep torpor that last from consecutive days to several weeks and are reliant either on stored food caches or body energy reserves built up in preparation for hibernation.

The third form of dormancy is estivation. It has been observed in several taxa including mammals, molluscs and amphibians under dry and hot environment conditions. Similar to hibernation and torpor, estivation is characterised by a reduction of MR (Hinds & MacMillen 1985). It may not be entirely associated with shortage of food supply issues, as with hibernation, but as a response to unfavourable biotic conditions such as extreme heat and drought that makes it difficult or impossible for the animal to survive.

Different combinations of dormancy, such as hibernation or estivation as well as daily torpor, have been observed in some animal species including bats (Hock 1951, Jonasson & Willis 2012), some squirrels (Shaw 1921, Shaw 1925, Bartholomew et al. 1970, Bartholomew & Hudson 1960) and mice (Bartholomew & Cade 1957, Bartholomew & MacMillen 1961). One species in particular, the edible dormouse (*Glis glis*), has shown the ability to display all three forms of dormancy (Wilz 1999) and was the subject of an in depth investigation suggesting that all three forms of dormancy are based on the same physiological mechanism of thermal and metabolic regulation (Wilz & Heldmaier 2000).

According to Bradshaw & Holzapfel (2006), the main effect of climate warming on biotic systems results from increasing the length of the growing season and altering the optimal time for life-history transitions such as development, reproduction, dormancy and migration. Dormancy, in a rapidly changing climate, may be an important adaptation for animals that may enable those capable of such physiological changes to cope with arising unfavourable conditions.

Habitat selection in animals

Adequate resources within habitats are required to sustain animal populations. It is particularly important for conservation purposes to identify what these resources are in order to preserve species, especially those that are endangered or rare. Establishing the resources that are selected more often than others provide fundamental information about the nature of animals and how they met their requirements for survival (Manly et al. 2007). According to Boyce & McDonald (1999), habitat selection is a behavioural consequence of animals actively selecting where they live, or passively persisting in certain habitats.

Different species have different resource requirements, and this differential is thought to be one of the principal relationships which permit species to coexist (Rosenzweig 1981). It is often assumed that a species will select and use resources that best match their needs, depending on the balance between rewards and risks (Mayor et al. 2009), and that high quality resources are preferred over lower quality ones.

Resource usage is defined as the quantity of a given resource that is utilised by an animal, or populations of animals, in a fixed period of time, while resource availability is the quantity accessible to the animal or populations of animals during that same period of time (Boyce et al. 1999, Boyce & McDonald 1999). Resource availability in nature is not uniformly distributed and resource usage is related to how available they are. Selective use of resources occurs when they are sought out disproportionately to their availability.

The way resources are used is a consequence of the influence of selection on survival and reproduction, and the connection between habitat characteristics with organisms' life history strategies, which determines fitness in various habitats (Southwood 1977). Based on this view of habitat centred ecological systems, Fretwell and Lucas (1969) suggested that the extent of habitat use is directly associated with the quality and abundance of resources in those areas, which in turn reflects fitness in that habitat, although there is no guarantee that the presence of individuals in a given habitat is positively related to its quality (Van Horne 1983).

Resource selection and preference are often used as synonyms in the wider literature, but some authors defend the clear differentiation between the two terms: selection being the process in which an animal chooses a resource, and preference is the likelihood that a resource will be selected if offered on an equal basis with others (Johnson 1980). The literature on resource selection functions has its origins over forty years ago by Johnson (1980) and followed by another influential text on the subject published years later by Manly et al. (2007).

The main habitat selection concept, as it stands today, is based on the assumption that organisms select habitat at multiple hierarchical levels and at different spatial and/or temporal scales (Manly et al. 2007, Mayor et al. 2009). The scales within habitat selection are well explained and simplified by Mayor et al. (2009) where they state that an animal eating the leaves of a plant is using that plant part, that individual plant, that patch, that vegetation community, landscape, population range, species range, and so on, the animal may be selecting a habitat at only one or a few of these levels. McGarigal et al. (2016) considered that the main conceptual origins of the multi-scale perspective include: a) space and time scaling of ecological systems pioneered by Stommel (1963), where ecological patterns and processes interact across scales in space and time, such that as the spatial scale of the phenomenon increases so does the temporal scale over which it operates; b) organism centred perspective (Wiens 1989), which removes our own anthropocentric conception of environmental scale and concentrates on the perceptions of organisms; c) multi-level habitat selection (Johnson 1980), originates from the first two concepts and presents these ideas in a multiscale, hierarchical framework; and d) the “ecological neighbourhood” of an organism for a given ecological process is the region within which that organism is active or has some influence during the appropriate period of time (Addicott et al. 1987).

Another important element in habitat selection are the density-dependent theories, which are essential to our understanding of population dynamics, spatial distribution and dispersal, species interactions, niche evolution, patch use, and speciation (see review in Morris 2003). The idea behind these theories is that consumer habitat selection patterns often vary with consumer abundance, as discussed by Morris (1987) and Rosenzweig (1981, 1991). With an increase in consumer density, resources within preferred habitats can become restricted due to exploitation through intra competition, so that it can be beneficial for consumers to become less selective in their habitat use by including habitats of lower quality in their space use (Avgar et al. 2020).

Habitat selection therefore is to be understood as a mixture of complex behavioural and environmental processes and that habitat use (e.g. the use of specific sites as basking places, as hibernaculum, foraging grounds or nesting spots) is the outcome of the habitat selection processes. Most of the studies published in the literature on resource selection are related to food (i.e. prey species, size, colour, shape) or habitat selection, which may be among discrete habitat categories (open field, forest, pond) or among continuous array of habitat attributes such as plant density, canopy height/cover, water depth, temperature, shade, etc. (Manly et al. 2007, Viejou et al. 2018, Bearman-Brown et al. 2020).

The use of remote sensing for ecological studies

Ecological research involves the investigation of organisms and their physical environment. Traditionally, this has been achieved by the manual collection of data observations in the field, where scientists observe variability across time and space in the abiotic and biotic components of ecosystems (McIntosh 1986). This approach can be labour intensive and generally unfeasible over large areas (Aplin 2005). Early ecologists did not have the technology or concepts to explicitly deal with spatial heterogeneity and there was a tendency to develop explanations by grouping organisms into uniform and recognisable units, using models that treated the environment as spatially homogeneous (Clark 2010).

During the 1980s, advances in technology and the increased accessibility of computing, revolutionised the way data in ecological research is analysed. This rapid development allowed more complexity in research questions being asked, empirical methods used, studies conducted, and interpretations offered (Crowley 1992). Gradually, the type, quality, quantity, and availability of data for ecological research also changed. In a relatively short space of time, ecologists gained access to remote sensing technology, satellite and aerial imagery, geographic information systems, and spatial statistical methods (Dale & Fortin 2014), enabling them to observe and analyse spatial heterogeneity, ranging from local habitats to entire continents (Clark 2010). This new emphasis on broad spatial scales and the ecological effects of the spatial patterning of ecosystems led to the emergence of landscape ecology as a sub-discipline within ecology (Turner 1989, Wu & Loucks 1995, Naveh & Lieberman 2013, Risser 1987, Wiens 1989)

Remote sensing was quickly adopted by the scientific community because of its potential for ecological research (Roughgarden et al. 1991). Remote sensing is an effective tool for conducting ecological investigation at landscape scale (Frohn 2018), that has transformed the monitoring of life on Earth by revealing spatial and temporal dimensions of biological diversity through structural, compositional and functional measurements of ecosystems (Cavender-Bares et al. 2022). Early remote sensing systems produced imagery that averaged information over tens or even hundreds of square meters, which is useful for broad scale habitat mapping, but considered too coarse for detailed investigations (Turner et al. 2003).

The need to assess and predict ecosystem responses to global environmental change and its impacts on biodiversity (Bonan & Doney 2018) as well as human well-being (Pettorelli et al. 2014) are high priority targets for the scientific community. With rapid emergence of new technologies, from drones to airborne laser scanning and new satellite sensors providing imagery with very high resolution, new opportunities for monitoring the state of biodiversity and ecosystems are being opened (Vihervaara et al. 2017, Nagendra 2001) and remote sensing has now established itself as an indispensable technology for this purpose (Sánchez-Díaz & Mata-Zayas 2019).

Since the beginning of this century, much research has focused on mapping species distribution and using the resulting information to identify habitat availability and suitability (Hao et al. 2019, Booth 2018, Gomes et al. 2018, Randin et al. 2020). Accurate distribution models require spatial predictor variables that are relevant to the species being studied and are described at a relevant spatial scale (Franklin 2010, Franklin 1995). As such, climate and topographic data have been increasingly applied in the modelling of species distribution and habitats (Franklin 2010, Title & Bemmels 2018, Lembrechts et al. 2019a). One of the recent developments in the ever improving quality of remotely sensed data is airborne Light Detection and Ranging (LiDAR) technology from which high resolution structural and topographic data can be extracted (He et al. 2015, Dong & Chen 2017). The LiDAR derived fine scale data allows for microclimate investigations and associated species distribution across vast areas of the landscape (Lembrechts et al. 2019b, Zellweger et al. 2019, Rhodes et al. 2022).

Population Biology

Population is defined as a group of individuals of the same species that have a high probability of interacting with each other and population biology is basically the study of biological populations (Hastings 2013). It emerged in the 1960s from different areas of natural history including taxonomy and spatial distribution of organisms, their ecology and behaviour, and studies of heredity and hypothesis that organisms are related by descent (Neal 2018). Population biology implies that populations have two components: a genetic one (individuals belong to the same species) and a spatial one (individuals live in the same area) whilst recognising genetic and spatial heterogeneity (Silvertown & Charlesworth 2009).

Population biology employs the traditional empirical approach of observing the numbers of individuals in a population with the purpose to detect temporal and spatial changes, as well as the measurement of abiotic factors and biotic factors that may affect population numbers (Hastings 2013). For this purpose of understanding, explaining, and predicting dynamics of population biology, mathematical models are necessary (Thieme 2018).

As summarised by Silvertown and Charlesworth (2009), the essence of population biology can be explained by a simple equation that relates the number of individuals per unity area of an organism N_t at some time t to the numbers N_{t+1} time unit (e.g. year) later:

$$N_{t+1} = N_t + B - D + I - E,$$

Where B is the number of births, D the number of deaths and I and E refer to immigration and emigration respectively. B, D, I and E are known as demographic parameters central to population dynamics as well as evolution.

Whilst the above equation is relatively simple, a plethora of mathematical models have been developed over the years for numerous applications associated with the complexities of population biology (Levin et al. 1997). Of special interest is demography, the statistical study of populations that focuses on how vital rates, such as fecundity, population growth, dispersal and mortality, influence population processes (Boyce et al. 2006) and are essential for understanding species trends (Beissinger & Westphal 1998, Lebreton et al. 1992, Mills 2012b). Amongst other important vital rates, survival of individuals is one of the pivotal determinants of population dynamics that should be monitored in both threatened and recovering populations (Väli et al. 2021). Life-history theory assumes increased mortality at key life stages such as hibernation and yet variation of survival rates of hibernating mammals has rarely been estimated (Sendor & Simon 2003) and remains a gap in the knowledge on the ecology of many species that adopt hibernation as a survival strategy.

Climate change and effects on biodiversity

Human activities, such as habitat loss, habitat fragmentation, pollution, invasive species and over exploitation, impose an increased pressure on species and ecosystems of the Earth (Barnosky et al. 2011, Steffen et al. 2007, Tilman et al. 2017). Already, 26% of all mammal species, 13% of all bird species as well as 40% of plant species are threatened with extinction (Antonelli et al. 2020).

The scale of impact of human activities on the Earth system including land surface transformation and changing the composition of the atmosphere, has led to the suggestion by some authors that we have entered a new geological epoch, the Anthropocene epoch which marks the end of the Holocene as it is currently formally referred to (Crutzen 2006). Despite detailed reviews of the evidence, the status of this new geological epoch is unclear. Lewis & Maslin (2015) suggested that, out of the various proposed dates, two do appear to conform to the criteria to mark the beginning of the Anthropocene: 1610 and 1964. Despite this ambiguity, human induced changes to the natural environment increased dramatically from about 1950 onwards. The change in magnitude and rate of the human imprint increased sharply towards the end of the twentieth century making this period, also known as the Great Acceleration (Hibbard et al. 2006), the most rapid transformation of the human relationship with the natural world in the history of humankind (Steffen et al. 2006).

Amongst these pressures and impacts imposed by human activities, studies suggest that climate change is emerging as one of the most significant factors that could surpass habitat loss as the greatest global threat to biodiversity over the next several decades (Leadley et al. 2010). Climate change, however, is not a new topic in science and its biological impacts have long been described in scientific literature earning its first mentions in the early 1900’s following many years of observation of range shifts in parallel with changes in climatic conditions (Parmesan 2006).

A global analysis focused on greenhouse gas emissions involving >75,000 common and widespread species of terrestrial plants, birds, mammals, reptiles, and amphibians shows that without mitigation, 57±6% of plants and 34±7% of animals are likely to lose ≥50% of their present climatic range by the 2080s (Warren et al. 2013). If mitigation is considered (effective reduction in emissions of greenhouse gases), Warren et al. (2013) indicated that losses can be reduced by 60% if emissions peak in 2016 or 40% if emissions peak in 2030.

In Europe, potential socio-economic change imposed by high end climate change is thought to pose high risks to biodiversity across the continent. Under the current scenario, it is likely that land-use change will be unavoidable giving rise to considerable risk of major transformations of many ecosystems in southern Europe (Berry et al. 2017).

Currently, as reviewed by Bellard et al. (2012), there are various effects originating from climate change that are anticipated to affect all levels of biodiversity, from organism to biome level; concerning various strengths and forms of fitness decrease on individuals, populations, species, ecological networks and ecosystems. These effects tend to trigger species responses to climate change challenges by shifting their climatic niche along three non-exclusive axes: time (e.g., phenology), space (e.g., range) and self (e.g., physiology).

It is expected that with increased temperatures, especially around the equator, climate change will force a shift of species distributions (e.g. range) towards higher latitudes, leading to extinctions of species unable to adapt or move to more appropriate conditions. Already, there is compelling evidence that this is occurring with several species (Parmesan & Yohe 2003). The lack of suitable habitat and/or habitat connectivity may present a serious concern for endemic species, many of which are already conservation priorities, as they are often restricted to specific geographic range and cannot be replaced with taxa from elsewhere (Leadley et al. 2010).

One of the methods used to assess impact of climate change in biodiversity has been niche-based models. These models are based on statistical relationships between spatial distributions of plant or animal species and key environmental factors controlling their distribution such as temperature, precipitation, etc. Although there are limitations, such as lack of species migration, inter-specific interactions, key environmental factors controlling distributions (e.g., rising CO_2 concentrations for plants) and adaptive mechanisms (Thuiller et al. 2008), niche-based models are extremely useful when using climate variables to predict species range when taking account their own caveats. Another approach is the use of species-specific, process-based models used to predict the response of an individual or a population to environmental conditions by incorporating biological processes with incorporated observations on individuals in natural populations. Because of existing limitations in both methods, Morin & Thuiller (2009) demonstrated that both approaches can be used together to obtain more robust results and that comparisons among models are recommended to increase accuracy of predictions regarding range shifts under climate change.

Models have also been used to predict species extinctions associated with a changing climate. However, because of differences in approaches, predictions about extinctions risks vary greatly and some studies have suggested that 0 to 54% of species could become extinct because of climate change (Foden et al. 2013, Thomas et al. 2004, Malcolm et al. 2006, Warren et al. 2013). Despite the lack of modelling consistency, Urban (2015) pointed out that extinction risks were highest in South America, Australia, and New Zealand, that risks did not vary by taxonomic group and realistic assumptions about extinction debt and dispersal capacity substantially increased extinction risks.

With the predicted warming climate, species need to adapt and this will result in populations needing to shift their distribution of phenotypes such that the average fitness for the shifted phenotypic distribution is higher than that of the original distribution when compared within the current environment. For each individual species, the magnitude of ecological consequences will be strongly related to their adaptation rate to the changing environment (Visser 2008).

The change in seasonality, that is, the difference over time in the timing of climatic events, resulting from climate change can lead to populations altering the timing of seasonal activities such as migration, flowering, dormancy or breeding, with potential consequences for the demography and population dynamics of species and communities. These time-sensitive relationships may in turn alter the rates of reproduction and survival, leading some populations to decline and others to increase in abundance (Miller-Rushing et al. 2010).

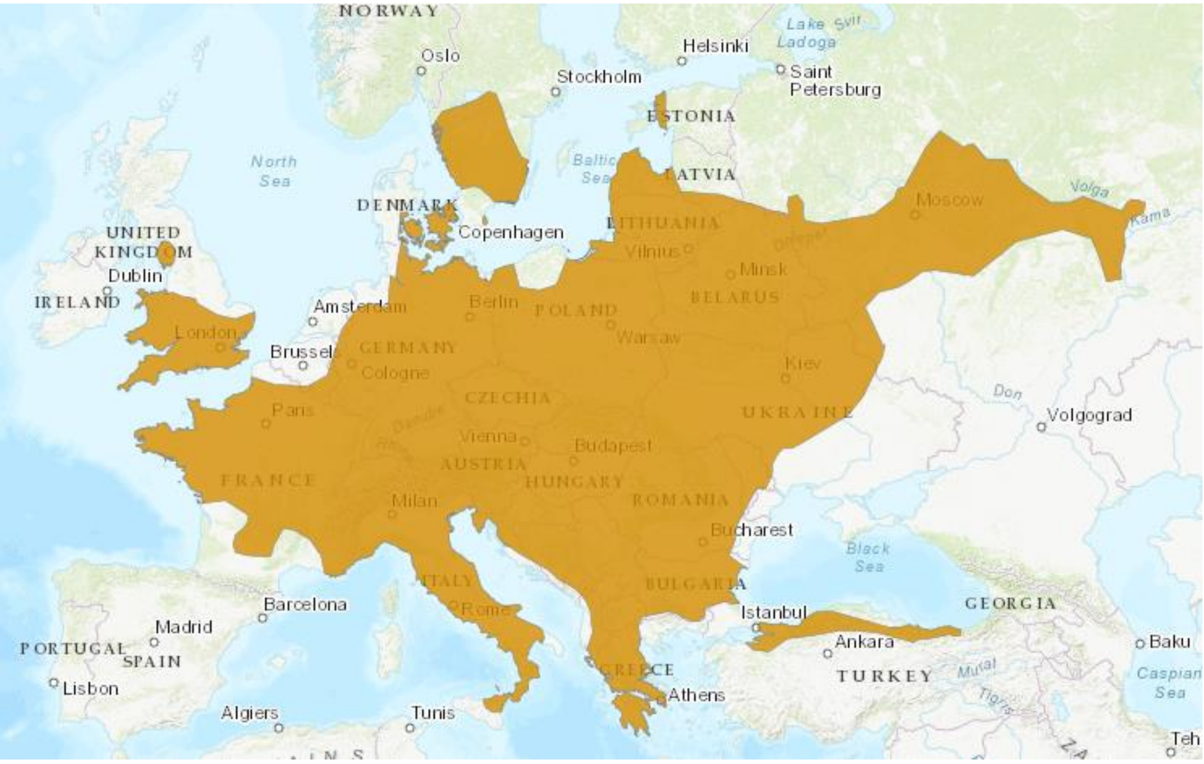
The Hazel Dormouse

The hazel dormouse *Muscardinus avellanarius* (Linnaeus 1758) is a small rodent member of the family *Gliridae*, which comprises 26 species grouped in nine genera, and the only extant member of the *Muscardinus* genus (Daams & De Bruijn 1995). The word dormouse comes from the French word “dormir” – to sleep, for their long, dormant hibernation period that can last several months. It is a nocturnal and arboreal species of golden fur and large black eyes with a head to tail length of between 115 and 164 mm and weight around 15-30 grams (Morris 2004).

The geographic range of the hazel dormouse (Fig 1.1) covers large parts of Europe, but it is absent from Iberia, south-west France, and northern parts of Fennoscandia and Russia. It is also absent from eastern Ukraine and southern Russia. Island populations occur in southern Britain, Corfu and Sicily (Morris 1999, Rossolimo et al. 2001). In the Alps it occurs up to 1,920 m (Spitzenberger & Bauer 2001).

Across its distributional range, the hazel dormouse is considered a threatened species and in Europe is protected under Annex IV of the Habitat and Species Directive of the European Union (1992) and Appendix III of the Bern Convention (1979). In the UK, it is considered rare and vulnerable to extinction, receiving protection under Schedule 5 of the Wildlife and Countryside Act 1981 (as amended) and in England, the hazel dormouse is included in Section 41 of the Natural Environmental and Rural Act 2006 as a species of conservation concern. However, following an assessment in 2009, the status of the species in the IUCN Red List of Threatened Species was revised from “Near Threatened’ to “Least Concern” (Hutterer et al. 2021).

Figure 1.1. *Map of the geographical range of the hazel dormouse, in ochre, according to Hutterer et al (2021).*



Because of its relatively large range and occurrence in diverse environmental conditions, the hazel dormouse has been associated with a variety of habitats; a topic that has been the subject of much research in many countries (e.g. Bright & Morris 1990, Berg & Berg 1998, Juškaitis 2003b, Juškaitis 2007, Panchetti et al. 2007, Wuttke et al. 2012, Vilhelmsen 1996, Verbeylen 2006, Hecker et al. 2003). As summarised by Juškaitis (2014a), the hazel dormouse is mostly a woodland species, inhabiting deciduous or mixed deciduous-coniferous forests with a well-developed understorey but also found in other habitats such as heathland and culm grasslands (Chanin & Woods 2003), low growing scrub and reed (Bright & Morris 1990), along roadside (Chanin & Gubert 2012, Schulz et al. 2012) and railway planting (Verbeylen 2006), commercial conifer plantations (Trout et al. 2012a) and hedgerows (Wolton 2009, Ehlers 2012).

The population density of the hazel dormouse varies according to habitat type and quality (Berg & Berg 1999, Sara et al. 2001, Juškaitis 2003b), and animals are generally found in low numbers even in the best habitats (Bright & Morris 1996). In Britain, there are normally three to five (but sometimes up to 10) adults per hectare in early summer but the average, including suboptimal habitats, is 2.2 animals per hectare (Bright et al. 2006).

The dormouse is considered a *K*-strategist (Pianka 1970), a relatively long living species compared to other non-flying terrestrial mammals, with a life span of up to six years in the wild (Juškaitis 2014a). Within its British range, the dormouse year starts when animals awake from hibernation sometime between early March and the end of April but can be as late as May (Bright & Morris 1996). Although breeding may start immediately (Juškaitis 1999), juveniles are born after a gestation period of 22-25 days from early June until September in Britain (Bright et al. 2006) but occasionally from as early as May and as late as October (Gubert *pers. obs.*). Female dormice produce between one and two litters a year with an average of four juveniles per litter (Morris 2004). Juveniles become independent from their mothers at the age of 35-45 days (Likhachev 1966, Slastionenko 1990). Once independent, juvenile hazel dormice normally disperse, a phenomenon characteristic of the species in Lithuania that normally lasts a month (Juškaitis 1997, Juškaitis 2014a). Despite being an arboreal species of low dispersal ability (Dietz et al. 2018), that tends to avoid movements on open ground (Bright & Morris 1996), maximum recorded distances travelled by hazel dormice can be over a few kilometres (see summary in Juškaitis 2014).

During the active season, from spring until mid-autumn in Britain, the hazel dormouse forages in different strata of their three-dimensional habitat, moving to different feeding sites according to food availability as the season progresses (Bright & Morris 1991, Bright & Morris 1992). Faecal analysis from a study site in South Devon, England (Richards et al. 1984) revealed a varied omnivorous diet that includes insects (aphids and caterpillars), leaves, flowers (pollen and nectar), and fruit (berries and nuts). In the autumn, outside its Mediterranean range, dormice prepare for the hibernation season by accumulating fat reserves to maintain vital bodily functions through the period of inactivity (Juškaitis 2001, Morris 2004).

Figure 1.2. *Male and female hazel dormouse in torpor, photographed in the spring during the breeding season as part of nest box monitoring surveys in Devon, England.*

By mid to late autumn, in response to shortening photoperiod and lower ambient temperatures, hazel dormice build a nest on the ground to hibernate. They seek a cool and moist place where temperatures remain stable (Bright et al. 2006). During hibernation, the hazel dormouse body temperature will track that of the environment to save energy adjusting metabolic rates to just above freezing (Csorba 2003). Individuals may arouse in response to higher temperatures, a process of high energy cost that can speed the consumption of fat reserves by a raised metabolic rate (Bright & Morris 1996, Mills 2012a). Exhausting fat reserves before the end of the winter can increase mortality and affect populations (Juškaitis 1999, Reiners et al. 2012).

Even though hazel dormice and their habitat are fully protected in Britain, the population has been experiencing a steady decline since the 1990s for reasons that are not well understood (Goodwin et al. 2017). Despite extensive research on the hazel dormouse in the last 30 years, there remain many gaps in our understanding, particularly around the hibernation aspect of their ecology. As a species of principal importance that generates great public interest in Britain (Morris 2003), its distinct life stages make the hazel dormouse a good model to investigate the effects of a changing climate on individuals and at population level. Specifically, how increasingly warmer temperatures may influence habitat selection, affect population dynamics, and overwinter survival probabilities of a species that has evolved to hibernate during times of lower availability and quality of food sources. As an adopted flagship species for woodland habitat conservation (Bright et al. 2006) and habitat requirements that include successional food supply through the seasons, the hazel dormouse has a role of indicator for the monitoring of habitat and community status in the face of ongoing changes in environmental conditions.

Outline of the thesis

Whilst the hazel dormouse is a popular and charismatic species that has been the subject of much research across it range, some key aspects of its ecology is still virtually unknown. Despite all the effort by the scientific community so far, hazel dormouse populations are declining in many countries. As such, the main objective of this thesis is to delve into some of the least studied aspects of hazel dormouse ecology to fill some obvious gaps in existing knowledge whilst making the most of technological advances and latest research to ultimately benefit the conservation of the species.

In brief, I aim to:

I. Evaluate different methods of detecting hazel dormouse hibernacula in the wild, establish whether hibernation takes place within home range and assess the impact of hibernation on body mass.

II. Develop a novel method of characterising hibernaculum locations of the hazel dormouse using remotely sensed data.

III. Investigate the structure and materials of hazel dormouse hibernation nests.

IV. Assess methodology to estimate dormouse overwinter survival.

I will approach these aims based on field data collected by myself, volunteers and in collaboration with other researchers using high resolution remote sensed LiDAR data, specialist software and telemetry. Following this introduction, the thesis has been structured in four chapters followed by a conclusion summarising main points of this research.

In Chapter 2, different methods of locating dormouse hibernacula in the wild are tried and evaluated including telemetry, systematic searches, and wildlife detection dogs. The use of telemetry allowed me to assess movement prior and during the hibernation period as well as examine changes in body mass during the hibernation period.

In Chapter 3, I use the hibernaculum data I collected from the field, together with contributions from professional ecologists and researchers in the Netherlands to design a novel approach to characterise hibernaculum location using high resolution remote sensed LiDAR data. I do this by using specific computer software and GIS tools to analyse the data and develop predictive models capable of identifying suitable locations for dormouse hibernation.

In Chapter 4, I investigate whether hibernation nest materials are a limiting factor for hibernaculum site selection, examine the structure of winter nests, identify the different types of nest materials used and establish how far dormice travel to collect them. This chapter was published by Journal of Zoology in 2022.

In Chapter 5, I investigate hazel dormouse apparent survival and recapture rates based on field data I collected at four different sites using capture-mark-recapture techniques and then analysed it using open population models to investigate how populations change over time.

In Chapter 6, I summarise the findings of my work and place it in the wider context of hazel dormouse ecology. I also discuss the implication of my research on the conservation of the species and make pragmatic suggestions for methodologies involving habitat management and forestry practices.

Chapter 2

Ecology and behaviour of the hazel dormouse *Muscardinus avellanarius* prior to and during the hibernation period

Chapter 2: Ecology and behaviour of the hazel dormouse *Muscardinus avellanarius* prior to and during the hibernation period

Abstract

The hazel dormouse is a mainly and arboreal species with nocturnal habits that, in northern European countries, move down to the ground to hibernate in the autumn where they stay until spring at locations not well understood. To prepare for hibernation, dormice accumulate fat reserves necessary to maintain vital bodily functions when food supply is lower and the energy cost of staying active supersedes the amount of energy that can be harvested in their habitat.

In this study, different methods to identify dormouse hibernacula were used: telemetry, systematic searches, and wildlife detection dogs. As part of the telemetry exercise, the movements of 31 individuals prior to and during hibernation were observed. Weight measurements of eight wild hazel dormice were recorded during the hibernation period and the rate of weight loss of each individual calculated as proportion of body mass per day.

A total of 44 hazel dormouse hibernacula were identified: 24 by telemetry, 20 by systematic searches and none by wildlife detection dogs. Telemetry results indicated that dormice selected sites for their hibernaculum within 43 m (SD=30) from the place where they were captured while active, suggesting that hibernation normally takes place within their home range. The timing of hibernation varied amongst individuals, with some dormice remaining active and feeding throughout the month of December. On average dormice lost 0.47% of their body mass per day during hibernation bouts

Despite dormice hibernating largely in leaf litter on the woodland floor, often at conspicuous locations, detecting hibernacula without the use of telemetry proved labour intensive but nevertheless effective through systematic searches. The fact that hazel dormice lose a relatively high proportion of their body mass during the winter highlights the challenges wild animals face to survive hibernation.

Introduction

The hazel dormouse is known for its ability to hibernate for long periods of time in temperate climates, but hibernation is still one of the least known aspects of the species' ecology. The hibernation season marks the end of the dormouse year: after litters are born in the spring and summer, young dormice remain dependent on their mothers for around four weeks before being fully weaned. Juveniles then start venturing away from the nest and foraging in the canopy to continue their development and prepare for the winter months to come (Bright & Morris 1996).

Adult dormice are primarily arboreal rodents; they are relatively sedentary and have home ranges of around 0.5–1.0 ha during the active season (Bright & Morris 1991, Goodwin et al. 2018, Juškaitis 1997). Juveniles generally settle in their permanent home ranges in the autumn of the year in which they are born. Most research on the species' movements and dispersal in temperate climates is focused on the active season between spring and autumn (Juškaitis 1997, Bright & Morris 1991). During this period, travelled distances between summer nest sites accounting for hundreds of metres have been reported, particularly by juveniles that are born earlier in the year (see summary in Juškaitis 2014a). Hazel dormice typically build natural nests in thick scrub, hollows and crevices in shrubs and trees and along hedgerows feeding on different foods varying with their availability throughout the year – feeding on insects, pollen, nectar, fruits, nuts, seeds, etc. (Juškaitis & Siozinyte 2008, Bright & Morris 1993).

At the end of the year, when food supply is low and the energy cost of staying active exceeds the amount of energy that can be harvested in their habitat, hazel dormice hibernate (Bright et al. 2006). For that purpose, hazel dormice abandon their usual arboreal behaviour to find a suitable location on the ground in which to hibernate, although little is known about how far they travel to find such places. In the United Kingdom, it is thought that hibernation takes place between October and May. In preparation for the winter, hazel dormice increase their body weight by accumulating fat reserves to increase their chances of survival, a task that is normally achieved by mid-autumn (Bright & Morris 1996). This influence of body weight and surviving hibernation is supported by a study of captive animals by Csorba (2003) suggesting that initial body weight is critical and attributed that the 44% mortality rate overwinter (n=18) were from animals weighing <15g (predation excluded). A similar long-term study on the mortality of wild hazel dormice based on capture-mark-recapture methodology using nest boxes in Lithuania suggests that 64%-72% of the populations do not survive the winter months due to starvation (e.g. animals failing to accumulate enough fat reserves) and predation (Juškaitis 1999), with animals losing on average 33% of their body weight over the hibernation period.

Once on the ground, hazel dormice build nests for individual use (Vogel & Frey 1995). These nests are constructed in a similar way to the ones built in the canopy earlier in the year, using locally sourced materials (Verbeylen et al. 2017, Gubert et al. 2022) and can be occupied for several months of the duration of hibernation (Juškaitis 2014a).

Although there has been some research on dormouse hibernation, many studies have focused on the physiology of hibernation in captive animals (Walhovd 1976, Walhovd & Jensen 1976, Pretzlaff et al. 2021). Others describe where winter nests have been found (Verbeylen et al. 2017, Bright 1992) as well as the size of winter nests (Kahmann & von Frisch 1950, Vogel & Frey 1995). Little is known about their behaviour in the wild - from the moment they stop using artificial nests boxes and tubes and natural summer nests, until the following spring when they emerge and become active once again. In particular, dormouse movements and dispersal between the autumn and spring is largely unknown and, apart from Lemmers et al. (2022), there is virtually no published information about the distance between summer nest sites and hibernaculum.

A key challenge in studying wild hibernating dormice is the difficulty of finding their hibernacula in the wild. Because of their low density and the inconspicuous nature of their hibernation nests, it is not an easy task and has historically been recorded through incidental finds by people involved in woodland management or recreation. There have also been many anecdotal reports of hibernating animals being found in garden sheds, flowerpots, compost heaps, and other unusual locations (Juškaitis & Büchner 2013). Identifying hazel dormouse hibernacula in the wild is not only useful for understanding the species' ecology, but also has crucial implications when it comes to its conservation. With hibernation being one of the key stages of the hazel dormouse life cycle, habitat disturbance during this period can greatly affect overwinter survival rates (Trout et al. 2012b). Whilst in hibernation, hazel dormice are unable to immediately react to any disturbance their hibernacula and are as vulnerable to predators as they are to trampling by domestic animals or human activities, such as recreation or woodland management (Bright & Morris 1996). It is during the hibernation season in the autumn and winter months that most woodland management and forestry operations take place to avoid other ecological constraints such as bird nesting season. Development activities, such as housing and large infrastructure projects can also lead to further habitat loss, fragmentation, and disturbance.

Many studies on hazel dormice ecology during the active season, such as investigations on home ranges, foraging habits and habitat preferences, have successfully employed telemetry (see summary in Juškaitis 2014a) and also, to a lesser extent, used as a way to locate hibernacula in the last 30 years (Verbeylen et al. 2017, Bright & Morris 1996, Lemmers 2022). This technique, using the transmission of radio signals to locate transmitters fitted to wild hazel dormice, might be helpful in addressing gaps in behaviour during the period prior to hibernation, particularly with respect to the use of resting places and ranging.

Systematically searching for hibernacula is another method that has recently become more widely used for development purposes in the last ten years or so in the UK. These involve ground “fingertip” searches of suitable habitats during the hibernation season prior to habitat clearance and is often a condition of project specific derogation licences to minimise the risk of death or injury to hibernating animals.

Although there is little published information from the UK on the use of wildlife detection dogs and ecological monitoring surveys, there is substantial collective evidence that trained dogs can be an effective tool in detecting several different species of mammals. Detection dogs have been used on species such as bush dogs in South America (Dematteo et al. 2009), bats and hedgehogs in the United Kingdom and North America (Arnett 2006, Mathews et al. 2013, Stanhope 2015), grizzly and black bears in Canada (Clare et al. 2015, Harrison 2006, Wasser et al. 2004), bobcats in United States (Clare et al. 2015) and even to locate invasive species of plants (Goodwin et al. 2010).

The aim of this paper is to establish whether hazel dormice hibernate within their home range by investigating Euclidean distances from rest sites in the autumn to hibernaculum, measure weight loss during hibernation and detail aspects of behaviour prior to and during the hibernation period.

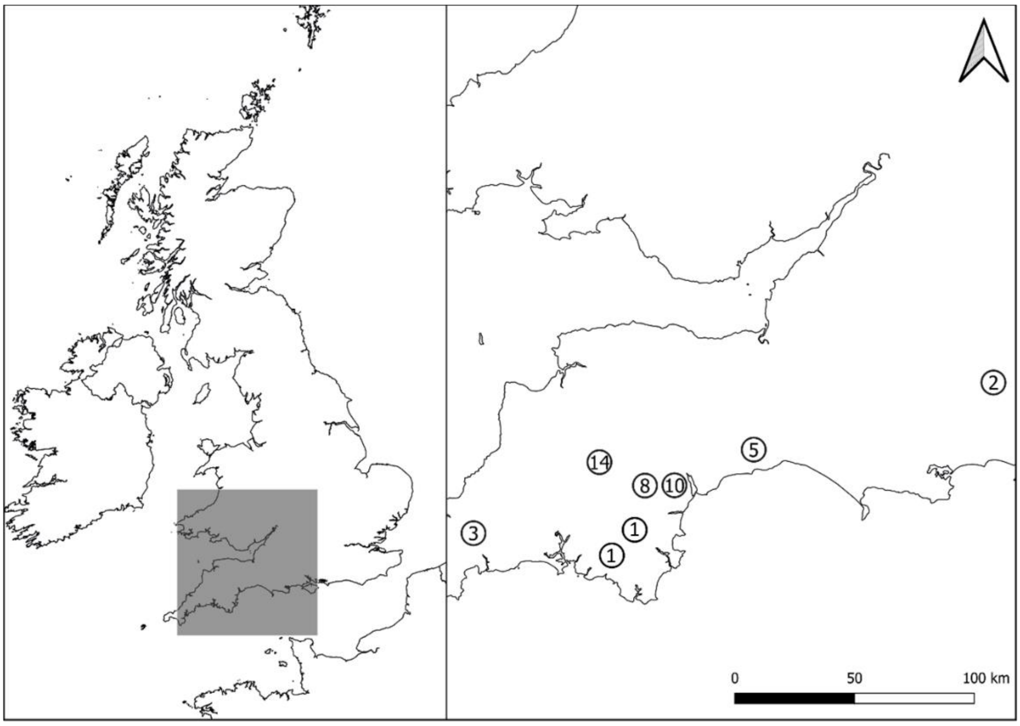
Methods

Study areas

The study was conducted at 18 sites in southwest England (Fig 2.1), in areas of broad-leaved and coniferous woodland, roadside habitats, and hedgerows in different central and southern areas of England where dormice had previously been recorded (Table 2.1). These locations represent the main habitat types used by the hazel dormouse in Great Britain. Apart from hedgerows, the study areas included other vegetation types that formed a mosaic of habitats, comprising scrub, grasslands, marginal vegetation, and woodland edge.

At each position where a hibernaculum was located, records of habitat characteristics such as vegetation type, dominant tree or shrub plant species, ground cover were taken.

Figure 2.1. *Location of the study areas in southern England. Numbers in dots indicate number of hibernacula identified in the area.*



Methods used to identify hazel dormouse hibernacula

Radio tracking (Telemetry)

Thirty-two wild dormice were captured from nest boxes at eight different sites in Devon, southwest England, between 28 October and 24 November 2016. The animals captured were 14 males (11 adults and three juveniles) and 18 females (nine adults and nine juveniles). The captures were timed just before the arrival of the first cold weather front in autumn whilst dormice were still active in the canopy and using nest boxes. Each captured dormouse was weighed, sexed, scanned for PIT tags at sites where this method was being used as part of a parallel investigation, fitted with a radio-transmitter collar (Type PIP3 mounted on a Teflon ribbon collar (tag size 13mm x 7mm x 4mm and total weight of 0.89 gram), Biotrack Ltd, Wareham, Dorset, UK, Fig 2.2) and released back into the same nest box immediately after. Initially, all animals were fitted with a lighter version of the radio-transmitter collar with a battery life of four to five weeks and at the end of this period, nine animals had their collars replaced by a slightly heavier collar with a bigger battery with expected life of 12 weeks (tag size 13mm x 8mm x 9mm and total weight of 1.4 gram). Since the Teflon ribbon collar design was relatively new, trials using dummy tags were carried out on three bank voles in the lab and on a captive dormouse at the Paignton Zoo in Devon, UK, over a three-week period to test and practice collar fitting methodology and assess any impacts on animal welfare.

Radio tracking in the field was undertaken using an Australis 26 scanning receiver and a handheld Yagi three element directional folding antenna (Titley Scientific, Coppull, Lancashire, UK). Positions of collared animals were recorded every one to five days at each site using Survey 123 for ArcGIS (version 1.1 for Android mobile phone) with an estimated accuracy of up to 5 metres and mapped using QGIS system (QGIS Development Team 2020). At every handling opportunity, a visual assessment of the general health of each radio tracked dormice (looking for signs such as fur loss, weight loss and any visible injuries) was made to ensure that the collar had no obvious detrimental impact on the welfare of animals. Records of losses to predation and/or natural causes were taken, and dead animals were submitted to the Zoological Society of London for post-mortem examination.

Systematic searches

Details of hibernation nests have been collected from systematic searches, often carried out as part of protected species licensing conditions, by the research team and a wider community of ecologist. This method involved searching the woodland floor for dormouse hibernation nests by hand. This ‘fingertip method’ is often used to locate hibernating dormice for development purposes, although no clear protocol yet exists. For this study, the woodland floor was thoroughly searched through leaf litter, moss and ivy *Hedera helix* covered ground, root systems, tree bases, crevices, burrows (as far as practicable), under moveable stones, fallen tree branches and brash, and ground vegetation.

Wildlife detection (search) dog

A 3-year-old Labrador retriever with previous experience in wildlife detection was specifically trained to detect dormouse hibernation nests by a skilled trainer (Mick Swindells of Search Dogs United Kingdom) during the winter of 2016 and a follow up training session in 2017. Hibernation and summer nests were provided to aid the dog to identify the scent and training was completed within 6 weeks. Regular training was given throughout the winter to reinforce the search protocol with practice sessions involving hidden nests at typical hibernaculum locations in woodland, woodland edge, scrub and grassland habitats.

Once training was complete, the search dog was taken to six different locations within known hazel dormouse territories to search for hibernacula during February and early March in 2016 for a period of 10 days. At four of these sites, dormouse hibernacula locations had already been previously identified by another method (e.g. telemetry) and was used to determine search dog capability to detect dormouse hibernacula in the wild. The sites were revisited again during late autumn 2016 over a period of four days, once the search dog completed the refresher training session.

Analysis of Euclidean distances from place of capture to hibernation sites from telemetry data

The Euclidean distances between paired points of 32 hazel dormice, classified as place of capture, canopy nest(s) and hibernation nest(s), were calculated on QGIS and rounded up to the nearest metre. Linear mixed-effects models were then run separately, including/excluding points obtained from nest box locations since these locations are not randomised. Using the distance between paired points as a response variable, the models were used to test whether the classification of the paired points, the fixed response variable, predicted the distance between the points using individual animal id as random effect.

This model assumes that if hibernation nests tend to be outside, or at the margins of animal’s home range, distances containing hibernation nests are expected to be further than other nest types. The significance of results was tested using Analysis of variance (ANOVA).

Analysis of weight loss during hibernation

Daily weight loss of eight individual dormice was calculated as proportion from the last weight measurement before entering hibernation and the subsequent readings obtained during collar changes or releases. Weight measurements were taken to the nearest 0.5g using a Pesola spring scale with an estimated accuracy of 0.3%. Weight loss is modelled as a linear function of time with individual’s weight as response variable, days between consecutive measurements over hibernation bouts as a fixed linear effect and individual id as random effect.

All statistical analyses were conducted using R (v 4.03) within the R studio environment (R Core Team 2017, R Studio Team 2020) and package ‘lme4’.

Results

The locations of 44 hazel dormouse hibernacula were identified as part of this study: 24 by telemetry and 20 by systematic searches. The wildlife detection dog found no nests. The location of hibernacula varied but the majority were found in the leaf litter on the woodland floor (n=33, Fig 2.4), the remaining under or anchored in ferns (n=3), in hazel stools (n=3), open ground adjacent to woodland or hedge (n=3), on a hedge bank (n=1) and surprisingly, on highway concrete structure under moss and grass (n=1). Despite the arrival of cold weather fronts and the leaf fall within their habitat, most dormice were still active at the beginning of November often using inconspicuous natural nests (Fig 2.2).

Figure 2.2. *Photographs detailing methodologies used in dormouse searches and examples of ‘summer’ natural nests. a) dormouse fitted with radio collar, b) example of pre-hibernation nest location in tree crevice, c) example of low “summer” nest in bramble, d) dormouse “summer” nest at the base of a hazel shrub, e) dormouse “summer” nest in grass tussock just above ground level, f) nest in gorse being used late in autumn when deciduous trees are dropping their leaves, and g) wildlife search dog in action.*

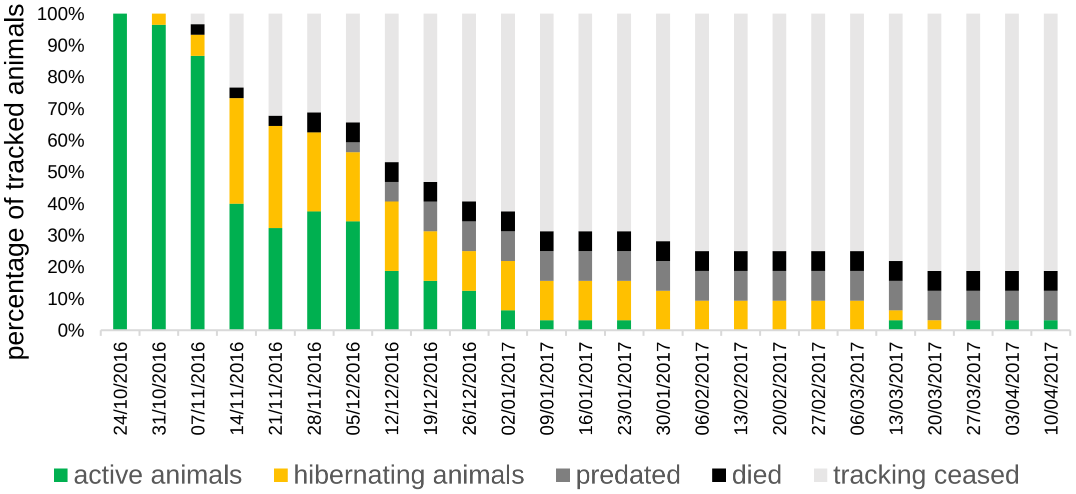
Identifying location of hazel dormouse hibernacula

Radio tracking

In total, 32 hazel dormice were fitted with radio collars from late October to mid-November resulting in 1241 tracking days and an average of 44 days per collared dormouse. A maximum of 28 individuals were tracked simultaneously during a period of two weeks at the beginning of November. Within one month from the beginning of the radio tracking exercise, five active individuals could not be located within 1 km radius of the study areas; three were recaptured in nest boxes wearing damaged/chewed tag casings (with the electronic components exposed) that were removed; one collar was found on the ground and another individual, recognised by its subcutaneous microchip, was found without the collar in a nest box near to where it was originally captured. Contact with four other dormice was lost once they had left hibernaculum later in the winter, possibly due to malfunction, predation, or collar damage by other dormice.

By mid-November nearly half of the tracked dormice were hibernating (Fig 2.3). At the end of November, the collars fitted with a battery life of four weeks were being removed or replaced. Dormice that had collars replaced whilst they were in hibernation, moved their hibernaculum location in every instance from as soon as the following night following collar removal to up to two weeks later, except for one adult male that remained in the same nest for a further eight weeks until emerging from hibernation by the beginning of April.

Figure 2.3. *Weekly summary of dormouse activity during radio tracking between October 2016 and April 2017 at eight different sites in Devon, southwest England.*



In total, fifteen dormice were tracked to their hibernaculum (see Fig 2.4 for examples). Some animals moved to new hibernaculum locations hence tracking resulted in the discovery of 24 different hibernacula. Four individuals moved once to new hibernacula, one moved twice, and another built four different hibernacula moving three times over its hibernation period.

Systematic searches

The time spent on searches varied according to ground conditions, vegetation cover, depth of leaf litter, moss cover, scrub cover, topography, presence of rocks and fallen branches, cavities, burrows, etc. Sites with a thick, well established ground layer of ivy, proved to be the most difficult for fingertip searches as these plants often sits above the leaf litter and, at wetter sites, a sublayer of mosses is often present. With these conditions considered, one hour of thorough ground searches covered between $70m^2$ to $150m^2$, taking on average approximately four hours of searching time to find one hibernaculum, based on data from 10 nest searches by the same surveyor at four different sites with distinct ground cover.

Wildlife detection (search) dog

Despite the intensive training and 14 days of attempts at different sites, ground cover and weather conditions, the search dog was not able to accurately identify wild dormouse hibernacula. The dog was able to detect summer and hibernation nests hidden by the research team in vegetation and leaf litter up to a day in advance of the survey within a radius of 25 metres but failed to identify the location of wild hibernacula that had been previously identified by telemetry in several instances. Curiously, the search dog proved capable of identifying remains of dormouse summer nests on the woodland floor that had been cleared out of nest boxes two months earlier.

Mortality during radio tracking period

Predation in the hibernaculum was observed in two occasions: one individual seemed to have been predated by a mammalian predator with clear marks of chewing, and the other was likely to have been by bird as parts of the skin was “pulled off” rather than chewed; in both circumstances there were parts of the body still recognisable. Another dormouse was depredated in the same nest box in which it had been captured, after emerging from a weeklong hibernation bout at a site 141 metres away, with clear marks of chewing at top the skull being the only visible lesion.

Two other dormice, one juvenile male and an adult female were found to be in poor health whilst active in a nest box and natural nest respectively and had their collars removed immediately but were found dead at later visits. A post-mortem examination of the adult female carried out by veterinarians at Zoological Society of London on the adult female identified pneumonia as main cause of death.

Pre hibernation movements

Results of the linear mixed-effects models indicated that there were no significant differences in the distances from places of capture to canopy nests or hibernacula including ($p=0.221$) or excluding ($p=0.113$) capture events in nest boxes, suggesting there is no evidence that dormice move beyond their home range to hibernate. We found that the mean distance from place of capture to hibernaculum location was 43 m (SD=30). Juveniles were found to move further away from place of capture to other canopy nests than adults while active ($\bar{x}$=73m (SD=53) and 44 m (SD=35) respectively) and chose to hibernate at further locations than adults ($\bar{x}$=48 m (SD=29) and 42 m (SD=32) respectively).

Our findings indicate that 10 of the 32 radio tracked dormice moved beyond distances of >100 metres prior to hibernation, which is likely to be beyond their expected home range (Fig 2.5). During this period of pre-hibernation activity, whilst broadleaved trees and shrubs were dropping their leaves making natural nests in scrub and shrub layer conspicuous, dormice were tracked to natural nests in mature trees such as oak *Quercus robur*, willows *Salix spp*, and alder *Alnus glutinosa*, often with thick ivy cover (n=10), grey squirrel *Sciurus carolinensis* dreys (n=3), concealed wild nests in low growing scrub such as gorse and bramble (n= 8), purple moor grass *Molinia caerulea* tussocks (n=2), and low nests at the base of hazel *Corylus avellana* shrubs (n=2, Fig 2.2). Except for one adult female that moved 141 m from its place of capture to hibernaculum location, most animals chose to hibernate within their expected home range. One male juvenile did not move nests during the six weeks tracking period and was consistently tracked back to the same nest box where it was captured. The animal was found both active and in torpor, it was also noted that the body weight varied between monitoring visits, indicating that it must have been actively feeding at night.

By the week commencing 31 October, 28 hazel dormice were being radio tracked and only one moved to a hibernaculum. In the following week hibernating animals increased to two and by the week commencing 21 November the number of active individuals matched those in hibernation. Active dormice were detected through the whole month of December, with those choosing to nest high up (>5 m) in the canopy of mature trees Those that remained active were largely juveniles engaged in foraging activity.

Figure 2.4. *Examples of hibernation nests and hibernaculum locations. a) nest constructed with bracken and pine needles next to Scots pine Pinus sylvestris, b) hibernaculum location in hazel coppice, c) hibernaculum location anchored in leaf litter on steep slope, d) hibernaculum located in hazel stool in hedgerow, e) inconspicuous hibernaculum constructed with bracken bark in south facing exposed clearing by woodland edge, f) hibernaculum in woodland floor by hazel stool, g) well-hidden hibernation nest in leaf litter under sparse bramble and, h) hibernaculum constructed at the base of hard fern* Blechnum spicant *next to footpath.*

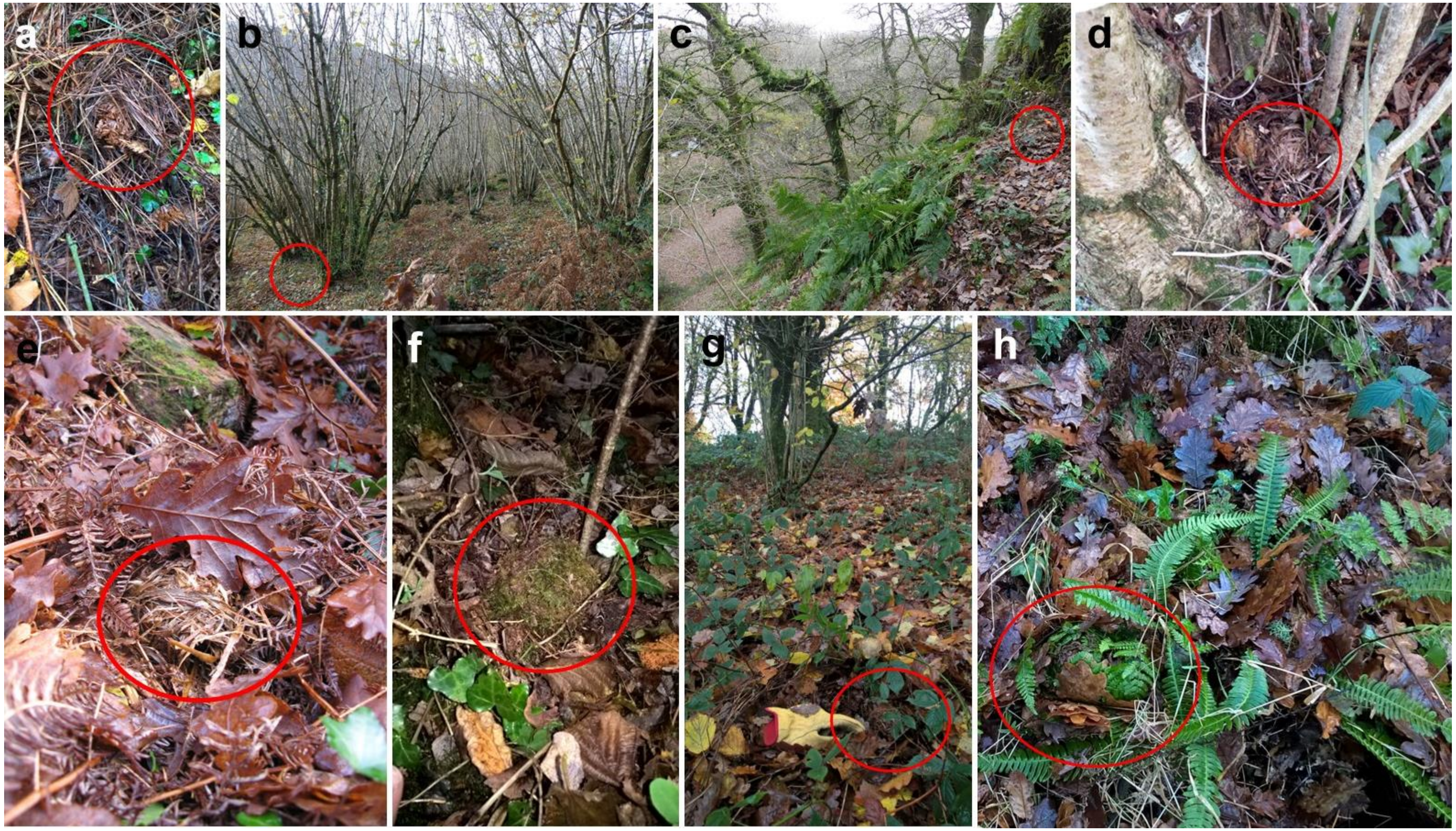
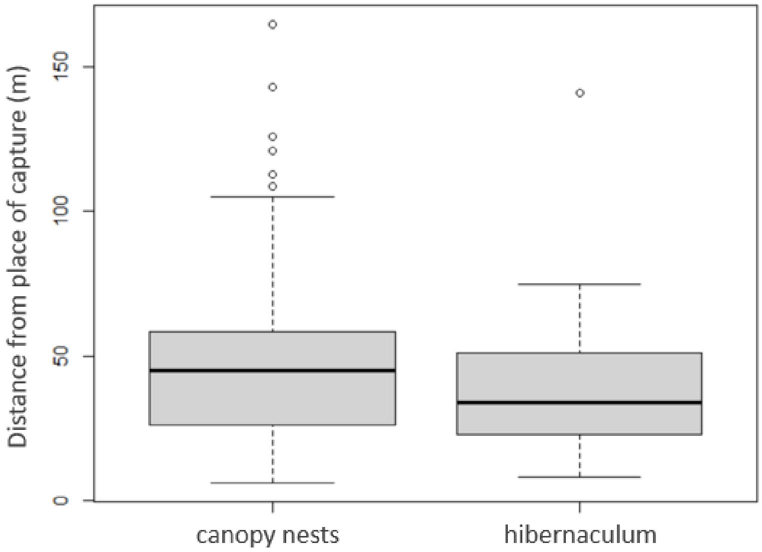


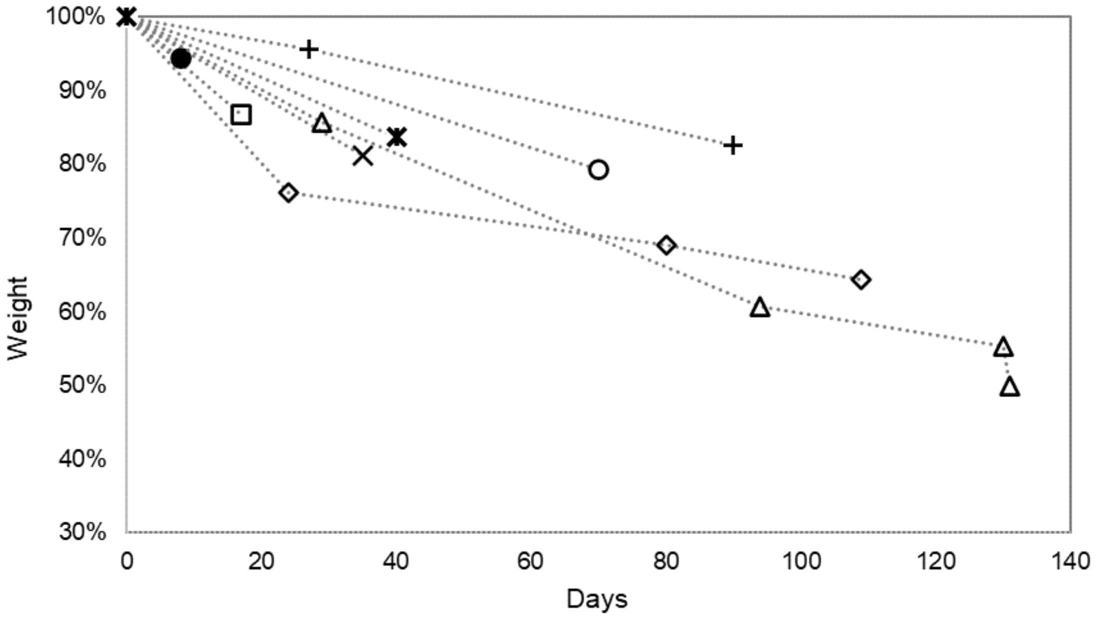
Figure 2.5. *Euclidean distance from dormouse place of capture to natural nests (places of rest) in the canopy and to hibernaculum. Boxes represent the range of distances recorded, black lines inside the boxes are the median markers whilst error bars extend upward from the third quartile to the maximum and the other extends downward from the first quartile to the minimum. Dots (outliers) represent the Euclidean distances by individuals above the upper quartile.*



Weight loss during hibernation

Results of the linear mixed-effect models indicate that on average dormice lost 0.47% of their body mass per day during hibernation bouts (Fig. 2.6). During the radio tracking period, an adult female started hibernating on 1 November at a mass of 28g, and at the last capture occasion in mid-March, 131 days later, it had a mass of 14g. This individual moved hibernaculum location three times and, between the last two weighing events taken on two consecutive days (15.5g and 14g respectively), revealed a loss 10% of its body weight over night after full arousal and leaving hibernaculum for a nest at the base of a hazel shrub over 50 metres away. Another tracked juvenile male weighing 13g in late October remained active and feeding through November and was recorded weighing 18g in early December, moving to a hibernation nest on 2 January at 15.5g. It remained in the hibernaculum for two weeks before moving to a nearby nest box where it stayed between bouts of torpor and activity. The final weight, recorded at the end of January when the radio collar was removed, was 13g, the same as when radio tracking started.

Figure 2.6. *Percentage of body weight loss during hibernation period of eight individual wild dormice in southwest England.*



Discussion

Both radio tracking and systematic searches proved efficient in locating dormouse hibernacula. The use of telemetry with the exception of a few studies (Bright & Morris 1991, Verbeylen et al. 2017, Lemmers 2022, Bright et al. 1996, Vogel & Frey 1995), is a methodology that has not been used to a great extent to investigate hazel dormouse behaviour in winter months.

Telemetry proved an effective and unbiased method to identify hibernaculum locations whilst providing opportunities to investigate aspects of the species ecology such behaviour and habitat use, timing of hibernation, movements, selection of resting sites and weight gain/loss prior and during hibernation period. However, equipment is costly (each radio collar £150, telemetry receiver and antenna approximately £1500 in August 2016), liable to faults, requires training, while permits and licenses that can be expensive and time consuming to obtain are also required. Systematic searches, on the other hand, are a relatively simple method for locating hazel hibernacula, but can be difficult to conduct over large areas, it is intrusive by causing disturbance to woodland floor cover, its accuracy is associated with survey effort, habitat characteristics, surveyor thoroughness, and it is inevitably a biased method (Juškaitis 2008), and hence not as useful for further investigations as telemetry.

Notwithstanding its advantages, radio tracking wild dormice prior to hibernation can be challenging in many aspects. For example, it was not expected that animals would remain active during late autumn often choosing to remain in the tree canopy during spells of warmer temperatures. Fitting radio collars to animals that were at the top of their weight just before hibernation also proved challenging as collars cannot be fitted too tightly, to avoid discomfort to the animal, or too loosely because it might to come off with expected weight loss. Conversely, animals that were still relatively 'light' and active foraging, could not have their collars fitted too tightly as weight increase was still expected. Another issue that became apparent is that autumn is a period of higher social interaction, when nest box sharing increased and it became common to find animals in pairs or groups of three or more individuals (Bright & Morris 1990, Morris 2004). It was probably during such social events that resulted in some radio tags being gnawed beyond repair, as once the casing is broken, the electrical components are easily damaged.

Despite reports of at least two previous cases of dogs finding hibernating hazel dormice on the forest floor in the literature (see summary in Juškaitis 2014) and the effective use of search dog in many wildlife species' surveys where success rate has been much greater than human surveyors (del Valle et al. 2020, Mathews et al. 2013, Harrison 2006, Long et al. 2007), this approach did not prove viable as a hazel dormouse hibernaculum survey method on this occasion. However, it is important to point out that a limiting factor that only one dog of a particular breed was used in this study. We concluded that the scent originating from hibernating dormice, as well as their nests was not conspicuous enough, even for a trained and experienced animal. A similar conclusion was drawn by a team of researchers in Germany where two search dogs were used but unable to detect dormouse hibernacula (B Schulz pers. comm. 2017). With the reduction in metabolic functions during hibernation, dormice are likely to have evolved to avoid disturbance and detection by potential predators using olfaction to locate prey. Dormouse hibernacula are often constructed amongst leaf litter and sheltered by a layer of fallen leaves in the autumn that settles impeding/reducing scents from dissipating. Furthermore, the diversity of habitat around their hibernacula (see Chapter 3) and the use of abundant local materials to build hibernation nests may disguise their location (Gubert et al. 2022, Verbeylen et al. 2017), may contribute to the fact that dormice are unlikely to be found often enough for a predator to develop a ‘search image’ which would lead to systematic finding and predation, as suggested by Bright & Morris (1996).

Although the verified mortality of radio tracked individuals during field observation affected 16% (n=5) of the individuals, it could be as high as 47% if equipment failure is discarded (e.g. battery/tag failures). High overwinter mortality of wild hazel dormice is reported in the literature (Bird et al. 2012, Juškaitis 2014*a*, Csorba 2003) and has been described as being around two thirds of the population based on mark-recapture techniques (Juškaitis 1999) but without distinguishing the numbers lost to predation and natural causes. Overwinter mortality under controlled conditions with predation excluded has been reported as being 44% (Csorba 2003).

We observed predation at the hibernaculum in two instances, but Verbeylen et al. (2017) reported that near a third of the hibernating animals being studied (n=17) were lost in this way to different suspected predators and can be considered a significant factor influencing overwinter survival rate. Predation during the active season just before hibernation was also observed and confirmed at least once during our study with a female adult found with head injuries in a nest box whilst the animal was likely to be vulnerable in torpor. Similar incidents have been reported elsewhere and attributed to wood mouse *Apodemus sylvaticus* and yellow-necked mouse *Apodemus flavicollis* as they are known to predate on torpid hazel dormice (Bright & Morris 1996, Verbeylen et al. 2013, Lemmers 2022) although the latter is absent from the study areas. It is possible that some of the animals that disappeared from the study area could have been predated and radio tags could not be recovered because of damage or carried further away (>1km).

The results of the radio tracking exercise suggest that dormice largely remained within their autumnal home range during the onset of hibernation choosing hibernaculum locations close to their places of rest during the late stages of their active period in autumn. As suggested by Juškaitis (1997), at this time most juveniles have already dispersed and those that stayed have become sedentary.

In this study, however, juveniles moved further away from the place of capture than adults, but this may be associated with searches for better foraging areas as they prepare to enter hibernation which is normally later than in heavier adults (Juškaitis 2014a). During the pre-hibernation period, hazel dormice were found to nest in a range of concealed locations, notably mature trees, squirrel dreys and in low growing scrub, highlighting the importance of habitat structural diversity. We found that the longest Euclidean distance from place of capture to hibernaculum was 160m which is an intermediate value between the maximum distance of 81m reported by Verbeylen et al. (2017) in Belgium and 250m reported by Lemmers et al. (2022) in the Netherlands.

As animals entered hibernation, we found that the rate of weight loss was 0.47% bodyweight/day, which is relatively high when compared to mean estimates of 0.17% bodyweight/day (n=18, including animals that died during the study) reported in a study in a controlled environment where animals fed *ad libitum* (Csorba 2003). However, the highest rate of weight loss was recorded by Csorba (2003) was 0.64% bodyweight/day by a juvenile that died during the experiment after 96 days in hibernation. The highest rate recorded amongst those that survived hibernation was 40% bodyweight/day. Difference is also evident with a capture-mark-capture study (Juškaitis 2001), where a mean of 33% body weight decrease was observed from the first half of October until the recapture of marked individuals in the spring (males in April and for females in April – early May). For example, marked males weighed an average of 30g in the first half of October and 20g in the spring; using our data, the same individual would be weighing close to 13.5g during similar period of 170 days, representing a loss of 55% of pre hibernation body weight. It is important to bear in mind that in mark recapture studies using nest boxes, the real duration of the dormouse activity season may be a little longer than the period of nest box use, both in spring and in autumn (Juškaitis 2014) so that the actual weight immediately before and after hibernation is not considered nor is the possibility of extended foraging periods in the autumn that may result in further weight gain. On the other hand, negative impacts of radio collars on individual dormice cannot be ruled out as it has been observed in similar radio tracking exercise (Verbeylen et al. 2017) and may exacerbate weight loss before and during hibernation.

The findings of this study indicate that there are suitable locations for hibernation to take place within the usual home range of the hazel dormouse. The timing of hibernation varied amongst individuals with some dormice remaining active through the month of December and other alternating bouts of hibernation and activity. Hibernaculum identification proved not to be a simple task but can be facilitated using telemetry, and, to a lesser extent, systematic searches. This study highlighted that the hazel dormice can lose body weight rather quickly during hibernation and revealed that weight gain occurred during the hibernation season, suggesting that animals were able to find food sources during the winter.

Supplementary Table S2.1. *Location and habitat description of study areas in England.*

Site ref	Latitude	Longitude	Habitat description	Habitat patch size
S1	50.640	-3.541	Coniferous forest with occasional broadleaved trees and shrubs such as oak, beech and hazel. Bramble and bracken are often abundant	1400 ha
F2	50.686	-3.728		170 ha
S2	50.735	-3.979	Linear belts of broadleaved shrubs and trees often with conifers, scrub, ferns, and bracken that forms part of roadside verge planting along dual carriageway trunk roads or railway corridor, in most cases well connected to other habitat patches in the wider landscape.	2 ha
RS2	50.436	-4.764		3 ha
RS3	50.725	-3.653		3 ha
RS4	50.478	-3.777		12 ha
RS5	50.384	-3.909		4.5 ha
RS6	50.461	-4.694		3.5 ha
RS7	51.02	-1.696		10 ha
RS8	50.501	-4.679		0.9 ha
RW1	50.773	-3.086		4 ha
F3	50.726	-3.942	Mature deciduous woodland consisting of pedunculate and/or sessile oak, ash, sycamore, with occasional rowan, beech, and birch. Bramble and bracken are often abundant.	16 ha
S3	50.725	-4.011		12 ha
S4	50.73	-4.007		7 ha
F4	50.564	-3.651		70 ha
F5	50.606	-3.722	Hazel coppice	40 ha
G1	50.726	-3.947	Gardens planted with native and exotic plant species surrounded by broadleaved woodland and scrub habitats.	2 ha
F6	50.951	-3.074	Early succession scrub with birch and bramble connected to mixed woodland.	>100 ha

Supplementary table S2.2. *Description of the location where dormouse hibernacula were found and associated search method.*

Site ref.	Nest id	No. of nests	Search method*	Hibernaculum location
S1	1	11	SS	Woodland floor under moss
	5		SS	Woodland floor under ivy layer
	10		SS	Woodland floor under ivy layer
	11		SS	Woodland floor in leaf litter
	12		SS	Woodland floor in leaf litter
	13		SS	Woodland floor in leaf litter
	14		SS	Woodland floor under ivy layer
	15		RT	Woodland floor by foot of tree
	16		RT	Woodland floor at base of fern
	17		RT	Earth bank of hedgerow
	18		RT	Woodland floor in bracken litter
F2	19	3	RT	Woodland floor in leaf litter
	20		RT	Woodland floor by hazel stool
S2	27	2	RT	Under moss on concrete wingwall
	28		RT	On steep slope in leaf litter
RS2	7	1	SS	Woodland floor in leaf litter
RS3	43	1	SS	Woodland floor in leaf litter/moss
RS4	42	1	SS	Woodland floor in leaf litter
RS5	64	1	SS	Woodland floor in leaf litter/ivy
RS6	4	1	SS	Woodland floor by foot of tree
RS7	47	2	SS	Woodland floor in leaf litter
	48		SS	Woodland floor in leaf litter
RS8	9	1	SS	Woodland floor in leaf litter
RW1	58	4	SS	Woodland floor in leaf litter
	59		SS	On grassland by woodland edge
	60		SS	Woodland floor in leaf litter
	61		SS	Woodland floor in leaf litter
	62		SS	Rank grass/short scrub on slope
F3	34	5	RT	Woodland floor in hazel stool
	35		RT	Woodland floor in leaf litter
	36		RT	On steep slope in leaf litter
	38		RT	Woodland floor in leaf litter
S3	21	2	RT	Woodland floor by hazel stool
	22		RT	Woodland floor in leaf litter
S4	29	5	RT	Wet woodland floor at base of fern
	30		RT	Woodland floor in leaf litter
	31		RT	Woodland floor in leaf litter
	32		RT	Woodland floor at base of fern
	33		RT	Woodland floor in leaf litter
F5	23	4	RT	Open ground in bracken area
	24		RT	Woodland floor in hazel stool
	25		RT	Woodland floor in leaf litter
	26		RT	Woodland floor by hazel stool
G1	37	1	RT	Woodland floor in leaf litter

* SS= systematic searches, RT= radio tracking, SD= search dog

Chapter 3

Using high-resolution LiDAR-derived canopy structure and topography to characterise hibernaculum locations of the hazel dormouse *Muscardinus avellanarius*

Chapter 3: Using high-resolution LiDAR-derived canopy structure and topography to characterise hibernaculum locations of the hazel dormouse *Muscardinus avellanarius*

Abstract

The Hazel Dormouse is predominantly an arboreal species that moves down to the ground to hibernate in the autumn in temperate parts of its distributional ranges at locations not yet well understood. The main objective of this study is to test whether environmental characteristics surrounding Hazel Dormouse hibernacula can be identified using high-resolution remote sensing and data collected *in situ*. To achieve this, remotely sensed variables, including canopy height and cover, topographic slope, sky view, solar radiation and cold air drainage, were modelled around 83 dormouse hibernacula in England (n=62) and the Netherlands (n=21), and environmental characteristics that may be favoured by pre-hibernating dormice were identified. Data on leaf litter depth, temperature, canopy cover and distance to the nearest tree were collected *in situ* and analysed at hibernaculum locations in England.

The findings indicated that remotely sensed data were effective in identifying attributes surrounding the locations of dormouse hibernacula and, when compared to *in situ* information, provided more conclusive results. This study suggests that remotely sensed topographic slope, canopy height and sky view have an influence on hazel dormice choosing suitable locations to hibernate; whilst *in situ* data suggested that average daily mean temperature at the hibernaculum may also have an effect.

Remote sensing proved capable of identifying localised environmental characteristics in the wider landscape that may be important for hibernating dormice. This study proposes that this method can provide a novel progression from habitat modelling to conservation management for the hazel dormouse, as well as other species using habitats where topography and vegetation structure influence fine-resolution favourability.

Introduction

Detailed knowledge of environmental conditions suitable for individual species across the landscape is crucial for understanding species' ecology and conservation. The use of remote sensed data to generate topographic data (Mallet & Bretar 2009, Passalacqua et al. 2015, Rose et al. 2015) and information on canopy structure (Dalagnol et al. 2021, Frolking et al. 2009, Liu et al. 2020) is a powerful tool that has increased knowledge of woodland species distributions (De Frenne et al. 2019, Stark & Fridley 2022).

As remote sensing technology constantly develops, increasingly high-resolution data have allowed researchers to investigate habitat quality (Olsoy et al. 2018, Spanhove et al. 2012) and species distribution at increasingly fine scales (de Vries et al. 2021) as well as to improve models of species' ecological niches, by including measures such as habitat quality, and seasonal or life-cycle events (Leitão & Santos 2019).

Airborne Light Detection and Ranging (LiDAR) is an established and reliable means of generating data on the physical structure of topography, vegetation and man-made structures that have been used for diverse purposes, including forestry (Næsset & Økland 2002), landscape mapping (Wang et al. 2021), habitat modelling and assessment (Getzin et al. 2022, Hagar et al. 2020), landcover types and habitat classification (Koma et al. 2021), natural resource management (Garabedian et al. 2017) and wildfire modelling (Botequim et al. 2019, Rosa & Stow 2014). Airborne LiDAR at resolutions of <1 m is capable of providing information to the scale of individual trees (Jaskierniak et al. 2021, Lichstein et al. 2010), which can be important for a variety of forestry activities and environmental modelling (Khosravipour et al. 2015). Such high-resolution spatial data also have the potential to identify landscape features that are important for the survival of individual organisms, whilst highlighting ecological variations at multiple scales, in local areas, regions and countries. Such approaches offer greater accuracy than many methods that are traditionally used in landscape ecology, for example, coarser-scale remote sensing and land cover mapping. The greater level of detail that can be extracted from LIDAR offers a novel advance for habitat modelling and/or species distribution modelling.

To improve the scope of ecological models it is important to take into consideration the spatial and temporal distribution of climate at the landscape scale. For habitat modelling, microclimate has long been acknowledged as a key factor in the spatial distribution of numerous species. Landscape-scale modelling of microclimates can be a powerful tool for conservation actions, including habitat creation, restoration, management, and species reintroductions (Bennie et al. 2010, de Vries et al. 2021, Lembrechts et al. 2019b, Massimino et al. 2020).

Many species use hibernation as a strategy to minimise the amount of energy spent in thermoregulation and, for this purpose, a suitable hibernaculum location capable of providing appropriate conditions is crucial to increase survival chances. For some species, such as bats (De Bruyn et al. 2021), ground squirrels (Goldberg et al. 2020) and bears (Cisneros-Araujo et al. 2021), these requirements may be different from those during the active season (Goldberg et al. 2020) and can include factors such as stable temperatures, correct level of humidity, safety from predators, low susceptibility to flooding, proximity to important resources, and others.

The hazel dormouse *Muscardinus avellanarius* is a mainly nocturnal animal that spends most of its active season in the shrub layer or canopy and, in northern European countries, they move down to the ground to hibernate in the autumn where they stay until spring at locations not yet well understood (Juškaitis 2014a). During the pre-hibernation period in temperate climates, the tendency for dormice to enter daily torpor increases with decreasing ambient temperature and day length (Mills 2012a). By the beginning of November, dormouse use of natural nests above ground and artificial nest boxes tends to decrease as they prepare for hibernation at ground level (Juškaitis 2014). The preference for dormice to overwinter on the ground is thought to be associated with more stable temperatures at which to hibernate. A humid site is preferable to prevent the animal from dehydration over winter (Morris 2004), where they have always been found to hibernate alone in individual nests made from plant material occupying all the interior nest volume available (Gubert et al. 2022, Vogel & Frey 1995, Juškaitis 2014a).

In Britain, pre-breeding population densities of hazel dormice range from 5-8 adults/ha (Bright & Morris 1996) but can be less, depending on quality and type of habitat. With their low population density, behaviour and nest size, dormouse hibernacula are notoriously difficult to find and apart from some targeted studies (Gubert et al. 2021, Lemmers 2022, Verbeylen et al. 2017, Vogel & Frey 1995, Walhovd 1976), hibernation of wild animals remains one of the least known aspects of the species' ecology.

The minimum area of continuous habitat able to support hazel dormouse populations in the long term varies hugely with habitat quality and connectivity (Bright et al. 2006). Adult hazel dormice are sedentary and have fixed home ranges of around 0.5–1.0 ha during the active season (Bright & Morris 1991, Juškaitis 1997, Goodwin et al. 2018). However, there is little information on their preferred hibernaculum and when it comes to dormouse conservation, there is limited evidence of where they hibernate and whether there is more that can be done in terms of habitat management as well as improving associated protocols for such activities to increase the chances of over-winter survival.

Remote sensing has been successfully used for investigations in hazel dormouse spatial ecology, and this technique is capable of identifying short term habitat preferences (Goodwin et al. 2018) as well as establishing broad-scale habitat descriptors associated with the current distribution populations (Cartledge et al. 2021).

In this study we have collected information of where hazel dormouse hibernation takes place in England and the Netherlands to identify habitat features at local and landscape scales, through an approach integrating high resolution remote sensing and data collected *in situ*. We have also investigated the feasibility of a predictive model to aid identification of potential hibernaculum locations to aid species' conservation.

Methods

Study areas

We analysed 12 study areas (Fig. 3.1) where dormouse hibernacula had been located by a range of methods, comprising of broadleaved, coniferous, and mixed woodlands, roadside habitats, hedgerows, scrub, and gardens, in England and southern Netherlands. These habitat types of variable age and structure are typical of those occupied by hazel dormice and often form a connected mosaic of habitats in the wider landscape. The study areas in these two countries are similar to a certain extent in their underlying geology, with the Netherlands comprising of eroded limestone with high contents of loess and clay, and the sedimentary formations of mudstone, siltstone and sandstone in England, which is also subject to higher winter rainfall.

Figure 3.1. Location of the study areas in England and the Netherlands. Dots represent hibernaculum location and the numbers hibernacula clusters in the area.

Methods used to locate hibernacula

Hazel dormouse hibernacula were located through telemetry in both countries with additional records generated from systematic searches and incidental observations in England. Hibernation nests were identified by their typical structure and characteristic location at ground level.

Radio Telemetry

Wild dormice were captured under licence from nest boxes and tubes installed at locations where the species' presence had previously been confirmed. In England, dormouse captures were timed just before the arrival of cold weather fronts during autumn 2016, when lower temperature was expected to trigger hibernation and while dormice were still active and using nest boxes. In the Netherlands, radio tracking was undertaken between October and January in 2018 and 2019. Animals were fitted with a VHF radio-transmitter collar (in

England with Type PIP3, Biotrack Ltd, Wareham, Dorset, UK and in the Netherlands with Holohil BD-2C, Holohil Systems Ltd., Ontario, Canada) and released back into the same nest box or tube immediately thereafter. Radio tracking was carried out at each site in England using Australis 26 scanning receivers and handheld Yagi three element directional folding antennas (Titley Scientific, Coppull, Lancashire, UK) and in the Netherlands with ICOM IC-R20 or Communication Specialist Inc. R-1000 receivers and a four-element Yagi antenna (Followit Sweden AB).

Systematic searches

This method involves searching the woodland floor for dormouse hibernation nests by hand. This ‘fingertip search’ is normally used to locate hibernating dormice at sites where habitat is likely to be disturbed or destroyed for development purposes. This methodology often forms part of protected species mitigation licence conditions in the UK. For this study, searches were carried out through leaf litter, moss cover and ground vegetation; only moving material such as branches and stones that could be done relatively easily but inspecting surroundings of larger logs and boulders. Records collected in this way for this study were originated by LG but drew on a wider community of dormouse ecologists to increase sample size.

Incidental observations

These records refer to findings originating from the research team and the wider community, as well as from members of the public where hibernation sites were identified by coincidence whilst engaged in other activities (such as walking, gardening, hedge laying, woodland management) but where they were not the object of deliberate searches.

Nest site characteristics

Once located, hibernaculum locations were recorded using handheld GPS devices (Survey 123 for ArcGIS version 1.1 for Android mobile phone in England and QFIELD version 1.2.0 for Android mobile phone in the Netherlands) with an estimated accuracy of up to 5 metres and mapped using QGIS system (QGIS Development Team 2020). Using the hibernation nest as a central location, random points were established between 10 metres from the nest (to allow variations to be detected) to a maximum of 50 metres radius, representing a typical dormouse home range (Bright & Morris 1991, Goodwin et al. 2018, Juškaitis 1997) using the random point generator feature in QGIS research tools. Random points were only selected within suitable dormouse habitat and features such as roads, footpaths, built up areas and open fields (>5 m from adjacent suitable habitat) were excluded from the modelling exercise.

At 44 hibernacula in England, leaf litter depth and distance to nearest tree/shrub (> 2 metre in height) were collected using a measuring tape whilst a visual canopy cover estimate was recorded *in situ*. At these locations, random points were generated *in situ* using Random UX for Android (UX Apps), with a set of random numbers to inform direction in degrees (1-360) and another to establish distance in metres (10-50) from nest using the same principle as the QGIS methodology described above. Additionally, temperature profiling of 19 hibernaculum locations in England and their respective random points were obtained by placing thermal data loggers (Thermochron iButton, Dallas Semiconductor, California USA) next to hibernation nests for 74 consecutive days. Temperatures were recorded hourly and from these the standard deviation, mean daily maximum, minimum, mean and variance of temperatures were calculated.

Topography and canopy structure profiling

In England, airborne Light Detection and Ranging (LiDAR) data in the form of Digital Surface Models (DSMs) and Digital Terrain Models (DTMs) from surveys carried out in the winter months (November to April) were obtained from the UK's Department for Environment, Food and Rural Affairs Data Services Platform (DEFRA 2020) at a one metre resolution and BlueSky International (BlueSky International Ltd. 2020) at a 50 cm resolution and were resampled to 1m resolution using average values to make the datasets comparable. For the Netherlands site, 1 m resolution LiDAR data were obtained from PDOK (Kadaster 2021). DSMs and DTMs were then used to assess topography and vegetation structure at landscape level surrounding hazel dormouse hibernacula and randomly selected points for comparison. At each hibernaculum location and respective random point, buffers of five metres were established using QGIS and details of microclimate were modelled for each point using the Microclima R package (Maclean et al. 2019). This package contains tools for modelling the mechanistic processes that govern fine-scale variation in temperature arising from variation in altitude, coastal influences canopy cover, cold air topographic drainage, solar radiation, surface albedo and wind speed.

The information extracted from the LiDAR data and Microclima package (Fig 3.2) is defined as following:

Canopy height and cover: forestry structure is known to be an important factor in the habitat of the hazel dormouse (Goodwin et al. 2018). Canopy height and cover were obtained by subtracting DTMs from DSMs using “raster” and “rgdal” packages in R (R Core Team 2017). Canopy height is the value of difference between the DSM and DTM; canopy height was calculated at the focal pixel and minimum, mean and maximum values were calculated from within a 5m radius of the focal pixel. Canopy cover is defined here as the proportion of pixels with a canopy height above 0.1 m within a 5m radius of the focal pixel. These canopy metrics will also reflect, to some extent, variation in the amount of light penetrating the canopy.

Slope: Field observations suggested that dormice selected well drained sites, on slopes that are not prone to flooding. Slope refers to the steepness or the degree of incline of a surface and is associated with drainage and hydrology. Slope was extracted using DTMs at 1 m resolution and the terrain function in R (2007) “raster” package.

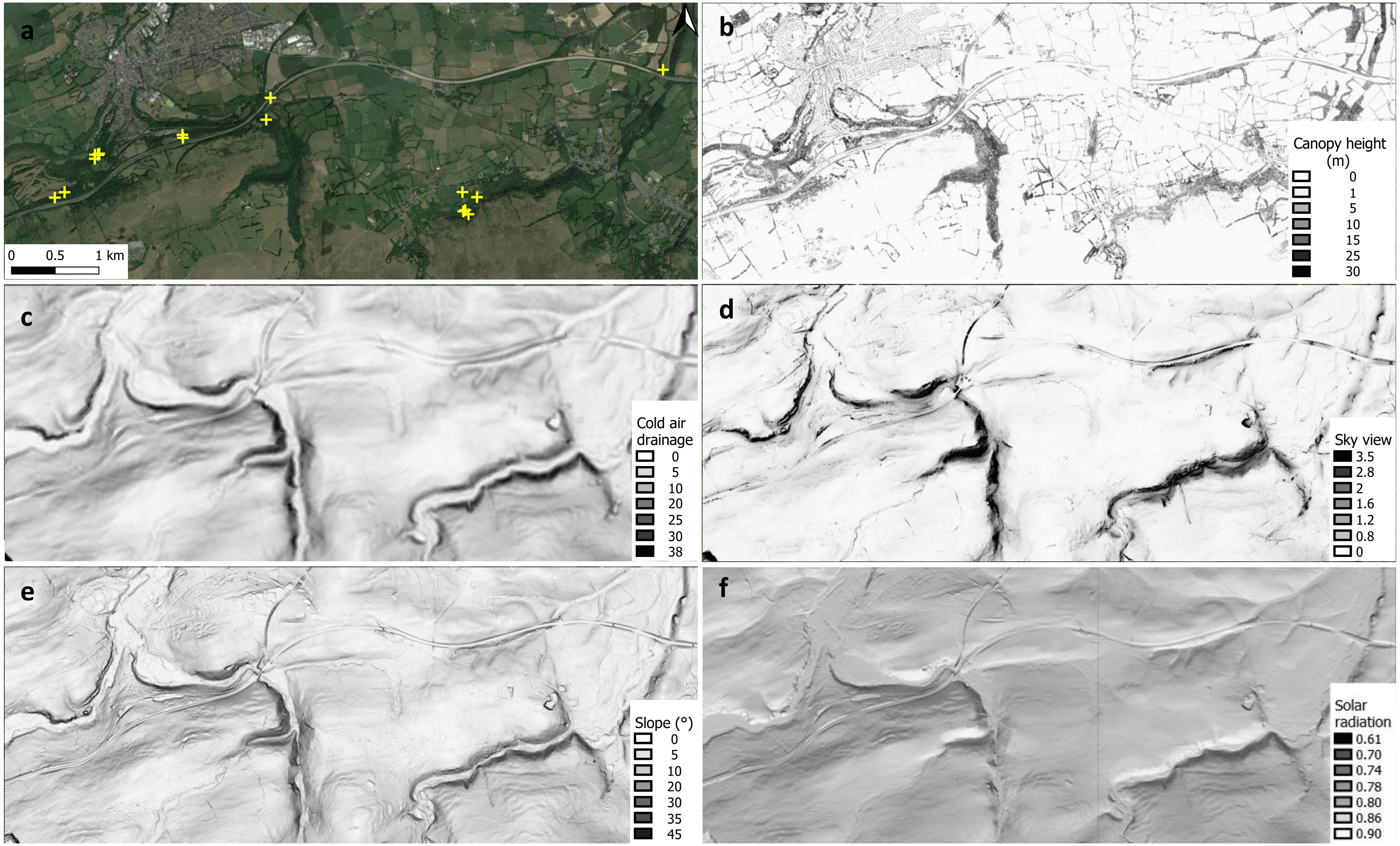
Sky view: linked to topography, sky view is the proportion of sky dome obscured by terrain from the sampled location excluding canopy and is calculated using DTMs at 1 metre resolution with the Microclima package using the skyviewtopo function. Sky view can be a proxy for landscape position and for radiation exchange with the atmosphere and radiative warming of the ground surface. Extracted values were adjusted to facilitate illustration using the following formula: 1-sky view x 10^5 resulting in higher values in deep valleys and lower on flat ground or hill tops.

Solar radiation: considered to be an important factor for hibernaculum selection as existing literature suggests that dormice require low constant temperatures to hibernate. This index was calculated using the solarindex function in the Microclima package that measures the proportion of direct beam solar radiation that, as described by Bennie et al. (2008), is the main component of ground surface energy balance and influences ecologically critical factors of microclimate, including near-surface temperatures, evaporative demand and soil moisture content. Solar radiation indexes were calculated based on the position of the sun integrated across daylight hours on 21st December.

Cold air drainage potential: is the potential for air in contact with terrain surfaces being cooled and flowing downslope and/or downvalley and in the context of this study may also be a proxy for both cold air (temperature), soil moisture and hydrological drainage. It is used in this context to indicate both aggregate downslope (katabatic) and downvalley flows and was calculated using the Microclima package using the pcad function.

Once the values of the remotely sensed terrain and canopy variables were obtained, the intercept and coefficients for each variable from the top model (lowest AIC value) for each country were used in the Raster Calculator function in QGIS to calculate an index of the relative probability of a nest in each map pixel. Vegetation cover (>0.1 m in height) was used as a masking layer, restricting modelled potential sites to areas with canopy cover. The output layer illustrates predicted suitable hibernation locations with topographic, microclimate and vegetation characteristics matching those of actual hibernacula.

Figure 3.2. *Maps in an area of southwestern England against backgrounds of (a) satellite imagery (Google Maps 2021) showing hibernaculum locations marked with yellow crosses, and spatial variation in (b) canopy height, (c) cold air drainage, (d) sky view, (e) slope and (f) solar radiation.*



Data Analysis

Data collected *in situ*: Wilcoxon tests were used to test for differences between recorded variables at each paired hibernacula locations and random points on a) distance to nearest tree, b) temperature, c) leaf litter depth and, d) between estimated canopy cover collected *in situ* and remote sensed.

Remotely sensed variables: To test whether hibernaculum locations differed significantly in site characteristics from the paired random locations a generalised linear mixed model was used to investigate the status of each location (hibernaculum or randomised) as a function of the remotely sensed variables. Remote sensed variables were rescaled to a mean of zero and unit SD and were included in the analysis as fixed factors. A site location code (shared between each pair of hibernaculum location and random point) was included as a random effect to account for the paired experimental design. General linear mixed models were run separately for both England (n=62), and the Netherlands (n=21), using pooled hibernation sites and random points with all possible combinations of remote sensed variables (slope, canopy height and cover, cold air drainage). Best models selection followed using R Package 'MuMIn' (Bartón & Barton 2020) and a model averaging procedure (Johnson & Omland 2004) to identify key explanatory variables. A "best" set of all models with AIC (Akaike's Information Criterion) values within 2 units of the lowest AIC value were selected, and effect sizes were calculated from this model set as the Akaike-weighted slopes of the standardized variables. The relative importance of explanatory variables was calculated as the proportion of the "best" set of models containing each explanatory variable.

Results

Hazel dormice hibernacula were predominantly located among leaf litter on the woodland floor, with varying degrees of concealment (Fig. 3.3). In England, dormice largely hibernated in the leaf litter on the woodland floor, occasionally under ferns and patches with dead bracken fronds, often metres away from the nearest tree or shrub. In hedgerow habitats, we found that dormice were often nesting nearby on adjacent grassland or field edge as well as within the hedge itself, at the base of hazel stools. Similar results were obtained in the Netherlands. There, most hibernacula were found in the leaf litter and covered with leaves on the sparsely vegetated woodland floor. Three nests were found in a hedgerow, also adjacent to field edges.

At sites with low gradients or waterlogged ground, some hibernation nests were built higher off the ground, on vegetation (e.g. ferns and grass tussocks) or other physical features (e.g. hedge bank and fallen branches), to reduce exposure to excessive damp or being flooded. We recorded a small proportion of the hibernacula (n=6) constructed in small depressions dug out in the ground in the form of a ‘cup’ to support the bottom half/third of the nest. Some (n=4) in leaf litter on sloped ground, securely positioned in the root systems of trees where the soil has eroded underneath. It was also noted that dormouse hibernacula in woodland seemed to have been selectively avoiding areas with clear evidence of other small mammals, particularly bank voles *Myodes glareolus*, such as feeding stations and networks of tunnels under moss and/or leaf litter.

Figure 3.3. *Examples of dormouse hibernacula in different locations: a) Nest in leaf litter in the Netherlands, b) nest above ground anchored at the base of a fern in waterlogged ground, c) conspicuous nest in leaf litter, d) hibernaculum built on hedge bank 30 cm off the ground on flood prone area, e) hibernaculum sited on concrete wingwall adjacent to highway and, f) hibernaculum constructed on top of branch on flat ground.*

Data collected *in situ*

Observed hibernaculum locations at UK sites did not differ from random points in distance to the nearest tree or leaf litter depth (all p>0.1). There were also no differences in canopy cover at hibernaculum locations and random points, whether cover was estimated remotely or *in situ*. However, average daily mean temperature at hibernaculum locations (n=19) was slightly lower (0.5°C) than at random points (p=0.038), but there were no significant differences in minimum, maximum, or daily variance in temperature (all p>0.1).

Remote sensing

Environmental characteristics surrounding hibernacula differed markedly between the two countries (Fig 3.4). In England (n=62), hibernaculum locations were positively related to slope gradient and sky view. Here, dormouse hibernacula were found predominantly on sloping terrain, avoiding deep valleys (lower sky view values and slope gradient). When analysing individual search methods utilised in England (telemetry. systematic search and incidental finds), the null model featured as the top model.

In the Netherlands (n=21), both slope and sky view had low importance, but the negative relationship with the percentage of minimum canopy cover within 5 metres radius of the hibernacula indicates that there is an effect of canopy cover on nest sites that is not evident in England (Fig. 3.4), suggesting that animals preferred locations by the woodland edge or near gaps in the canopy.

When both countries were analysed separately, the null models were outside the top model set, indicating that remote sensed variables had important, but contrasting, effects in both England and Netherlands (Fig 3.5). However, with the combined dataset, and interaction terms for country, we found that the null model (including no spatial variables) was within the top model set (selected using AIC values). Therefore, consistent patterns in nest location across both countries could not be detected with confidence.

Figure 3.4. *Summary of factors affecting the location of hazel dormouse hibernacula in England and the Netherlands. Effect sizes are from the top model set analysing variation in standardized variables from observed hibernaculum locations and random points nearby. The bars represent the effect size, calculated as the magnitude and direction of the Akaike-weighted coefficients of terms in the set of models within 2 AIC units of the best model. Figures at the end of bars represent the relative importance, defined as the proportion of models within the set in which the term is included. Variables with zero weight and zero effect were tested but did not feature with the top model set in one or both locations.*

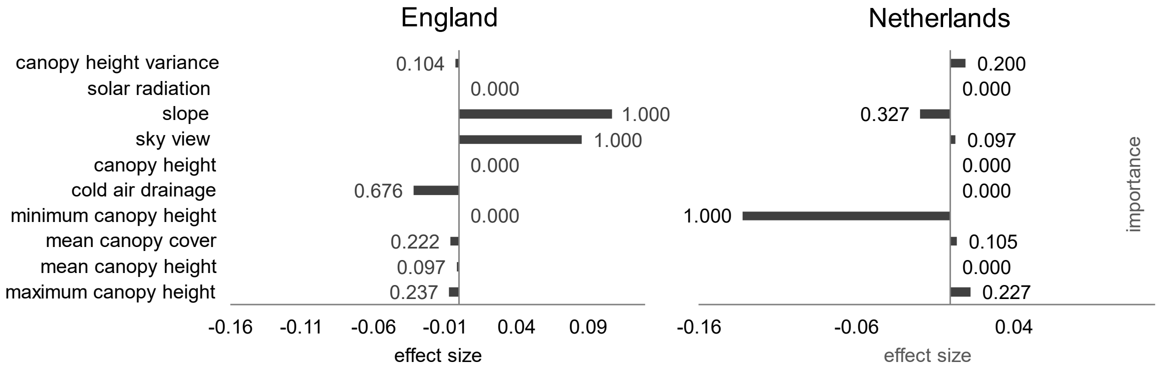
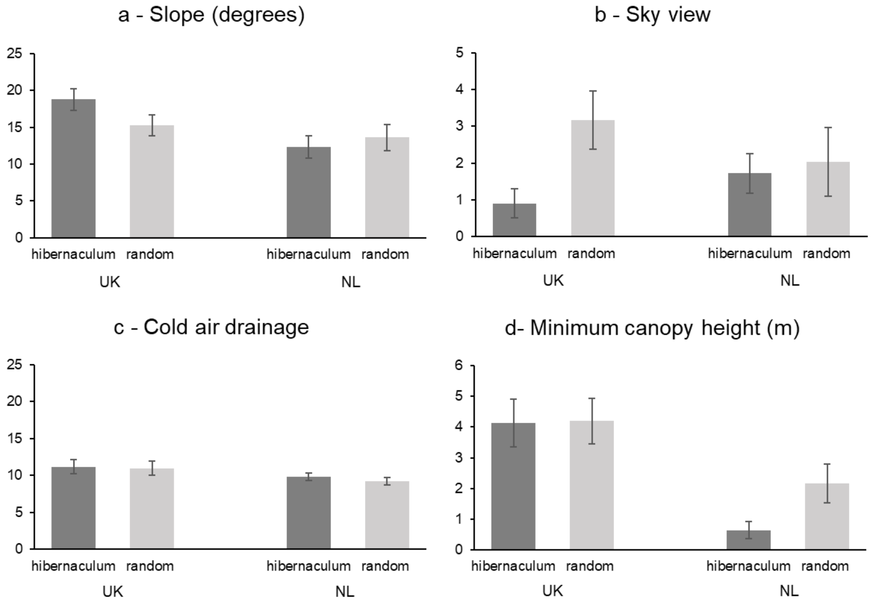
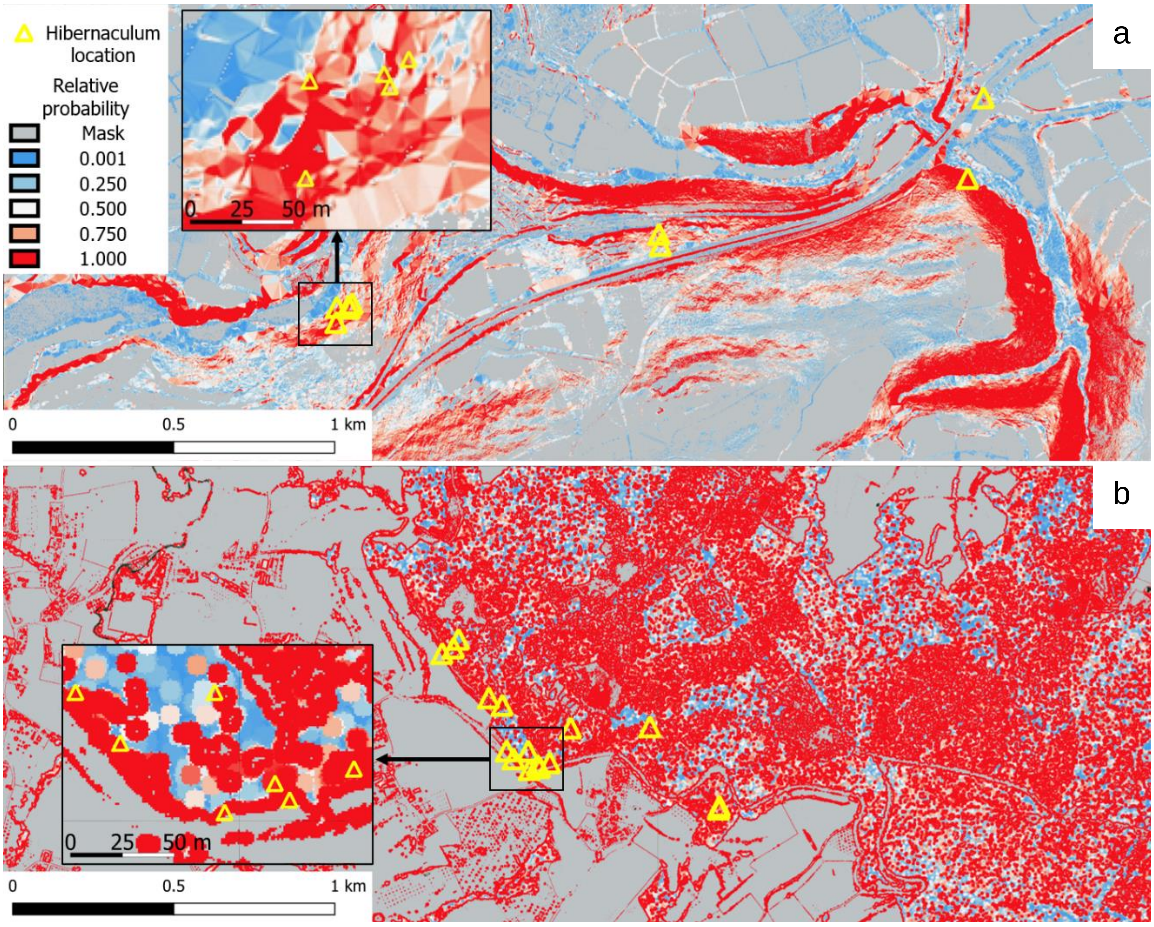


Figure 3.5. *Summary of variation in remote sensed variables measured at hibernation site locations and associated random points in England: a) slope, b) transformed sky view and c) cold air drainage, and the Netherlands: d) minimum canopy height. Columns indicate the mean and error bars represent standard error.*



Based on the remotely sensed predictive variable values, environmental conditions models based on the relative probability of finding dormouse hibernacula were created, indicating areas of similar characteristics across the landscape (Fig. 3.6).

Figure 3.6. *Example of predictive models of the suitability for hazel dormouse hibernaculum across landscapes in England and the Netherlands with inset maps. Observed hibernacula are marked by a yellow triangle for illustration in areas in a) England - based on sky view and slope, and b) Netherlands – based on minimum canopy height, highlighting the relative probability of the area to match habitat characteristics according to the relevant remotely sensed variable(s) of nearby hibernaculum locations.*



Discussion

One of the great advantages of using LiDAR in ecological models, is its ability to characterise a three-dimensional habitat structure of terrestrial environments in fine detail across large areas (Vierling et al. 2008). Despite the limitations that may affect accuracy of micro-topography and crown characteristics on tree height estimations of LiDAR canopy height models (Alexander et al. 2018) our remote sensed data was found to be effective in identifying topographic and vegetation features favoured by dormice in selecting hibernacula sites. We were able to demonstrate how specific features used by dormice when selecting hibernaculum location differed in distinct landscapes. Also, that there is an apparent difference in the variables that have explanatory power between the two studied countries and, although not readily transferable, they are able to indicate ecological variations at different scales. Additionally, our results indicated that remote sensing proved more efficient at identifying highly localised environmental characteristics in the wider landscape that may be important for hibernaculum selection when compared to habitat data collected *in situ* alone.

Similar to results reported by Cartledge et al. (2021) where slope featured as an important habitat descriptor for dormice during the active season, we found that topography was a key factor in hibernaculum selection in England with both slope and sky view variables distinctly featuring in top model sets. There, dormice built their hibernacula on slopes, avoiding narrow bottoms of deep valleys and largely building their hibernacula in leaf litter on the woodland floor. Additional subjective observations in the field suggest that where hibernacula were recorded on flat/low gradient landscapes, prone to or with the potential of being waterlogged, dormice built their nests slightly higher on grass tussocks, hazel stools, ferns or on top of fallen branches to avoid excessive dampness or being flooded during the hibernation period. In the Netherlands, although slope derived from the DTM did not prove a significant predictor of hibernacula location in this study, in a previous analysis using *in situ* field data gathered on the same nest-site dataset, Lemmers et al. (2022) found a significant difference in slope between nest sites and random locations, consistent with our observations in the English sites. This suggests that the field observations may have detected sloping features that were not well represented in the LiDAR data. Their study used a similar method but selected random locations within a 20m radius, rather than the 50m used in this study.

Cold air drainage, which can also be a proxy for water drainage, had a negative effect in England, suggesting dormice preferred to locate their hibernacula away from cold air flow and avoided areas such as ditches, trenches and gullies that may be a water conduit/accumulator. The positive effect of the sky view variable exerts, also indicate that locations such as the bottoms of valleys and gorges in general, where often cold air drainage values are higher, were avoided. In the

Netherlands, despite sloped terrain being present in the landscape, neither slope nor sky view index had explanatory power.

Surprisingly, solar radiation did not feature as a relevant variable capable of influencing hibernaculum location in neither country. Indeed, in England, some hibernacula were located under closed canopy away from forest edges, whilst others were fully exposed to sunlight, often recorded away from woody vegetation cover on open ground. The fact that solar radiation had little importance or effect is reflected by the negligible effect canopy cover had on hibernaculum location in both countries. Perhaps, due to nests being well insulated and constructed under leaf litter and other vegetation as well as the seasonal effect, solar radiation had no effect on hibernating animals during low temperature spells. With regards to canopy cover, many of the hibernaculum locations in England and the Netherlands share similar characteristics as described by Verbeylen et al. (2017) in Belgium, where they were often found in open areas within or surrounding woodland blocks. Dormice also seemed to avoid localised areas of woody scrub cover such as bramble *Rubus fruticosus*, mammal burrows and log piles, possibly as a measure to prevent predation or disturbance by other animals that actively seek out these features for shelter.

Whilst canopy height (vegetation above >0.1 m) was not an important factor for hibernaculum location in England, dormice seem to be clearly favouring woodland edges in the Netherlands. The effect size and importance of minimum canopy height extracted from the top model set showed the pronounced difference between the two countries. However, it is important to note that in the Netherlands dormice were captured and radio collared in nest boxes placed along woodland edges but even when considering their relatively small home ranges, the animals still opted to hibernate nearer to the woodland edge than randomised points in the vicinity of their capture locations. Similar observations were made with ground squirrel in North America by Goldberg et al. (2020) as hibernaculum locations had more canopy cover than random points but had less cover than sites used during the active season.

We have also found that data collected *in situ* on leaf litter depth, distance to nearest trees and canopy cover did not have significant predictive power in identifying hibernaculum locations. These are habitat features mentioned in the literature (see Bright et al. 2006) that were considered important for hibernating dormice, but do not alone seem to distinguish hibernaculum locations. Whilst some of our hibernacula shared similarities with the existing literature by being found at locations such as coppice stools, under moss and leaf litter, we did not find any under large stones, boulders, logs, tree roots or animal burrows. We found that distance between hibernaculum and nearest tree trunk or vine were not significant and mean distance was nearly three times greater (n=44) than the 0.5 metres reported by Bright (1992). Also, we were able to establish that the accuracy of canopy cover of the remotely sensed data could be compared with the information collected *in situ*.

Measured temperature had a minor influence in hibernaculum location. The average daily mean temperature at hibernaculum locations (n=19) was slightly lower than at random points collected at the hibernacula, indicating that dormice chose to hibernate at sites with lower average mean temperatures. This finding corroborates with Bright and Morris (Bright & Morris 1996) suggesting that dormice seek out a cool place on the ground to hibernate.

Our results suggest that using remote sensed data can be useful in detecting localised topographic features and climatic conditions that may be relevant to species that favour specific conditions during their life cycle or at certain life stages. With the relatively simplistic method and freely available high-resolution data, this methodology has the potential to provide more accurate species distribution and habitat suitability models.

As highlighted by Trout et al. (2012b), hibernating dormice are vulnerable to disturbance during hibernation at ground level, especially during forestry operations The predictive models can be useful to inform woodland and habitat management as well as development projects, potentially focusing survey efforts based on relevant habitat characteristics.

We found that the extent to which different remote sensed variables have explanatory power varied between countries and therefore cannot be considered species deterministic but context dependent. The explanatory variables were able to predict suitable dormouse hibernaculum locations across large areas of the landscape, indicating that these can be quite abundant and that dormice may be flexible or tolerant with regards to specific topographic features and environmental conditions in which to hibernate. This flexibility may also be an effective strategy to avoid predators such as birds, badgers, and foxes that could be biased to look for their hibernaculum at specific places on the woodland floor (e.g. next to tree trunk, on specific gradients or under closed canopy) whilst reiterating the benefit that a mosaic of microhabitats is capable of offering suitable conditions for hibernation.

Since the hazel dormouse and its habitat are fully protected throughout its European range, the modelling approach demonstrated here may prove useful in situations when habitat is being disturbed or destroyed by, for example, development, habitat management and forestry activities. In England and Wales, derogation licences issued to ensure legislation compliance against intruding activities within dormouse territory in the winter often require that systematic searches are undertaken to identify and/or move dormouse hibernacula to ensure the animal’s welfare. The predictive models presented in this study could highlight areas where searches should be focused, especially for large sites following verification using independent data or as more data becomes available.

Given the diversity of locations in which hibernating dormice were found, it is likely that suitable conditions for hibernation is relatively abundant within their home range as illustrated in our predictive models. Bright & Morris (1996) suggested that suitable places for hibernaculum are available in most woodlands and are unlikely to be a limiting factor, their findings also highlight that during this period animals might then be vulnerable to floods, trampling and predation.

The results of this study demonstrated for the first time that there are specific variables favoured by dormice when choosing hibernaculum locations. Whilst conservation efforts such as habitat creation, enhancement and management are of great importance for dormice, they have the potential to negatively impact on local populations when carried out indiscriminately during the hibernation season. The use of predictive models to highlight areas where dormice are likely to site their hibernacula can be a useful tool to inform and guide woodland management as well as large scale forestry operations to safeguard local populations.

Chapter 4

The elusive winter engineers: structure and materials of hazel dormouse hibernation nests

Chapter 4: The elusive winter engineers: structure and materials of hazel dormouse hibernation nests

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Abstract:

Trade-offs between specialist use of particular resources and opportunistic use of widespread materials may present different strategies for survival. Hazel dormice *Muscardinus avellanarius* are arboreal mammals that in Great Britain hibernate from late autumn to mid spring in nests that are specially built at ground level. Hibernation nests are rarely encountered, and little is known about the types of construction or materials used. Specifically, it is not known whether nest materials are selected opportunistically, based on their availability or are specialised to suit local environmental conditions. We therefore conducted a study to characterise the main materials used to construct these nests, explore the distances travelled to collect materials and investigate whether regional climate and/or local microclimate have an impact on the types of nests built.

Thirty-three hibernation nests were located through radio-tracking, systematic searches and incidental finds. Structurally, hibernation nests were built similarly to summer nests; and were most commonly constructed with an outer layer of leaves and distinct core section made of woven material. We found no correlation between nest type and the temperature recorded at nest sites. Nests were built using a mean of two materials per nest, which were both in every case available within 3m of the nest. The most frequently used materials were bracken, hazel and beech leaves, and grasses. Dormice were flexible in their use of nest materials, using various materials harvested very locally. However, dormice travelled further to collect grasses, ferns, bracken and honeysuckle and these materials made up most of the nests in which they were found. There were also positive correlations between material abundance and usage, and suitable materials for hibernation nest construction were therefore readily available within their home range.

Keywords: hazel dormouse, hibernation, *Muscardinus avellanarius*, nest material, resource selection, winter nest.

Introduction

Conservation management of threatened species requires detailed understanding of their resource requirements. Establishing which resources are selected more often than others provide fundamental information about how animals meet their requirements for survival (Manly et al. 2007). Habitats can be defined in terms of the composition, structure and connectedness of resources (Dennis et al. 2003), and hence the availability of critical resources may determine whether a species can exploit a particular habitat.

At temperate latitudes, climatic conditions and habitat structure often differ markedly between the seasons, and this variation is commonly reflected in animal behaviour, resource use and habitat associations (Law & Dickman 1998, van Horne 1983). Evolutionary responses to seasonal variations include, for example, dormancy, migration, and hibernation (MacArthur 1959, Pérez-Tris & Tellería 2002, Buckley et al. 2012). Thus, species living in highly seasonal environments often require specific resources during each season and so focusing conservation efforts solely on their requirements during particular seasons or life stages may neglect other important components of habitat quality.

Nest building is a key aspect of the ecology of many species and the use of resources from which to build nests has been observed across many different taxa, including mammals, birds, fish and insects, which are used to lay eggs and/or raise offspring (Hansell 2000) and also for shelter and roosting (Rosalino et al. 2011). Resource selection has been observed in birds where the use of nest materials was associated with local availability and geographical location (Briggs & Deeming 2016, Deeming et al. 2012) and their design and function are complex (Mainwaring et al. 2009).

The hazel dormouse *Muscardinus avellanarius* is a mainly nocturnal, arboreal mammal that spends most of its active season in the shrub layer or canopy, coming down to the ground to hibernate in late autumn (Bright & Morris 1991, Bright & Morris 1996). In Great Britain, the dormouse hibernation period is mainly from October to May, depending on local climatic conditions. The striking variation in their behaviour over the course of the year makes the hazel dormouse a particularly suitable species to explore changes in habitat requirements according to seasonal conditions.

Adult dormice are relatively sedentary and have home ranges of around 0.5–1.0 ha during the active season (Bright & Morris 1991, Juškaitis 1997, Goodwin et al. 2018). During this time, they typically build natural nests in thick scrub, hollows and crevices in shrubs and trees and along hedgerows.

Over the year, dormice build two main types of nests. Summer nests are used for shelter and/or breeding (Foppen et al. 2002) and are usually situated above the ground at varying heights, from tussocks of grass close to ground level to high in the canopy of mature trees (Hurrel & McIntosh, 1984, Foppen et al. 2002, Juškaitis and Remeisis 2007, Müller-Stiess 1996, van Laar 1979). Winter hibernation nests are normally constructed at ground level (Bright & Morris 1996, Eden 2009, Juškaitis 2014, van Laar 1984), under moss, in the leaf litter, or at the bases of coppice stools and of thick hedges (Bright et al. 2006). Summer nests are normally built using grass, leaves, moss, bark and ferns (Bertolino et al. 2016, Bracewell & Downs 2017, Kahmann & von Frisch 1950, Vilhelmsen 1996, Wachtendorf 1951, Zaytseva 2006,) though the use of anthropogenic materials has also been observed (L. Gubert, pers. obs.). Dormice build summer nests using nearby materials (Kahmann & Frisch 1950; Vilhelmsen 1996), though the plant species used as materials will differ between regions, based on botanical composition (Juškaitis 2014) and individual preference (Kahmann & Frisch 1950; Wachtendorf 1951). Eden (2009) suggested that dormice tend to choose large leaves such as hazel (*Corylus avellana*) and beech (*Fagus sylvatica*) to build summer nests, avoiding small-leaved species (such as blackthorn *Prunus spinosa*), whilst Wachtendorf (1951) suggested that the frequent use of certain material is related primarily to their abundance.

An existing classification of dormouse nests was proposed by Wachtendorf (1951) based on nest structure and materials: foliar nests, built from dry or fresh leaves of trees or shrubs; mixed nests made from woven leaves of trees and shrubs together with grass leaves and stalks that are used to form the walls; layered nests that have two distinct layers, the outer layer consisting of leaves with a core section made of finer, often woven material, such as grasses and stripped honeysuckle *Lonicera periclymenum* bark; and grassy nests in the shape of spheres made of woven grass leaves, stripped bark and stalks.

Despite the limited amount of information on materials used for the construction of hibernation nests, previous studies have suggested that dormice use similar materials for the construction of both summer and hibernation nests (Walhovd & Jensen 1976, Vogel & Frey 1995, Morris 2004, Juškaitis 2014). Verbeylen et al. (2017) is one of few studies that details hibernation nest material usage based on 19 nests constructed mainly of stripped bark, stems and leaves of several species including clematis (*Clematis vitalba*), grasses, herb stems, ferns, honeysuckle , bark and leaves of several trees including hazel, ash (*Fraxinus excelsior*), sycamore (*Acer pseudoplatanus*) and oak (*Quercus robur/Q. petraea*); whilst Vogel & Frey (1995) reported wide use of beech leaves and occasionally grass blades in 10 hibernation nests. Other previous studies have focused on their size, shape and thickness (Walhovd & Jensen 1976, Vogel 1997, Morris 2004) but lacked detail of what materials are used. The scarcity of information on hibernation nests can be attributed to the fact that they are difficult to find and in most cases are only found incidentally.

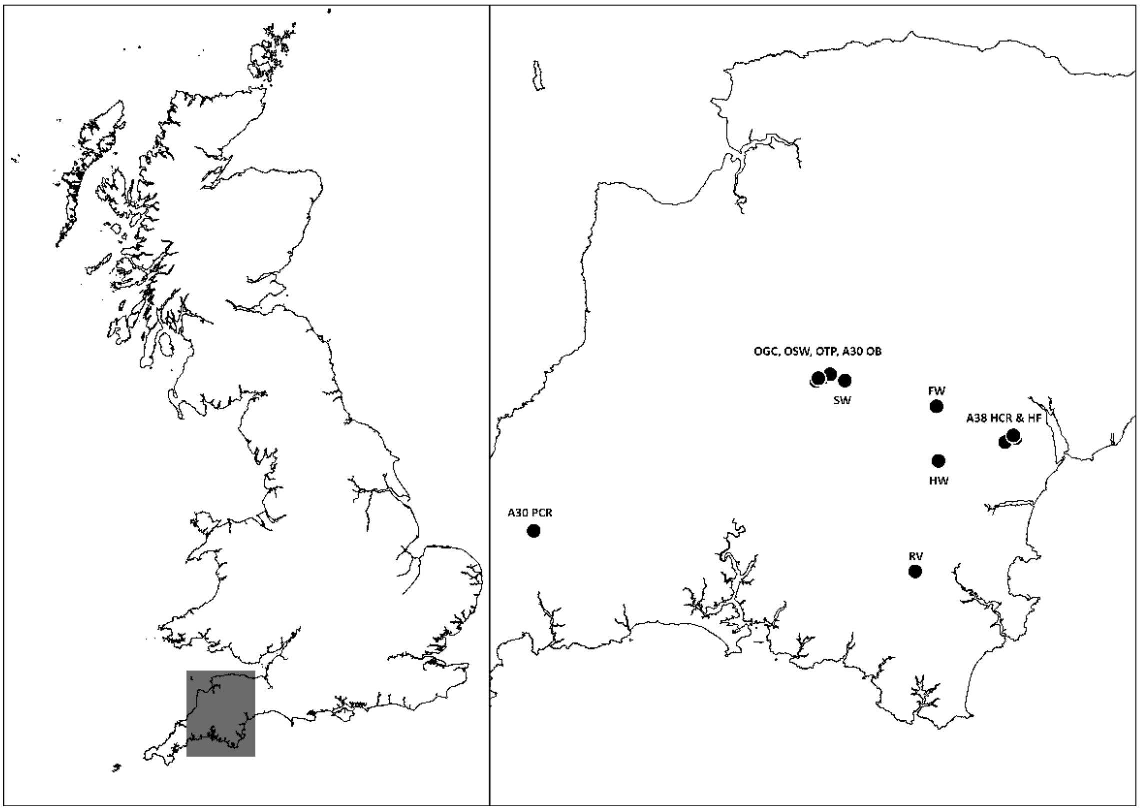
The objectives of this study are to establish a) whether there are different types of construction of hibernation nests, as has been observed to be the case for summer nests (Wachtendorf 1951), and the extent to which construction and materials correspond to those in summer nests; b) whether there is a relationship between the composition of materials in the nest and availability of potential materials in the surroundings; c) how far dormice travel to collect each nest material; and d) whether ambient temperatures are linked with nest materials and/or construction.

Methods

Study areas

The study was conducted in areas of broadleaved and coniferous woodland, roadside habitats, and hedgerows in southwest England (Devon and Cornwall) where dormice had previously been recorded (Fig. 1). These locations represent the main habitat types used by hazel dormouse in GB. Apart from hedgerows, the study areas included other vegetation types that formed a mosaic of habitats, comprising scrub, grasslands, marginal vegetation, and woodland edge.

Figure 4.1. *Locations of study sites in Devon and Cornwall in the southwest of England.*



Hibernation nest survey

Nests were found by three methods: radio tracking of 30 individual dormice (of which 15 led to hibernation nests) during the pre-hibernation period in winter 2016/17, systematic 'fingertip' searches of the ground within known hazel dormouse habitat and incidental findings where animals were detected during woodland/hedgerow management.

Studies on summer nests use deconstruction methods to measure the dry weight of each component (see Bracewell & Downs 2017 and Zaytseva 2006) but this was not possible here because most nests were occupied or there was a chance that animals might return to the nests that were empty. Hence, nests were generally left onsite and not removed for further analysis.

The materials used in the construction of each nest were identified whilst empty, and a visual estimate of the proportion of each item was recorded. Materials such as leaves and conifer needles were identified to species, except for ferns, grasses and mosses. Samples of nesting materials that could not be identified *in situ*, e.g. pieces of stripped bark, were taken to the lab for accurate identification using a hand lens and/or microscope. Materials that made up <1% of the nest, such as fragments of leaves and bark, were not identified or accounted for. Bracken was recorded separately from other ferns owing to its ability to tolerate a range of habitat conditions as well as its capacity to quickly dominate ground cover.

At each site, materials that were available for nest construction were visually assessed and the percentage of ground cover of each species was recorded within a 300 cm radius of the nest, and the linear distance between the nest and the nearest source was measured using a tape.

To test the hypothesis that temperature is linked with choice of nest materials or the method of nest construction, the temperature at each precise nest location was recorded. Individual thermal data loggers (Thermochron iButton (Dallas Semiconductor, California USA) were used simultaneously next to hibernation nests at 22 nest sites for 75 consecutive days between 12 November 2016 and 26 January 2017 recording hourly readings from which mean daily maximum, daily minimum and daily average temperatures were calculated.

Data analysis

Statistical analyses were conducted using R within the R studio environment (RStudio Team 2020, RCore Team 2017). The relationships between the proportion of materials in the nest and availability of that material within 0-100 cm, 100-300 cm and within the 300 cm radius from the nest, were tested. Confidence intervals were calculated using the Wilson Method as recommended by Brown et al. (2001) and Agresti & Coull (1998). This analysis has been extended to incorporate the effect of the availability of alternative materials within hibernacula vicinity. General linear models were used to test whether the proportion of a given nest material was linked to availability of all materials in the surrounding environment. The logit transformed proportions (Warton & Hui 2011) of each of the recorded vegetation types within a 3m radius of the nest were specified as predictor variables. The most parsimonious model was selected using backward removal of variables with highest p-values and assessment of the change in the AIC (Akaike's Information Criteria) value. Due to multiple testing of nest material types, Bonferroni corrections were applied to reduce experiment-wide error rate. Bonferroni correction has been criticized as being too conservative, particularly when the tests performed are highly correlated (Cabin & Mitchell 2000, Moran 2003); therefore, both corrected and uncorrected results are presented.

Kendall’s Tau correlation tests were used to test whether the distance to get a nest material is negatively related with its use (i.e. if animals have to travel further, they use less). Kruskal-Wallis rank sum tests were carried out to establish whether temperature at the hibernaculum varied among nest types (Layered, Grassy, Foliar, Mixed).

Results

In total, 33 hibernation nests were found between 2008 and 2017; 24 by radio-tracking, 5 by systematic searching and 4 were found incidentally. Radio tracking identified that four animals moved once to new hibernacula, one individual moved twice and another that moved hibernaculum three times building four different nests over its hibernation period.

Types of nests

The classification used for summer nests could be applied satisfactorily to winter nests (Fig. 2). Layered nests were the most common (42.4%), followed by Grassy (30.3%), Foliar (18.2%) and Mixed (9.1%). Grassy nests included those constructed entirely by grass and/or long and thin materials of similar shape of grass blades (e.g. stripped honeysuckle/bracken (*Pteridium aquilinum*) /fern bark, dry bluebell (*Hyacinthoides non-scripta*) stems or fern stems) arranged in the characteristic sphere shape. Foliar nests included those made of bracken fronds.

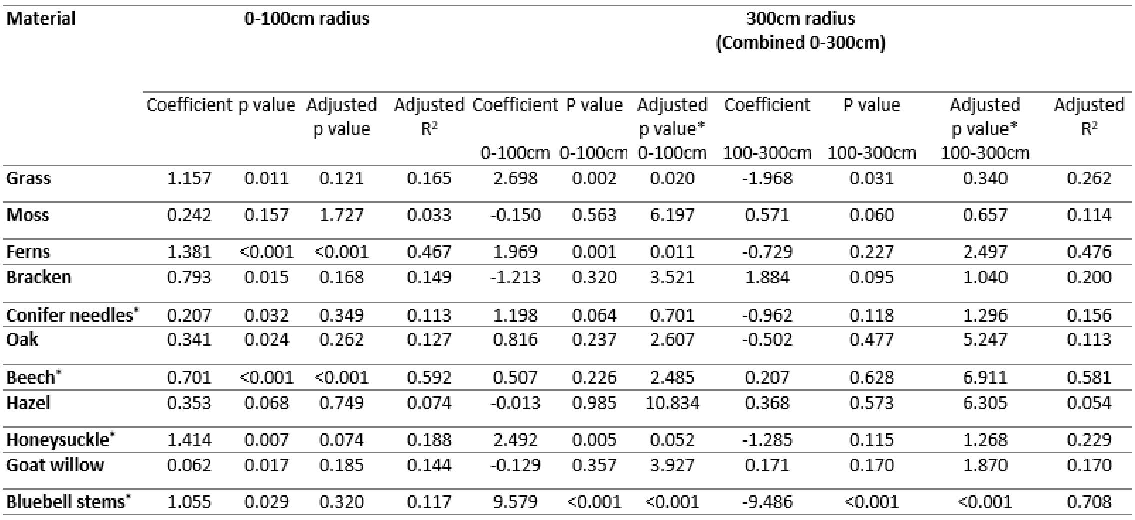
The radio tracked animals that moved nests once or twice built a different nest type in all instances and the animal that moved three times built four nests of three different types.

Figure 4.2. *a) layered nest with an outer layer made of moss with a distinct core of stripped fern stems and grass, b) typical woven structure of grassy nests or core of layered nests (this example is built mostly with honeysuckle bark and the dormouse has been made visible), c) a foliar nest utilising ferns and broad-leaved tree leaves, and d) an in situ mixed nest made of leaves and grass stems.*

Nest materials used

The number of different materials used in each nest ranged from one to five (n=33, mean= 2.2, SD=1.6). Although 31 potential known nest materials known in the literature for their use in summer and hibernation nests were identified within 300 cm of hibernacula, only 11 materials were used in construction (Table 1). Nine of the 11 materials constituted > 50% of the composition of a nest on at least one occasion. All materials used for the construction of hibernation nests were present within a 300 cm radius of the nests (Table 2).

Table 4.1. *Regression values for the proportion of used materials in the nest (all nests were taken into account including sites where certain materials were not available in the radii) against proportion available within 100 cm radius and 0-300 cm radius. The only materials with significant results between 100-300 cm radius were fern and beech and were omitted from the table for clarity. The adjusted p values were obtained using Bonferroni correction to control the overall probability of a false significant result after multiple comparisons were carried out, with number of comparisons (n) set to 11 to match the number of nest materials presented on the table. Where p ≤ 0.05, there is a significant positive relation between the proportion of materials found in the nest and proportion available in the immediate surrounding area.*

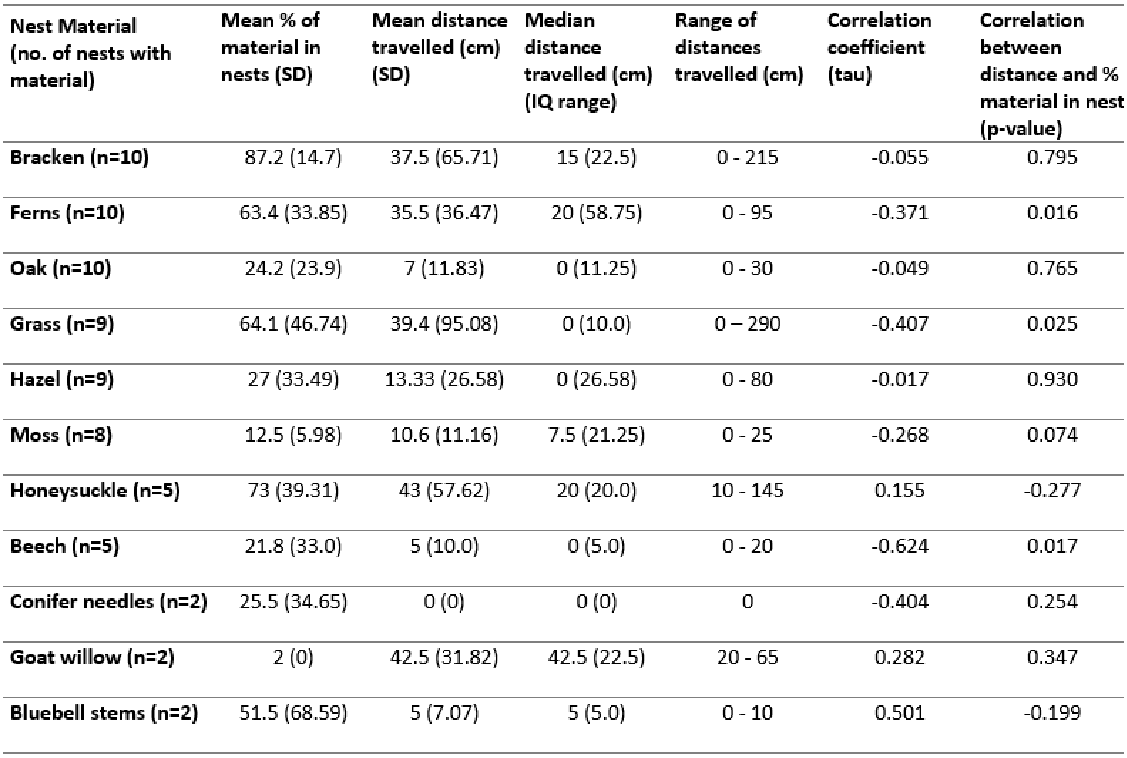


Material	**0-100cm radius**				**300cm radius (Combined 0-300cm)**						
	Coefficient	p value	Adjusted p value	Adjusted R^2	Coefficient 0-100cm	P value 0-100cm	Adjusted p value* 0-100cm	Coefficient 100-300cm	P value 100-300cm	Adjusted p value* 100-300cm	Adjusted R^2
Grass	1.157	0.011	0.121	0.165	2.698	0.002	0.020	-1.968	0.031	0.340	0.262
Moss	0.242	0.157	1.727	0.033	-0.150	0.563	6.197	0.571	0.060	0.657	0.114
Ferns	1.381	<0.001	<0.001	0.467	1.969	0.001	0.011	-0.729	0.227	2.497	0.476
Bracken	0.793	0.015	0.168	0.149	-1.213	0.320	3.521	1.884	0.095	1.040	0.200
Conifer needles*	0.207	0.032	0.349	0.113	1.198	0.064	0.701	-0.962	0.118	1.296	0.156
Oak	0.341	0.024	0.262	0.127	0.816	0.237	2.607	-0.502	0.477	5.247	0.113
Beech*	0.701	<0.001	<0.001	0.592	0.507	0.226	2.485	0.207	0.628	6.911	0.581
Hazel	0.353	0.068	0.749	0.074	-0.013	0.985	10.834	0.368	0.573	6.305	0.054
Honeysuckle*	1.414	0.007	0.074	0.188	2.492	0.005	0.052	-1.285	0.115	1.268	0.229
Goat willow	0.062	0.017	0.185	0.144	-0.129	0.357	3.927	0.171	0.170	1.870	0.170
Bluebell stems*	1.055	0.029	0.320	0.117	9.579	<0.001	<0.001	-9.486	<0.001	<0.001	0.708

*Honeysuckle bark and beech leaves were found in five nests each whilst bluebell stems and conifer needles were present only in two nests, so the results for these materials should be interpreted with caution.

The most common materials recorded within 300 cm of the nest sites were pleurocarpous mosses (mainly *Thuidium tamariscum*, *Hylocomium splendens* and *Rhytidiadelphus squarrosus*), oak (*Quercus robur* and *Q. patrea*) leaves, grasses, hazel leaves and honeysuckle. Three of the materials (ferns, bracken and oak leaves used either individually or in conjunction) were used in > 66% of nests, whereas conifer needles, goat willow (*Salix caprea*) leaves and bluebell stalks were rarely used (only 18% of nests).

***Table 4.2**. Percentage of nest materials used, and distance from nest to source of nest material measured in a straight line. SD = standard deviation. IQ range = inter-quartile range. Correlation between distance and % material in nest presented as p-value obtained from Kendall's tau coefficient (values are negative signifying that a lower proportion of material was used when it was available further away from the nest).*



Nest Material (no. of nests with material)	Mean % of material in nests (SD)	Mean distance travelled (cm) (SD)	Median distance travelled (cm) (IQ range)	Range of distances travelled (cm)	Correlation coefficient (tau)	Correlation between distance and % material in nest (p-value)
Bracken (n=10)	87.2 (14.7)	37.5 (65.71)	15 (22.5)	0 - 215	-0.055	0.795
Ferns (n=10)	63.4 (33.85)	35.5 (36.47)	20 (58.75)	0 - 95	-0.371	0.016
Oak (n=10)	24.2 (23.9)	7 (11.83)	0 (11.25)	0 - 30	-0.049	0.765
Grass (n=9)	64.1 (46.74)	39.4 (95.08)	0 (10.0)	0 – 290	-0.407	0.025
Hazel (n=9)	27 (33.49)	13.33 (26.58)	0 (26.58)	0 - 80	-0.017	0.930
Moss (n=8)	12.5 (5.98)	10.6 (11.16)	7.5 (21.25)	0 - 25	-0.268	0.074
Honeysuckle (n=5)	73 (39.31)	43 (57.62)	20 (20.0)	10 - 145	0.155	-0.277
Beech (n=5)	21.8 (33.0)	5 (10.0)	0 (5.0)	0 - 20	-0.624	0.017
Conifer needles (n=2)	25.5 (34.65)	0 (0)	0 (0)	0	-0.404	0.254
Goat willow (n=2)	2 (0)	42.5 (31.82)	42.5 (22.5)	20 - 65	0.282	0.347
Bluebell stems (n=2)	51.5 (68.59)	5 (7.07)	5 (5.0)	0 - 10	0.501	-0.199

Some materials such as honeysuckle were rarely used but formed a high proportion of the nest when they were present (Fig. 3). Moss on the other hand, despite being the most common material widely available (97% of sites) was only used in around 24% of the nests.

There was an overall positive relationship (R2 = 0.54, p = 0.005) between the number of sites where a material was available and its use in nests, but no correlation was found between availability and the tendency for a material to form the main nest component (R2 = 0.078, p = 0.060).

Grasses, ferns, bracken and honeysuckle made up most of the materials in the nests they were found (Table 2). Dormice had also travelled further to collect these materials than others (minima distances between 95 and 290cm; minima for all other materials were <= 80 cm). However, most materials were collected very close to the nest (<50 cm). For grass, ferns and beech, the proportion of the material used in the nest was greater when it was found closer to the nest site (negative correlations between use and distance), potentially suggesting some opportunistic exploitation of these materials for construction.

Figure 4.3. *Relationship between material availability and their use in dormouse hibernation nests in southwest England. a) Number of nests including the material and b) Number of nests where the material was the main nest component, both plotted against the number of sites where the material was found within a 3oo cm radius from the nest.*

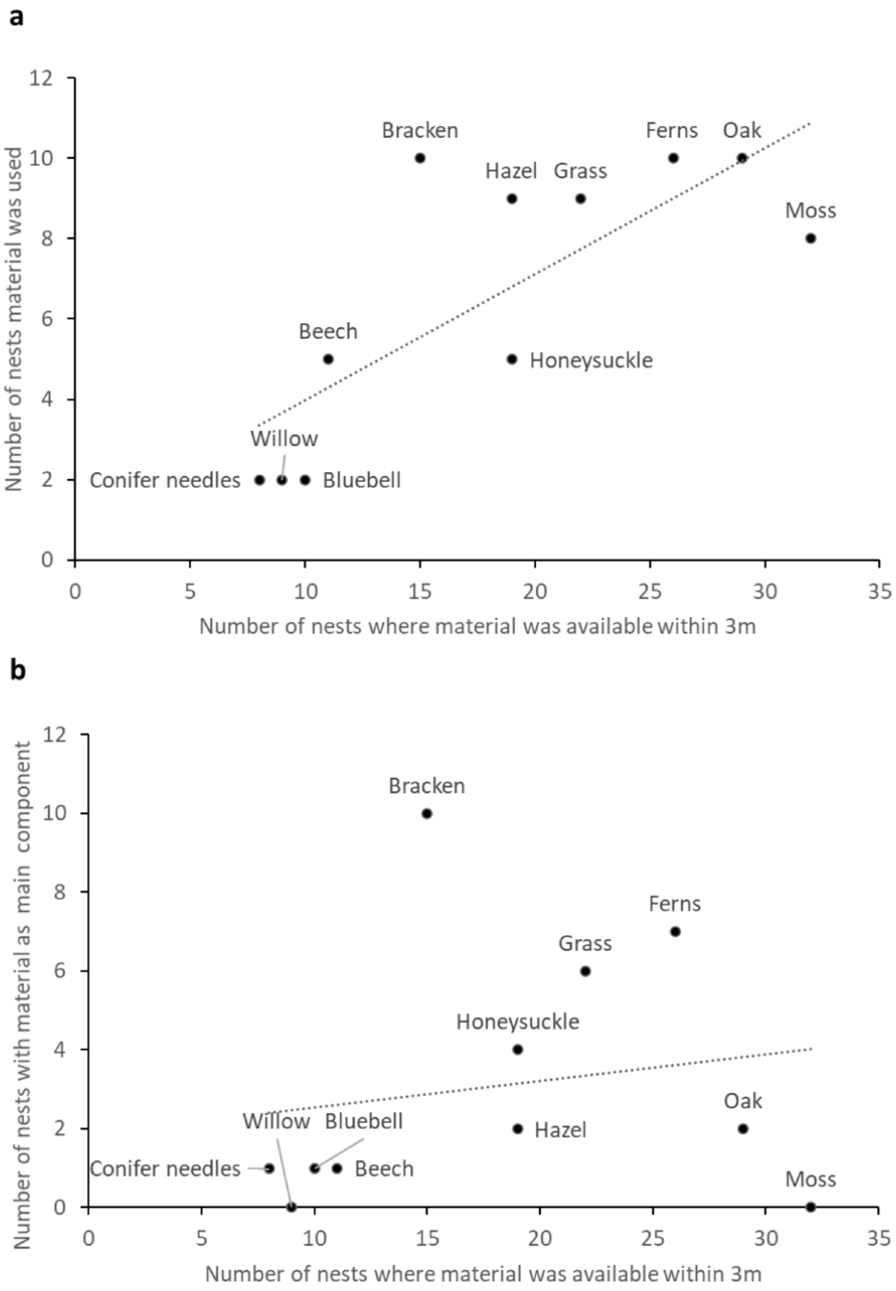
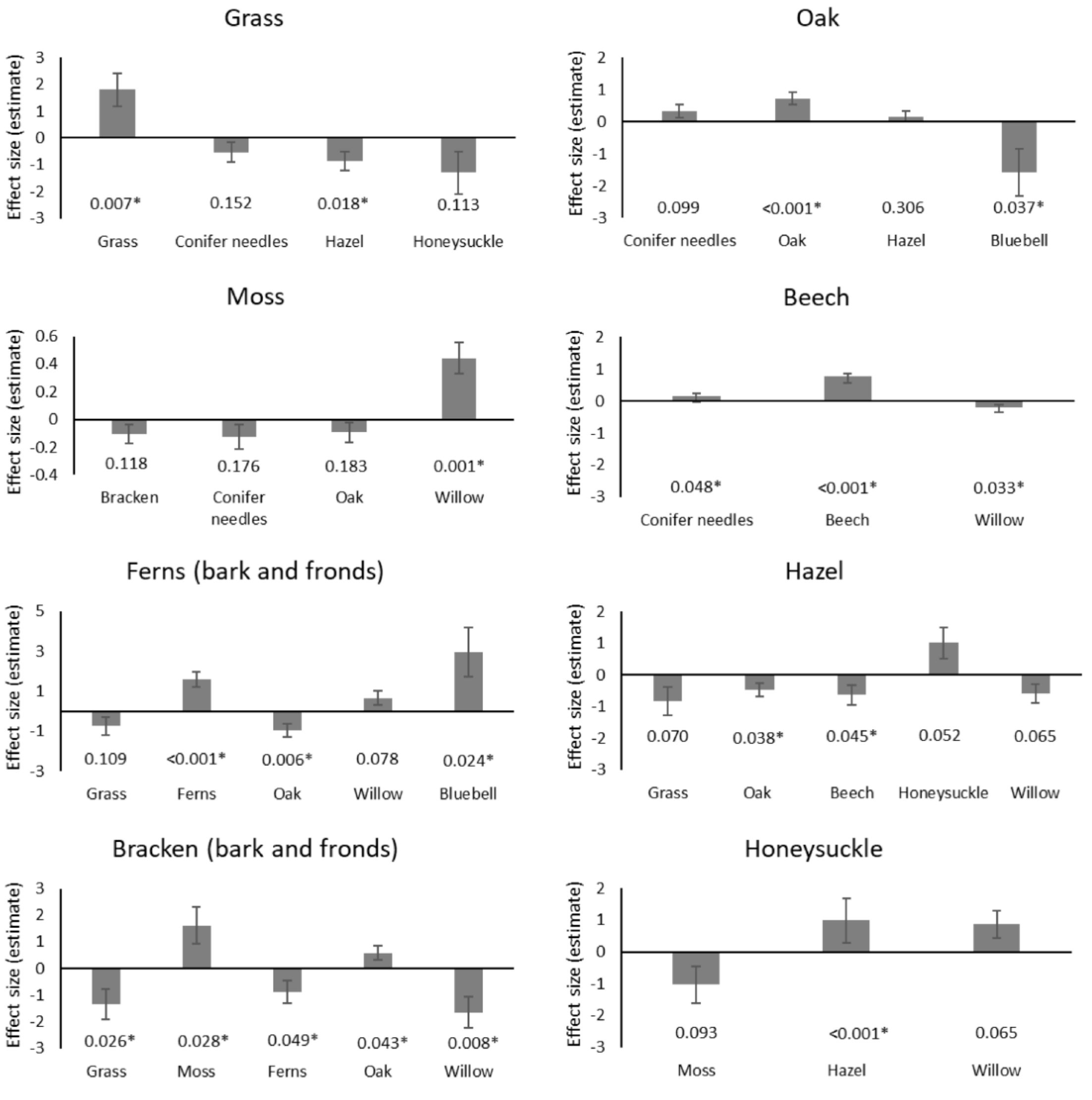


Figure 4.4. *Result of generalised linear models to test whether use of one focal nest material was affected by the presence of other known nesting materials within a 300 cm radius of the hibernaculum. Bars represent other availability nesting materials; a positive effect suggests that the presence of this material increases the likelihood of usage of the focal material, a negative effect suggests a decreased likelihood. Only predictor variables included in the parsimonious models are shown. P values are given under each bar. Error bars represent 95% confidence intervals.*

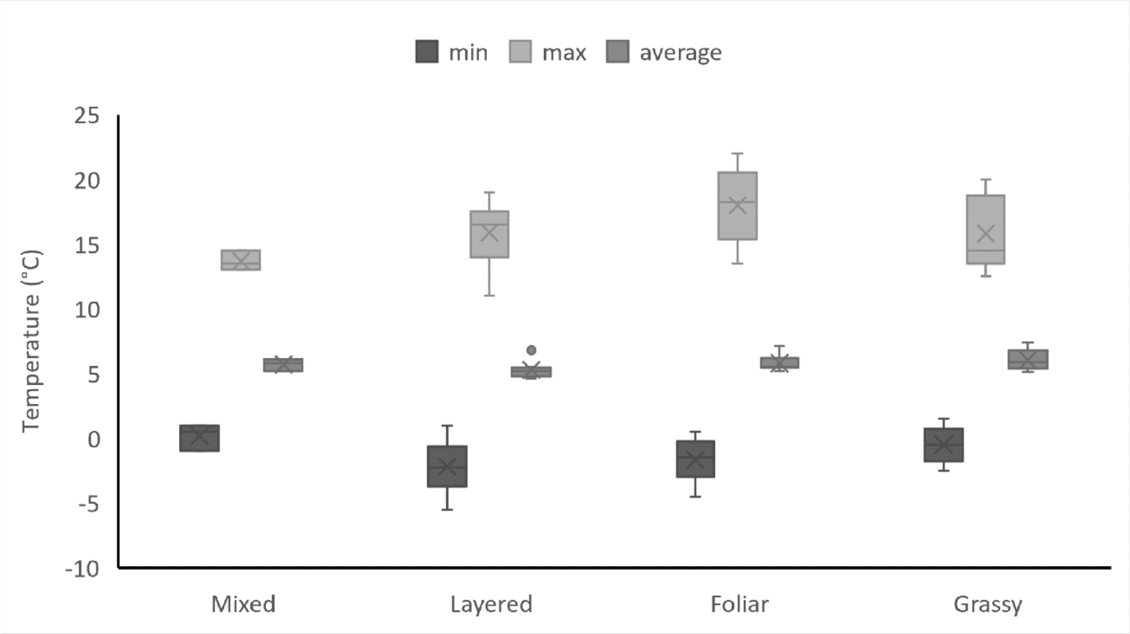


The results of the generalised linear models highlight whether the proportion of each material used within the nests was related to the abundance of other available items known to be used in dormouse nests that were recorded within a 300 cm radius of the hibernaculum (Fig. 4). The lowest achieved AIC (Akaike's Information Criteria) for the most frequently used materials indicated the most parsimonious model. For example, grass was preferred in areas where conifer needles, hazel and honeysuckle were least abundant; honeysuckle was mostly used where grass was not common, bracken was preferred in areas where oak was present but with little grass, ferns and willow whereas moss usage was associated with abundant willow where bracken, conifers and oak were scarce.

Nest site temperature profiling

Different types of nest construction (Layered, Grassy, Foliar, Mixed) were not associated with differences in ambient temperature (Kruskal-Wallis rank sum tests for T_{min} were p = 0.101, T_{max} p= 0.192 and $T_{avereage}$ p= 0.147; Fig. 5).

Figure 4.5. *Nest types and temperature recorded at nest sites. Daily mean minimum, maximum and average temperatures reflect values recorded simultaneously at 22 nest sites for 74 days. Boxes represent the range of temperatures recorded, crosses are the mean markers, and the lines are the median values whilst error bars extend upward from the third quartile to the maximum, and the other extends downward from the first quartile to the minimum.*



Discussion

This study is based on one of the largest datasets available for dormouse hibernation nests. It shows that the species uses similar nest structures as those deployed in summer. We discuss these results in the context of nest material use according to their availability and effort required (distance covered) to collect them.

Nest material availability and use

Overall, a wide range of materials are used in nest construction, probably related to their availability within the home range, however the hazel dormouse used a relatively low number of materials to construct hibernation nests, ranging from 1 to 5 ($\bar{x}$ = 2.22) similar to results presented elsewhere in hibernation nests ($\bar{x}$ = 2.52 by Verbeylen et al. 2017) and summer nests ($\bar{x}$ = 3.54 by Bracewell & Downs 2017). There was plasticity in how the materials were used, with some being used on their own or in conjunction with others and there was positive relationship between proportion of materials available in the immediate surroundings and their use in the nest. A similar positive relationship was found for bird's nests by Briggs & Deeming (2016) where leaves found in pied flycatcher nests generally reflected their availability within individual's territories rather than showing evidence of selective use of materials.

The most frequently used materials from our dataset were bracken, hazel and beech leaves, and grasses. Bracken was one of the most extensively used materials, proving to be a versatile item as both fronds and stripped bark from the stems were utilised on their own or in conjunction with other materials. Although the use of bracken was not associated with its abundance, it was used where there was less grass and ferns, and in woodlands with oak and moss and occasional goat willow.

Our results also showed that moss was present at every site except for one, where the nest was in an area of abundant holly understory. Mosses are good indicators of high levels of ground moisture and humidity, which are thought to be an important factor in the dormouse nest site selection process to prevent dehydration over winter (Morris 2004). Despite its wide distribution, moss use in nests was not strongly associated with the local abundance of moss but was significantly more commonly used in areas with goat willow (wetter parts of woodland habitats) and less so in oak or conifer woodlands.

Beech was also popular and, when available, there was 50% uptake of beech leaves in nest construction and proved to be prominent at sites with conifers. The high usage could also be attributed to the fact that beech tends to shade the woodland floor outcompeting other species of plants for light and diminishing the diversity of other plants that could be used as nest material.

Distance travelled to collect materials

Most of the material used in hibernation nests were collected within one metre of the nest. Verbeylen et al. (2017) found similar results in Belgium, although some were collected up to 15 metres away. Bracewell and Downs (2017) found that dormice can cover long distances to collect summer nest materials (up to 50m), whereas materials for the hibernation nests studied here were available very locally, all within 3m and typically within 50cm of the nest. This may be because dormice have evolved to avoid movements on the ground (Bright et al. 2006). By collecting materials for hibernation nest in the immediate surroundings, dormice can reduce construction time and minimise exposure to potential predators. It is also possible that the use of local materials ensures that the nest blends in with the background making it less conspicuous. The use of materials from local vicinity has also been reported in other taxa although distances travelled may vary, for example, in a study investigating the use and distance of artificial nest material by various species of birds, Surgey et al. (2012) found that the proportion of birds using the material declined with increasing distance with a reported mean of 167.8 m and maximum of 860 m between source and nest.

Hibernation nest classification and temperature profiling

As opposed to some studies on bird nests where temperature and environmental conditions seem to have an effect on nest design and construction such as to create suitable microclimate for parents and developing offspring (Mainwaring et al. 2012 & 2014), there was no clear evidence from this study that temperature in the hibernaculum vicinity, which varied widely within and among sites during the hibernation period, influenced the type of nest construction.

Hibernation nests can be classified into the same categories as summer nests, and all four types were recorded in this study. Layered nests made up most of our records, followed by Grassy, Foliar and Mixed. Nest materials and structures will clearly vary widely among locations and between seasons (Juškaitis 2014), though detail of nests in Britain are scant, particularly for winter nests. Bright (1992), identified 14 hibernation nests, most frequently made of woven honeysuckle bark under sheets of moss, while Bracewell and Downs (2017) identified 56 summer nests in nest boxes, all of the Layered type. Across the species' wider range, the classification of summer nests in natural sites have received more attention, such as the study by Wachtendorf (1951) at the foothill of the Alps where 316 nests were classified with a higher proportion of Mixed nests (57%), then Foliar (20%), Grassy (13%) and Layered (10%). Nest types in nest boxes or tubes have also been reported such as the study in Ukraine by Zaytseva (2006), where Mixed nests in 41 nest boxes was the most common (54%), followed by Foliar (24%), Layered (20%) and Grassy (2%);and in Belgium by Verbeylen et al. (2017), where layered nests were the most common type in both nest boxes and nest tubes (55%) followed by Foliar (24%), Mixed (12%) and Grassy (8%, n=378: including only nests for which the type was accurately recorded).

Given the lack of elaborate structure and the simplistic way they are built, Foliar and Mixed nests may be quicker to construct than the Grassy and Layered types, but they were observed during this study to offer less protection against weather conditions as they quickly deteriorated once animals had left the nests. However, no significant relationships were detected between nest type and temperature, suggesting that there were no preferences for a particular nest type in cooler or warmer sites. It remains unclear why different types of nests were built, particularly by those animals that moved hibernaculum during hibernation and built a different type of nest. This may be because there is less variation in temperature in woodlands which function as a thermal insulator, cooling the understory when ambient temperatures are high and warming the understory when ambient temperatures are low, thus reducing temperature oscillation at nest sites under canopy cover (De Frenne et al. 2019).

Implications for dormouse conservation

Despite the use of different materials often in different ways, this study highlights the importance of certain species of plants, such as bracken, honeysuckle, and grasses, as source materials that are commonly used in hibernation nests in Southwest England. Bracken was found to be one of the most common materials found in hibernation nests and is often controlled or eradicated from sites due to their invasive nature or conflict with other conservation or economic interests. We also found associations of the use the use of certain nest materials according to what is available. For instance, the use of hazel leaves is associated with habitats with little grass, willow, oak and beech availability, and higher availability of honeysuckle. The latter proved to be used more at locations where hazel leaves were also abundant. Whereas the use of grass in nests increased where it is locally abundant, and slightly less in woodlands with a lot of hazel, conifers and/or honeysuckle. Oak leaves were used where they were more abundant but proved to be less preferred when grass, ferns or goat willow were present.

It is known that the hazel dormouse is adaptable and versatile, able to forage and build summer nests in a range of habitats incorporating trees and shrubs (Chanin & Woods 2003, Eden 2009). We found that this flexibility also extends to the colder months when it comes to the selection of hibernation nest materials. Given the high plasticity of nest material use it is expected that, in terms of nest materials at least, if a site is suitable for dormice in the active season, there should be suitable materials for hibernation nest construction as most of the species of plants described here are associated with dormouse habitats. The presence of bracken, grass and honeysuckle are capable to provide sufficient resources for nest construction. Even in areas dominated by conifers which are not considered a common source of nest material, dormice proved flexible and able to build nests with a range of materials available suggesting that nest materials alone may not be a defining factor for hibernaculum location.

Declarations

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Author contributions

The manuscript was created by LG. The fieldwork was planned by LG, PC, FM and RW and conducted by LG. Data was analysed by LG, with advice from FM, JB and RW. The manuscript was written by LG and reviewed and revised by FM, JB, PC, RMc and RW.

Permits

Fieldwork was conducted under license from Natural England 2015-11955-SCI-SCI, Home Office PPL 3003431 and PIL I69D694C7, and with the approval of the University of Exeter College of Life and Environmental Sciences (Streatham Campus) animal ethics committee. Work within designated areas were carried out under consent from Natural England and/or under landowners’ agreement.

Data accessibility Statement

The research data supporting this publication are openly available from the University of Exeter's institutional repository at: https://doi.org/10.24378/exe.3603.

References

Agresti, A. and Coull, B. A. (1998). Approximate is better than “exact” for interval estimation of binomial proportions. *The American Statistician,* ***52***(2): 119-126.

Berg, L. and Berg, A. (1998). Nest site selection by the dormouse *Muscardinus avellanarius* in two different landscapes. *Annales Zoologici Fennici,* ***35***(2): 115-122.

Bertolino, S., Büchner, F., Mori, E., Büchner, S. (2016). Presence of the hazel dormouse *Muscardinus avellanarius* at the limit of its altitudinal range. Hystrix **26**, 1–4.

Bracewell, M. and Downs, N. C. (2017). Hazel dormouse (*Muscardinus avellanarius*) nest material preferences and collection distances, in southern England. Mammal Communications **3**: 1-10, London.

Bright, P.W. (1992). Ecology and conservation of the dormouse (*Muscardinus avellanarius*). Doctoral dissertation, University of London.

Bright, P. and Morris, P. (1991). Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius*, in diverse low-growing woodland. *Journal of Zoology* ***224***: 177-190.

Bright P. and Morris P. (1996). Why are dormice rare? A case study in conservation biology. Mammal Review, **26**: 157–187.

Bright, P., Morris, P., & Mitchell-Jones, A. J. (2006). The Dormouse Conservation Handbook. English Nature, Peterborough.

Brown, L.D., Cai, T.T., DasGupta, A. (2001). Interval estimation for a binomial proportion. *Statistical science*, 101-117.

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography, **21**(9), 873-885.

Cabin, R. and Mitchell, R. (2000). To Bonferroni or not to Bonferroni: when and how are the questions. *Bulletin of the Ecological Society of America,* ***81***(3): 246-248.

Chanin, P. and Woods, M. (2003). *Surveying dormice using nest tubes: results and experiences from the South West Dormouse Project.* English Nature Peterborough.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Lenoir, J. (2019). Global buffering of temperatures under forest canopies. Nature Ecology & Evolution, **3**(5), 744.

Deeming, D. C., Mainwaring, M. C., Hartley, I. R., & Reynolds, S. J. (2012). Local temperature and not latitude determines the design of Blue Tit and Great Tit nests. Avian Biology Research, **5**(4), 203-208.

Dennis, R. L., Shreeve, T. G., van Dyck, H. (2003). Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. Oikos, 417-426.

Eden, S. (2009). Living with dormice. The common dormouse: real rodent or phantom of the ancient world. Papadakis Publisher, Great Britain. pp. 128..

Foppen, R., Verheggen, L.S.G.M. and Boonman, M. (2002). Biology, status and conservation of the hazel dormouse (*Muscardinus avellanarius*) in the Netherlands. Lutra, **45**(2), 147-154.

Goodwin, C.E., Hodgson, D.J., Bailey, S., Bennie, J. and McDonald, R.A. (2018). Habitat preferences of hazel dormice *Muscardinus avellanarius* and the effects of tree-felling on their movement. Forest ecology and management, **427**, 190-199.

Hurrell E. and McIntosh G. (1984). Mammal Society dormouse survey, January 1975 – April 1979. Mammal Review, **14**, 1–18.

Juškaitis, R. (1997). Ranging and movement of the common dormouse *Muscardinus avellanarius* in Lithuania. *Acta Theriologica, **42***(2): 113-122.

Juškaitis R. and Remeisis R. (2007). Summer nest sites of the common dormouse *Muscardinus avellanarius* L. in young woodlands of Lithuania. Polish Journal of Ecology, **55**, 795–803.

Juškaitis, R., Balčiauskas, L., Šiožinytė, V. (2013). Nest site selection by the hazel dormouse *Muscardinus avellanarius*: is safety more important than food?. Zoological Studies. Dec 1;**52**(1):53.

Juškaitis, R. (2014). *The Common Dormouse "Muscardinus Avellanarius": Ecology, Population Structure and Dynamics* (2nd ed.). Institute of Ecology of Vilnius University Publishers.

Kahmann, H. and von Frisch, O. (1950). *Zur Okologie der Haselmaus (Muscardinus avellanarius) in den Alpen.* Zoologische Jahrbücher, Abt. Systematik, **78**: 531–546.

Law, B. and Dickman, C. (1998). The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity & Conservation,* ***7***(3): 323-333.

Mainwaring, M.C., Hartley, I.R., Bearhop, S., Brulez, K., du Feu, C.R., Murphy, G., Plummer, K.E., Webber, S.L., James Reynolds, S. and Deeming, D.C., (2012). Latitudinal variation in blue tit and great tit nest characteristics indicates environmental adjustment. Journal of Biogeography, **39**(9): 1669-1677.

Mainwaring, M. C., Hartley, I. R., Lambrechts, M. M., & Deeming, D. C. (2014). The design and function of birds' nests. Ecology and Evolution, **4**(20): 3909-3928.

Manly, B.F.L., McDonald, L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. (2007). Resource selection by animals: statistical design and analysis for field studies. Springer Science & Business Media.

Mathews, F., Kubasiewicz, L., Gurnell, J., Harrower, C., McDonald, R. A., & Shore, R. (2018). A review of the population and conservation status of British mammals: Natural England.

Moran, M. D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos* ***100***(2): 403-405.

Morris, P. A. (2004). Dormice. British natural history series. Cromwell Press, Whittet Books Ltd., Linton, United Kingdom.

Müller-Stiess, H., 1996. Zur Habitatnutzung und Habitattrennung der Bilcharten (Myoxidae) Haselmaus (*Muscardinus avellanarius* L.), Gartenschläfer (Eliomys quercinus L.) und Siebenschläfer (Myoxus glis L.) im Nationalpark Bayerischer Wald. In: (H.Mùller-Stiess, ed.) Schläfer und Bilche. Tagungsbericht 1. Intern. Bilchkolloquium, St Oswald 1990. Verein der Freunde des Ersten Deutschen Nationalparks Bayerischer Wald e V., Neuschönau.

Pérez-Tris, J. and Tellería, J. L. (2002). Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines. *Acta Oecologica* ***23***(1): 13-21.

RCore Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL .

Rosalino, L. M., Ferreira, D., Leitão, I., & Santos-Reis, M. (2011). Selection of nest sites by wood mice Apodemus sylvaticus in a Mediterranean agro-forest landscape. Ecological research, **26**(2): 445-452.

RStudio Team (2020). RStudio: Integrated Development for R. RStudio, PBC, Boston, MA, USA. URL http://www.rstudio.com/.

Surgey, J., Feu, C. R. D., & Deeming, D. C. (2012). Opportunistic use of a wool-like artificial material as lining of tit (Paridae) nests. The Condor, **114**(2): 385-392.

van Horne, B. (1983). Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management:* 893-901.

van Laar, V. (1979). Summer nests of the hazel dormouse in north-eastern France. Acta Theriologica, **24** (37): 517–521.

van Laar, V. (1984). Geographical distribution and habitat selection of the hazel dormouse *Muscardinus avellanarius* (L., 1758) in the Netherlands. Lutra, **27**: 229–260

Verbeylen G., Andre A., Desmet A., Manzanares L., Mels B., Pulles R., Swinnen K., Vanseuningen I., Vermeiren M., and many more volunteers and students (2017). Nest site selection and use of other habitats by the hazel dormouse *Muscardinus avellanarius* in Voeren (Flanders). Report Natuur.studie 2017/3, Natuurpunt Research Department (Mammal Working Group), Mechelen, Belgium.

Vilhelmsen, H. (1996) The distribution, habitat requirements and nest sites of the common dormouse in Denmark. In: (H.Mùller-Stiess, ed.) Schläfer und Bilche. Tagungsbericht 1. Intern. Bilchkolloquium, St Oswald 1990. Verein der Freunde des Ersten Deutschen Nationalparks Bayerischer Wald e V., Neuschönau.

Vogel, P. (1997). Hibernation of recently captured Muscardinus, Eliomys and Myoxus: a comparative study. *Natura Croatica* ***63****:* 217-231.

Vogel, P. and Frey, H. (1995). The hibernation of the common dormouse *Muscardinus avellanarius* (Gliridae, Rodentia) in nature: nest, frequency of arousal and body temperature. *Bulletin de la Societe Vaudoise des Sciences Naturelles* ***83***(3): 217-230.

Wachtendorf W. (1951). Beiträge zur Ökologie und Biologie der Haselmaus (*Muscardinus avellanarius*) im Alpenvorland. Zoologische Jahrbücher, Abt. Systematik **80**: 189–204. [In German]

Walhovd, H. and Jensen, J. V. (1976). Some aspects of the metabolism of hibernating and recently aroused common dormouse *Muscardinus avellanarius* L.(Rodentia, Gliridae). *Oecologia* ***22***(4): 425-429.

Warton, D. I., & Hui, F. K. (2011). The arcsine is asinine: the analysis of proportions in ecology. Ecology, **92**(1): 3-10.

Zaytseva, H. (2006). Nest material of the common dormouse (*Muscardinus avellanarius L*.) used in nestboxes, Podilla (West Ukraine). *Polish Journal of Ecology* ***54***(3): 397-401.

Supplementary information

Table 1: Study sites used for nest material study.

Site name	Latitude	Longitude	No. of hibernation nests	Size	Habitat description
HF	50.640	-3.541	7	~1400 ha	coniferous forest with occasional broadleaved trees and shrubs such as oak, beech and hazel. Bramble and bracken are often abundant
FW	50.686	-3.728	3	~170 ha	
A38 HCR	50.634	-3.565	1	~ 2 ha	Linear belts of broadleaved shrubs and trees part of roadside verge planting beside dual carriageway trunk roads with conifers, scrub, ferns and bracken.
A30 OB	50.735	-3.979	2	2 ha	
A30 PCR	50.501	-4.679	1	0.9 ha	
SW	50.726	-3.942	5	~16 ha	mature deciduous woodland consisting of pedunculate oak, ash, sycamore, with occasional rowan, beech and birch. Bramble and bracken are often abundant.
OGC	50.725	-4.011	2	~12 ha	
OTP	50.730	-4.007	5	~7 ha	
OSW	50.732	-3.993	2	~4 ha	
HW	50.606	-3.722	4	40.3 ha	traditional hazel coppice. This area has been under management in the last 10 years as larch plantations are phased out.
RV	50.439	-3.778	1	~200 linear metres (0.05 ha)	mature hedgerow comprising mainly hazel with holly, honeysuckle and traveller's joy. The hedgerow is well connected to woodland blocks and a network of hedges.

Table 2: List of materials that were present in the areas where nests were found but were not used in nest construction.

Common name	Scientific name	Common name	Scientific name
rowan	*Sorbus aucuparia*	field maple	*Acer campestre*
holly	*Ilex aquifolium*	sycamore	*Acer pseudoplatanus*
bramble	*Rubus fruticosus*	wood rush	*Luzula* sp.
sweet chestnut	*Castanea sativa*	yew	*Taxus baccata*
gorse	*Ulex europaeus*	broom	*Cytisus scoparius*
silver birch	*Betula pendula*	Rushes	*Juncus* sp.
ivy	*Hedera helix*	hawthorn	*Crataegus monogyna*
blackthorn	*Prunus spinosa*	alder	*alnus glutinosa*
ash	*Fraxinus excelsior*	rhododendron	*Rhododendron ponticum*
wild cherry	*Prunus avium*	dogwood	*Cornus sanguinea*

Chapter 5

The will to live: Overwinter survival in different hazel dormouse *Muscardinus avellanarius* populations in southwest England

Chapter 5: The will to live: Overwinter survival in different hazel dormouse *Muscardinus avellanarius* populations in southwest England

Abstract

Knowledge of important demographic factors that influence the structure of animal populations is crucial for understanding species trends. Increased mortality during key life stages such as hibernation can have an impact on populations dynamics and yet, it is rarely estimated for most taxa. Using the hazel dormouse as a model species, an arboreal rodent that in Britain hibernates on the ground from late autumn to mid spring, apparent survival estimates were modelled based on capture-mark-recapture methodology. Animals were marked with passive microchip transponders and future recaptures recorded in four different populations in southwest England over periods between three and six years. In total, 465 hazel dormice were microchipped and 1054 encounter events were recorded. Apparent survival estimates were modelled according to age classes (juveniles and adults) and sex. Based on pooled data of the four populations sampled, apparent survival was estimated at 0.36 (0.29 - 0.44, 95% Confidence Intervals (CI)). The results indicated variations in the survival estimates amongst the populations studied, and at two sites, age was detected as an important factor affecting survival performance of juveniles more than adults. The outcomes of this analysis showed similarities with other studies using different methodologies in Britain and continental Europe. The findings of this study indicate that apparent survival rates amongst hazel dormice are relatively low and that this can present challenges for species that depend heavily on yearly reproductive success to self-regulate and maintain viable populations.

Introduction

Knowledge of demographic factors that influence the structure of animal populations is crucial for understanding species trends (Beissinger & Westphal 1998, Lebreton et al. 1992, Mills 2012b). Amongst other factors such as mortality, population growth and dispersal, survival of individuals is one of the pivotal determinants of population dynamics that should be monitored in both threatened and recovering populations (Väli et al. 2021).

For many animal species in temperate climates, survival through the distinct seasons is thought to be critical for the long term persistence of populations. The number of individuals at the beginning of any one season is dependent on the survivors from the previous seasons (Fretwell & Lucas 1969, Williams et al. 2015). The distinct winter conditions are important factors of species distributions, community composition, ecological interactions and can explain distinct life history strategies such as migration and hibernation (Pauli et al. 2013, Penczykowski et al. 2017, Williams et al. 2015). Several studies highlight that limited food availability and quality, together with harsh weather conditions during the winter season, poses a challenge for many small mammals (Solonen 2006, Shang et al. 2019, Rödel et al. 2004, Merritt et al. 2001).

The hazel dormouse, *Muscardinus avellanarius* is a small mammal that hibernates through the colder winter months in areas of temperate climate within its distribution range. To prepare for hibernation, the hazel dormouse accumulates fat reserves (Juškaitis 2001, Morris 2004) and gradually increases short bouts of daily torpor as the temperature drops before turning into longer hibernation periods that may last months (Juškaitis 2014a). Despite being a true hibernator, winter mortality amongst hazel dormice is thought to be quite high and many individuals that enter hibernation do not survive until the spring (Juškaitis 1999, Csorba 2003, Catzeflis 1984). Similarly, animals that emerge from hibernation in the spring are also vulnerable to erratic weather patterns, depletion of body fat reserves and lower foraging opportunities (Juškaitis 2014a).

With exception of some controlled experiments (Csorba 2003, Walhovd & Jensen 1976, Vogel & Frey 1995), survival rates for hazel dormice have mostly been derived from Capture-Mark-Recapture (CMR) methodologies. Early studies following this principle in Russia (Likhachev 1966), Sweden (Berg & Berg 1999) and Lithuania (Juškaitis 1999) indicated high mortality rates, with losses between 48% to 81% of marked animals overwinter, often in effect of age and sex of individuals (Juškaitis 2014a, Bieber et al. 2012). Age and sex specific survival estimates can be essential to understanding important life history characteristics, and variation in these estimates can be a key driver of population dynamics (Weldy et al. 2022). Adult survival is an important driver for long-lived vertebrates or declining populations, whilst impact of juvenile survival has been greater in short lived species or growing populations (Oli & Dobson 2003).

In Britain, there is little published information on mortality and survival rates of the hazel dormouse, apart from two studies. Information from a life table compiled for pooled data at the northern boundary of the British hazel dormouse distribution range reported survival rates of 0.2 for juveniles and 0.4 for adults (Bird et al. 2012); whilst in West Midlands region of England these rates were 0.25 and 0.6 respectively (Trout et al. 2018) by developing an Integrated Population Model (Abadi et al. 2010, Kéry & Schaub 2011).

However, true survival can be difficult to estimate because of losses to migration as well as the impact of imperfect detection on field surveys (Kellner & Swihart 2014) and the timing and causes of mortality are usually unknown (Sandercock 2020). The Cormack-Jolly-Sebber method (CJS, Lebreton et al. 1992) address these limitations involving live encounter data originated from CMR surveys by modelling conditions upon first capture and uses forward time modelling to estimate apparent survival adjusted by probability of encounter. The CJS models can provide a rich set of inferences about population survival (Nichols 2016) and is the fundamental model to use for live encounter data analysis. Many other different model forms for this type of data are considered extensions of the CJS (Sandercock 2020).

Using the CJS model, this study estimates the apparent survival of the hazel dormouse, the probability that an individual survives between sampling occasions and remains in the study area and hence is available for recapture, allowing for losses to mortality or permanent emigration (φ); and recapture rate, the probability that an individual is detected under field conditions given that it is available for encounters in the study area and includes individuals not available for detection or those present but not detected (p).

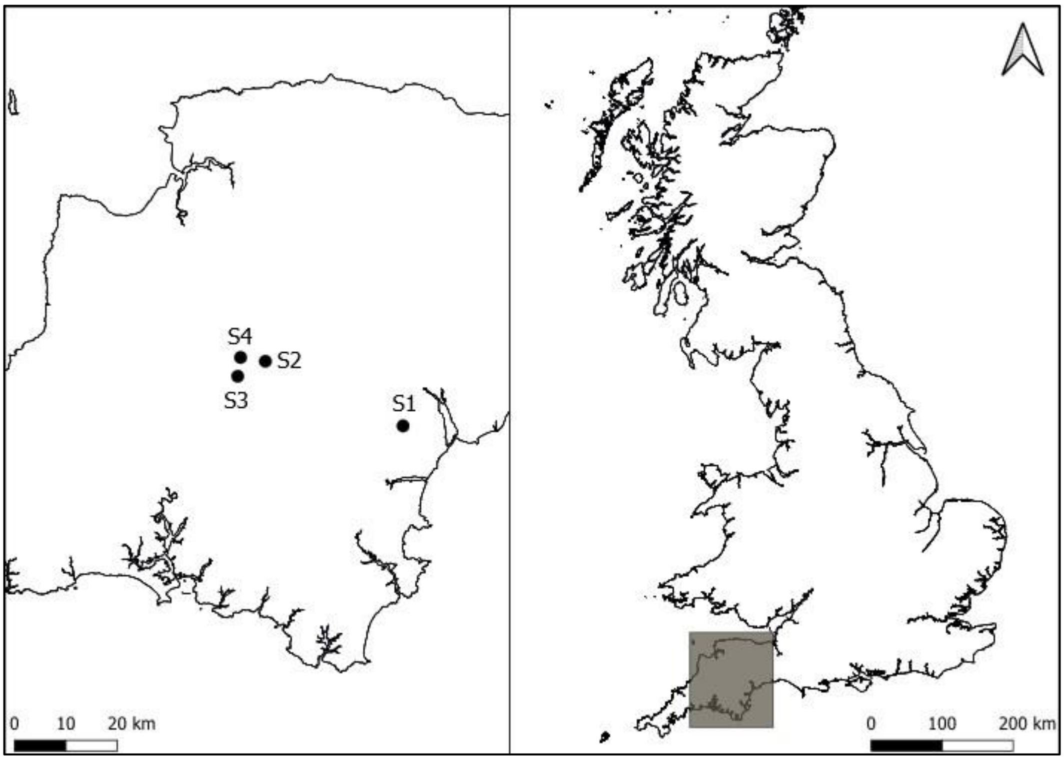
Methods

Wild dormice at four different sites were monitored using 50 nest boxes at each location in southwest England (Fig 5.1), between 2016 and 2021. The study areas comprise of typical dormouse habitats with two sites located in mature broadleaved woodland, S3 and S4, with sparse understorey; and two sites located in semi mature mixed woodland along two carriageway trunk roads, S1 and S2, with the first being contained within a 2 km section of a central reservation (Fig 5.2). Monitoring surveys were carried out at least five times a year between

April and November for a period of six years at S4, 5 years at S2 and S3 and for three years at S1. Captured dormice were sexed, classed as juvenile (animal born in the same year of the survey) or adult (individual that have overwintered at least once), weight measurements taken to the nearest 0.5g using a Pesola spring scale with an estimated accuracy of 0.3%, and their reproductive condition noted. Litter sizes in nest boxes were recorded at each site and refer to dependent suckling juveniles.

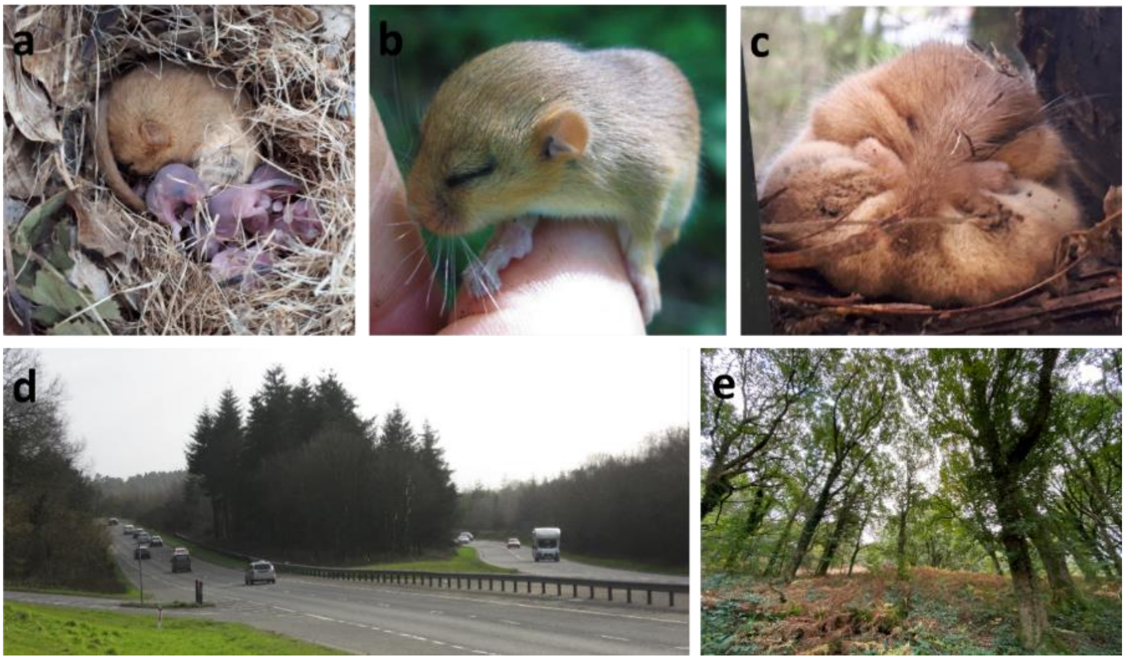
Adult and independent juvenile dormice (> 7.5g) were microchipped using 8mm passive integrated transponder (Trovan UniqueTM for animals ID-100A/1.4 mini passive integrated transponder (PIT)) injected subcutaneously using a specialist implanter gun between the back of the neck and shoulder blades. Future recaptures were recorded using a portable microchip scanner (Real Trace PetScan RT 100 V8BT) at the nest box site during monitoring visits whilst animals were weighed and sexed. Animals in visible distress, injured, heavily pregnant females or females caring for new-born litters, were not microchipped. The resulting CMR survey data was then analysed to investigate any differences in sex ratio and age classes between sites, and to quantify apparent survival rates and recapture probability.

Figure 5.1. *Location of the study areas in southwest England. Dots on the inset map represent location of individual study areas.*



Chi square tests were used to detect differences in sex ratio and age classes amongst the four sites and to investigate whether litters were being produced at a particular time of the year by classifying them according to the month they were born. ANOVA was then used to investigate relationships between sites and litter sizes. Statistical tests were undertaken using R (v 4.03) within the R Studio environment (R Core Team 2017; R Studio Team 2020).

Figure 5.2. *Photographs of hazel dormice of different age classes and examples of the habitat of study areas. Torpid female dormouse with new-born litter in the spring (a), young 'eyes-closed' juvenile dormouse (b), torpid adult male dormouse with visible accumulated fat reserves before hibernation period (c), roadside dormouse habitat in southwest England (d), broadleaved woodland with sparse understorey study area (e).*



Capture-mark-recapture statistical analyses were conducted using the Cormack-Jolly-Seber model (CJS, Lebreton et al. 1992) in Program MARK (White & Burnham 1999) applying the logit link to estimate apparent survival (φ), and recapture rate (*p*). Annual encounter histories for each site were compiled based on individual capture events and according to number of years surveyed (e.g. three to six years). The models using the pooled dataset covered the same three-year period across the four sites (2017 to 2019). Positive live encounters for any given year were recorded as a result of a single individual encounter regardless of how many recaptures were recorded within that particular year.

To evaluate the effect of sex and age on φ and *p* on the individual sites and pooled dataset analyses, marked animals were placed in four different groups: juvenile males, juvenile females, adult males, and adult females. To allow for the fact that juveniles age and become adults in subsequent years after marking, the time dependent φ model using the pooled dataset was adjusted to reflect this age effect, allowing the survival rate to be the same amongst adults regardless of whether individuals were marked as juveniles or marked as adults.

Model structures were chosen according to their ability to fit the data using Program MARK (1999) built in the bootstrap goodness of fit (GOF) procedure (White et al. 2001). This procedure was applied to the saturated model for each analysis with 1000 simulations. The saturated models are defined as being those which the number of parameters equalled the number of data points or data structures. In this study, the saturated models refer to φ (age/sex) *p* (constant) for the individual sites and φ (age/sex*time) *p* (constant) for the pooled dataset. The overdispersion parameter (c) was estimated for all models and c-hat was computed by the recommended method of dividing the deviance estimate of the original data by the mean of the simulated deviances (White et al. 2001). There was no overdispersion on individual site models, but the pool dataset model was adjusted to correct slight overdispersion as this may cause underestimation of the variance of parameter estimates leading to model choices that can be too complex for the data being analysed. Best models were selected using Akaike's information criterion (AIC) or quasi-AIC (QAIC) where over-dispersion was detected (Ver Hoef & Boveng 2007) to rank models in terms of their ability to explain the data. The intercept-only model, φ (.) *p* (.), was considered as the null model.

Results

Across the four study sites, 1054 hazel dormouse encounter events were recorded, and 465 dormice microchipped (Table 5.1). The mean number of dormouse live encounters recorded per survey session was much higher at the roadside sites S1 (26) and S2 (11) when compared to the broadleaved woodland sites S3 (5) and S4 (2). There were occasions when animals could not be marked because of their condition or escaped before being marked or scanned, but this number represents less than 1% of total encounter events.

The adult and juvenile ratio amongst all marked animals from the pooled dataset was very similar, with juveniles making up 52% of the total. However, there was a significant difference between the proportion of juveniles and adults amongst sites (Chi sq = 1.163, $p = 0.762$), with juveniles forming the majority of the marked animals in S2 and S3 (70%) whilst lower juvenile proportions were observed in S1 (35%) and S4 (52%, Fig 5.2). Dormice up to the age of four years old were recorded at every site and the oldest recorded individual was a ≥ 5 year old male at S3 that was marked as adult in 2016 and last recaptured in 2020.

The proportion of males and females amongst all marked animals were almost even at 51:49 respectively and similar trend was observed at individual sites. Sex ratio between adults was even at 50:50 and 51:49 amongst juveniles where a slightly higher number of males was observed. There was no significant difference in the proportion of males and females between sites (Chi sq = 1.1629, $p = <0.762$).

The number of litters recorded at each site varied as well as their sizes, which ranged from one to seven juveniles per litter, S1 ($n = 14, \bar{x} = 4.8$, SD= 1.1), S2 ($n = 16$, $\bar{x} = 4.5$, SD = 0.8), S3 ($n = 4$, $\bar{x} = 3.8$, SD = 0.5) and S4 ($n = 6$, $\bar{x} = 3.8$, SD = 2.1). However, there was no significant difference in litter size amongst sites ($F_{8,31} = 1.118$, $p = 0.378$). Litters were detected between May and October and based on the pooled data for all sites, there were no significant differences in the months in which litters were born (Chi sq = 20.247, $p = 0.163$). All recorded breeding females had one litter per year. Breeding amongst young-of-the-year females were recorded on five occasions, three at S1, one at S2 and one at S3.

Table 5.1. *Hazel dormouse capture-mark-recapture field survey results from four different sites in southwest England.*

Site	No. of survey sessions^ (years)	No. of dormouse encounters⁺	No. of marked animals	Marked as juvenile / adult	No. capture / recapture events	Total recaptures	No. animals recaptured / recapture rate *	Percentage of males / females
S1	17 (3)	450	224	78 / 146	355	168	83 / 38%	50 / 50
S2	31 (5)	354	115	80 / 35	244	195	34 / 30%	51 / 49
S3	35 (5)	181	103	72 / 31	184	108	36 / 35%	52 / 48
S4	36 (6)	69	23	11 / 12	37	22	8 / 35%	57 / 43

^ Number of survey sessions include events when no dormice were recorded

⁺ Total number of dormice recorded at the site during the monitoring visits including new-born and suckling juveniles

* Recapture count/rate includes recaptures in the same year

Apparent survival estimates

Overall, the effect of sex and/or age on apparent survival of the hazel dormouse was not significant (Table 5.2). Despite the age effect featuring on top models of the pooled dataset, both as constant in time and as variant over the survey years, it does not demonstrate that apparent survival from the juveniles in the first year differ as animals entered adulthood from the second year onwards. Sex featured in some of the top models but was not detected as a single significant factor effect or in combination with age and/or time.

Table 5.2. *Model rankings of estimated annual apparent survival (φ) and recapture probability (p) in respect of age and sex of hazel dormouse in four different populations in southwest England modelled with both φ and p constant over time (a), and pooled dataset modelled with φ time dependent (b). The null model is expressed as φ (.) p (.). Δ AICc = difference between model AICc and lowest AICc. k = number of model parameters. Deviance = total deviation between the computed model and a saturated model of the data). QAICc = quasi-AICc (used instead of AICc on the model corrected for overdispersion).*

a) Individual populations (φ and *p* constant over time)

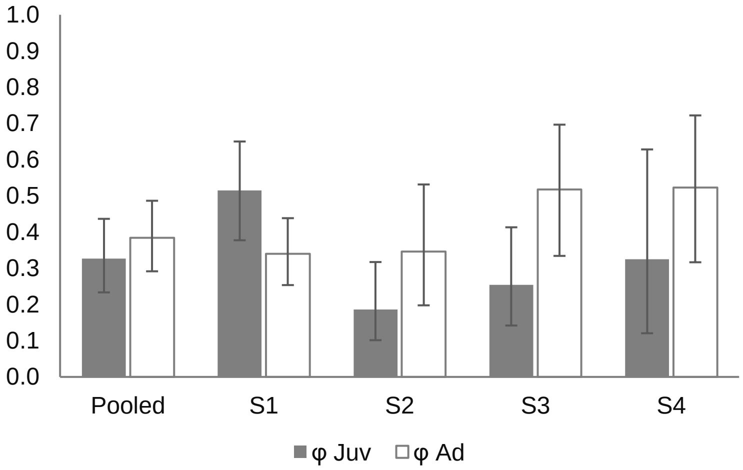
Site	**Model**	**AICc**	**ΔAICc**	**AICc Weight**	***k***	**Deviance**	**-2log(L)**
S1	φ (age) *p* (.)	265.054	0.000	0.699	3	17.600	258.927
	φ (.) *p* (.)	268.048	2.994	0.156	2	22.658	263.985
	φ (age & sex) *p* (.)	269.184	4.130	0.089	5	17.536	258.863
	φ (sex) *p* (.)	270.093	5.038	0.056	3	22.638	263.966
S2	φ (age) *p* (.)	125.317	0.000	0.508	3	38.919	119.097
	φ (.) *p* (.)	126.291	0.973	0.312	2	42.003	122.182
	φ (sex) *p* (.)	128.282	2.964	0.115	3	41.883	122.061
	φ (age & sex) *p* (.)	129.431	4.114	0.065	5	38.692	118.870
S3	φ (age) *p* (.)	128.845	0.000	0.495	3	44.494	122.58
	φ (age & sex) *p* (.)	129.519	0.674	0.353	5	40.758	118.85
	φ (sex) *p* (.)	132.502	3.657	0.079	3	48.151	126.24
	φ (.)*p* (.)	132.669	3.824	0.073	2	50.451	128.54
S4	φ (.) *p* (.)	58.297	0.000	0.497	2	40.059	53.922
	φ (age) *p* (.)	59.485	1.188	0.274	3	38.848	52.711
	φ (sex) *p* (.)	60.143	1.846	0.197	3	39.506	53.369
	φ (age & sex) *p* (.)	63.831	5.534	0.031	5	37.899	51.762

b) Pooled (φ time dependent, *p* constant over time)

Model	**QAICc**	**ΔQAICc**	**QAICc Weight**	***k***	**Deviance**	**-2log(L)**
φ (.)*p* (.)	327.420	0.000	0.394	2	18.178	420.396
φ (age*time) *p* (.)	327.668	0.248	0.348	5	12.274	412.720
φ (age) *p* (.)	328.664	1.244	0.175	3	17.385	419.364
φ (sex) *p* (.)	329.457	2.037	0.142	3	18.177	420.395
φ (sex*time) *p* (.)	331.789	4.370	0.044	5	16.395	418.078
φ (age & sex*time) *p* (.)	331.876	4.456	0.042	9	8.092	407.284
φ (age & sex) *p* (.)	332.773	5.353	0.027	5	17.379	419.356

Apparent survival estimates of the pooled dataset indicate that just over a third of individuals survive from year to year (Table 5.3). Between sites S1 and S3, where age was detected as a significant factor affecting apparent survival, juvenile estimates indicated a different trend when compared to adults. S1, the site with the lowest ratio of juveniles in the population, showed a higher apparent juvenile survival rate when compared to other sites and the pooled dataset (Fig 5.3).

Figure 5.3. *Comparison of estimates of adult and juvenile apparent survival between sites based on constant age (φ) and recapture probability (p) over time (model φ (age) p (.)). This simple model featured within 2 Δ AICc (difference between model AICc and lowest AICc) in all of the analysis of individual sites and with the pooled dataset. Error bars represent 95% confidence intervals.*



Discussion

Field survey results

Similar to other studies on the hazel dormouse, the sex ratio amongst the young was close to 1:1 with a slightly higher frequency of males that is considered normal amongst vertebrates (Caughley 1977). The average litter sizes recorded are similar to those recorded in other regions in continental Europe, but female dormice only produced one litter per season, whereas two or even three, have been reported by other authors in continental Europe (see Juškaitis 2014a for summary). Birth time of juvenile litters were spread over the active season with no clear seasonal peaks as this seems to be the case in regions where females have more than one litter per year as suggested by Bright & Morris (1996).

The pooled juvenile : adult ratio from this study is very similar to the 53% ‘marked as juveniles’ reported by Bird et al (2012) in the North Wales/Northwest England border, although there was variation between and amongst the sites. This variation can be attributed to self-regulation in populations of the hazel dormouse as the proportion of juveniles in the autumn is an index of reproductive success earlier in the year, and particularly associated with density of adult females (Juškaitis 2003*a*, Juškaitis 2014*a*). As a *K*-selected species, the reproduction process in dormouse populations is thought to be closely related to population density (Likhachev 1966). The breeding rate amongst hazel dormice has been reported to increase at low population densities, especially when adult female numbers are low, and may stimulate young-of-the year to breed to promote self-regulation in populations (Juškaitis 2014*a*). Similarly, high population densities can be counter balanced by increased proportion of non-breeding adult females to trigger reproductive suppression (Berg 1997) and may explain the higher number of adults at S1 when compared to other sites.

Apparent survival rates

From the published literature, dormouse survival rates have been found to vary widely depending on geographical location, length of the study and methodology used (Juškaitis 2014b). One of the main factors to consider is the sampling method as most studies on hazel dormice demography only account for animals that interact with nest boxes and, despite being a reliable method to survey and capture dormice (Chanin & Gubert 2011), individuals using only natural nest sites would be excluded. However, this factor is reduced by the chosen model structure that considers animals that are present in the study area but not captured and is one of the advantages of the CJS model.

The apparent survival estimates based on the top model of the pooled dataset was 0.36 (0.29 - 0.44, 95% Confidence Intervals (CI)) suggesting that only around a third of the population survives overwinter. Although age could not be distinguished as a significant factor from the pooled dataset, the survival estimates of 0.33 (0.23 - 0.44, 95% CI) for juveniles and 0.38 (0.29 - 0.49, 95% CI) for adults from one of the top models can be placed somewhere in the middle of the reported estimates in Britain that were assessed using different methodologies. Bird et al. (2012) reported survival rates from pooled data of two populations at the northern edge of the species British range of around 0.2 for juveniles and 0.4 for adults based on life tables; whilst Trout et al (2018) reported similar values of 0.25 for juveniles and slightly higher estimate of 0.6 for adults estimated using Integrated Population Models (Schaub & Abadi 2011) at locations subject to different forestry treatments.

The lowest survival estimates from this study, 0.24 (0.15 – 0.36, 95% CI) for both adults and juveniles at S2 over a period of 5 years is concerning. This estimate highlights how vulnerable local populations can be since an average litter size of 4.5 means, at this site, that only one of the juveniles is likely to survive. However, it is important to consider that sample sizes can influence apparent survival estimates because of the nature of CJS models. Although apparent survival estimates provided in this study take this into account through model selection, it cannot be discarded that results may reflect the difficulty of detecting unequal probabilities of capture in small data sets as highlighted by Hammond and Anthony (2006).

Estimates of survival rates for the hazel dormouse elsewhere in Europe also showed variation, from approximately 0.20 to 0.50 for adults and 0.19 to 0.55 for juvenile dormice (Berg & Berg 1999, Juškaitis 2014a, Likhachev 1966, Catzelis 1984, Catzeflis 1984) but in general, juvenile dormice had a lower survival estimates when compared to adults. Interestingly, S1, the roadside site within a central reservation, was the only site in this study, and elsewhere in the published literature for that matter, where juvenile apparent survival estimates were higher than adults. Given the location of this site and its fragmented nature, the lack of habitat connectivity could be a limiting factor constraining juvenile dispersal. According to Juškaitis (1997), dispersal is a necessary stage in the life of young dormice and, although lack of arboreal linkage may preclude dormouse dispersal (Bright & Morris 1991), roads are not considered to be complete barriers to hazel dormouse movements (Chanin & Gubert 2012, Schulz et al. 2012). Road crossings may even occur with a relative frequency by at least a percentage of the population, but the age classes of individuals and circumstances in which such crossings take place remains unclear (Kelm et al. 2015).

The apparent survival estimates presented in this study were somewhat similar to other studies using different methodologies but differed greatly when compared to Bieber et al (2012) using CJS and Program MARK whilst investigating timing of reproduction. In this study, adult survival estimates ranged from 0.96-0.98 over the hibernation period (October to May) and are considerably high when compared to other studies and almost double the estimates presented by Juškaitis (2014a) using life tables based on the same dataset.

Winter has always been thought to be a bottleneck for hazel dormouse survival and, as summarised by Juškaitis (2014), the main reasons for high winter mortality in hazel dormouse populations are associated with feeding conditions in the autumn, weather conditions in winter, and predation. Furthermore, in many places in Britain, where woodland management and forestry operations in dormouse habitat are normally carried out in late autumn and winter, together with wide public access, hibernaculum disturbance cannot be discounted and may affect survival rates at local population levels. Summer mortality has also been studied in Lithuania (Juškaitis 2014b), where it was estimated that approximately 38% of overwintered dormice were not recaptured again and many dormice that survive the winter die early in the spring, due to depletion of fat reserves and lower food availability as well as predation (Bieber et al. 2012).

Whilst it is useful to use other studies as benchmarks, it is important to mention that habitat characteristics differ from region to region. For example, the typical hazel dormouse habitat in Lithuania, where most information on the species survival rates originates, is described as mixed deciduous-coniferous forest dominated by birches *Betula* sp. and Norway spruce *Picea abis* (Juškaitis 2014a), whereas in the United Kingdom it is associated with different types of broadleaved woodlands, hazel coppice, hedgerows, scrub and conifer plantations amongst other suboptimal habitats (Bright et al. 2006). It is also relevant to highlight that the United Kingdom is the least wooded nation across the entire hazel dormouse distributional range (Forest Research 2015) and population dynamics of the species is likely to differ from other regions.

This study quantifies interannual survival rates at four populations of hazel dormouse in southwest England. Overall estimated survival rates were 0.36 (0.29 - 0.44, 95% CI). These rates are broadly similar to other estimates from populations in Britain and Europe; however, the use of the CJS models in this study allow assessment of uncertainty surrounding these estimates. As an elusive species that occurs at low densities where live encounters are infrequent, quantifying this uncertainty is important in understanding the limitations of models of population dynamics, and in propagating model uncertainty.

Chapter 6

Discussion

Chapter 6: Discussion

Introduction

Ecology, the branch of biology that focuses on how organisms interact with one another and their physical environment, has never been so relevant as it is in today’s rapidly changing world. During the new era of the Anthropocene (Crutzen 2006, Steffen et al. 2007), in order to fulfil human demands, natural ecosystems are being lost, modified, degraded, and fragmented at an unprecedented rate (Goudie 2018). Over exploitation of resources, human population growth and anthropogenic climate change are likely to have long lasting geophysical and biological impacts on the planet (Trexler 2015).

Over the millennia, species have evolved to respond to their environmental conditions. Seasonal changes can be strong determinants indicating optimal time for key life history transitions such as when to germinate, grow, migrate, feed, flower, mate, nest or hibernate. With a changing climate, unpredictable weather patterns are forcing species to alter their lifecycle and seasonal events (Badeck et al. 2004, Lane et al. 2012). While the effects of climate change on phenology have been well documented for some groups, such as plants and birds, others, including mammals, are less well studied.

Human activity also puts pressure on natural habitats. Woodlands and forests are among the habitats that are suffering most losses not only because of direct impact of human activities such as deforestation (Mataveli et al. 2021), fragmentation (Haddad et al. 2015), overexploitation (Goudie 2018), pollution, introduction of invasive non-native invasive species (Cazetta & Zenni 2020); but also, as consequence of climate change for example, pathogens outbreaks, diseases and pests (Linnakoski et al. 2019), hydrological changes (De Jong 2016) and wild fires (Jones et al. 2020).

For a woodland species with distinct life stages such as the hazel dormouse, unpredictable seasons, human pressure on their habitat, and knowledge gaps in their ecology can hamper conservation and monitoring efforts. With hibernation being one of the least studied aspects of the hazel dormouse ecology, research around the species has largely concentrated on captive animals during the winter or during the active season. Considering that hazel dormice can spend more time hibernating than active in some regions of their distributional range, every effort aimed at increasing scientific knowledge during this key life stage can result in more meaningful conservation efforts, which may also benefit other species that share similar habitats.

The findings I have presented in this thesis adds and develops the existing knowledge on dormouse ecology and population biology with a focus on hibernation in wild hazel dormouse of British populations. My objectives have been as follows. Firstly, in **Chapter 2**, I aimed to evaluate different methods of detecting hazel dormouse hibernacula, establish whether hibernation takes place within their autumnal home range and assess the impact of hibernation on body mass. Secondly, in **Chapter 3**, I developed a novel method of characterising hibernaculum locations of the hazel dormouse based on field observation and remote sensing. In **Chapter 4**, I investigated the structure and materials of hazel dormouse hibernation nests with a view to establish whether material availability was a constraining factor for selection of hibernaculum location. My final objective, covered in **Chapter 5**, was to assess a methodology to estimate wild hazel dormouse overwinter survival and demography of wild populations based on field observations.

In this concluding chapter I will summarise the findings, discuss the value and contribution this study makes in the wider context of conservation and lay out topics for future research

Methods of identifying hazel dormouse hibernaculum locations

One reason that little is known about the hibernation ecology of the hazel dormouse is that its hibernacula are cryptic and challenging to find in the field. Systematically collected datasets are rare, so much of our knowledge comes from serendipitous discoveries of individual nests. The difficulties involved in locating hibernacula also have implications for practical conservation; there is a lack of effective protocols for winter surveys for the species to protect populations from development or disturbance during woodland management. In **Chapter 2**, I evaluated different methods of identifying hazel dormouse hibernacula using telemetry, systematic searches, and wildlife detection dogs. The results indicated that telemetry and systematic searches are valid methods, but the use of detection dogs proved unsuccessful.

Telemetry, despite being the most intrusive method trialled, was the one that returned most useful information. I was able to accurately track individuals and collect novel information on species ecology, habitat use and behaviour that would not have been obtained otherwise. There were challenges involved with telemetry because shortfalls of technical failures, radio tag gnawing and difficulties in fitting collars during a period of considerable morphological change as the animals accumulation or lose of body weight were evident. Another disadvantage of telemetry is the high cost of radio tags and tracking equipment, something that can be unfeasible for small scale investigations. There is also the legal aspect and ethical constraints of this methodology as radio tracking is a regulated procedure under the Animals (Scientific Procedures) Act 1986 which requires training and specific licences.

Meanwhile, systematic searches for hazel dormouse hibernacula proved a simpler method, albeit with its own limitations as it only provides information of hibernaculum location and prone to surveyor bias.

Despite being a tried and tested methodology that works with other wildlife species (as well as numerous other purposes), the use of a trained wildlife detection dog to identify hibernaculum locations proved unsuccessful. One of limitations of this study was that I only used one dog and perhaps using others, specially of other breeds, could return better results. If proved successful, the used of wildlife detection dogs in dormouse surveys could enhance accuracy of systematic searches, especially those undertaken for the purpose of development (already used for great crested newt *Triturus cristatus* surveys), woodland management or forestry that involve habitat disturbance, fragmentation and/or destruction.

Hibernation ecology of the hazel dormouse

Interactions of any given organism with their surrounding environment is bound to be driven by complex mechanisms. As suggested by Southwood (1977), the connection between habitat characteristics with organisms' life history strategies is a key determinant of fitness in various habitats. However, hibernation as a distinct life history strategy, is often poorly studied in many species but may be vital to understanding how hibernating species respond to climate change. For the hazel dormouse in Britain, a species at the northwest edge of their range, the selection and availability of suitable habitats with adequate resources for its distinct life stages is crucial for their survival and maintenance of viable populations. While the habitat requirements for hazel dormice in summer are well understood, prior to this study little was known about habitat selection for hazel dormouse hibernacula in Britain, and the potential constraints on finding suitable sites for hibernation. This thesis addresses several key questions by identifying the topographic, structural, and microclimatic characteristics of chosen hibernaculum locations, demonstrating how dormice find suitable sites within their summer and autumn home range without having to venture further afield, and how far hazel dormice need travel to forage for suitable nesting materials.

In the interest of overwinter survival, their habitat must be selected by its ability to provide safe resting places, suitable foraging opportunities to boost fat reserves in preparation for hibernation, suitable locations in which to hibernate, with appropriate materials to build a hibernaculum, as well as adequate food sources and shelter for the following spring once hibernation ends.

Radio tracking results prior to hibernation indicated that hazel dormice are sedentary but with occasional movements further away from their home range (>100 m) potentially associated with location of available food sources. As autumn progressed, animals started to hibernate at different times, but juveniles stayed active longer than adults, as indicated by Juškaitis (2014a). Some animals remained active well into the winter, a period when the energy cost of thermoregulation is expected to be onerous but that can be offset by bouts of torpor and additional foraging.

As weight gain was detected during the early part of the winter, hazel dormice must be able to find food sources at this time of the year. It may an early indication that, with a warming climate, the dormouse hibernation season may be shortened as animals may have opportunities to counterbalance energy expenditure with winter foraging by reorganising their life cycles in response. During hibernation, I examined the weight loss rate of wild animals (**Chapter 2**) and my findings suggest that the rate was higher than studies carried out on captive animals fed *ad libitum* (Csorba 2003) or based on capture-mark-recapture studies using nest boxes (Juškaitis 2001).

In **Chapter 3**, I demonstrate how hazel dormice at the onset of hibernation face another challenge involving habitat selection when choosing hibernaculum location. Using remote sensing, I explain how animals favour locations with specific environmental characteristics for the location of their hibernaculum, at slopes in England and at the forest edge in the Netherlands. As part of the selection for hibernaculum location, I explain in **Chapter 4** that materials for nest building must also be present at the hibernaculum location as hazel dormice avoided travelling distances beyond one metre to collect them, but were flexible with regards to using different materials and in different ways. The plasticity in the use of different nest materials demonstrates how adaptable the hazel dormouse can be and suggests that materials alone may not be a defining factor for hibernaculum location.

The use of remote sensing to characterise hazel dormouse hibernaculum

High resolution remote sensing provides ecologists with opportunities to move beyond simple descriptions of habitat as vegetation type. Additionally, these technologies enable researchers to investigate the distribution of biotic and abiotic conditions that influence survival at different life stages. The main objective of **Chapter 3** was to develop a methodology to identify hibernaculum locations using high resolution LiDAR derived canopy structure and topography. For this study, I used data on hibernaculum locations from two countries, the Netherlands and England, where information of other habitat features were collected in situ for comparison. My findings indicate that remote sensed data identified environmental predictors that were not identified in the analysis of field measurements for sites in England where in situ data was collected. I also found that environmental characteristics surrounding hibernacula differed markedly between the two countries: topographic slope and sky view had a positive influence in hibernaculum location selection in England with animals choosing to hibernate on sloped ground, avoiding deep valleys; whilst canopy height was a more important driver in the Netherlands. The conclusion is that remote sensing proved capable of identifying highly localised environmental characteristics in the wider landscape and that there are specific variables favoured by hazel dormice when choosing hibernaculum locations.

The methodology using fine scale remotely sensed environmental data and habitat mapping I describe in **Chapter 3** gives a novel example of applying this technology to identify hibernaculum site selection by hazel dormice. It also opens opportunities to progress from habitat mapping and distribution modelling to identifying requirements for key life stages applicable not just for the hazel dormouse but also for other species.

Overwinter survival

Quantifying survival rates of wild animals is key to understanding the population dynamics and the viability of populations. Although this has been an area of central focus in ecological research (e.g. Berg & Berg 1999, Bieber et al. 2012), rare and elusive species are often overlooked. The hazel dormouse is one of the species that, despite the research interest it attracts, only a few studies have attempted to measure survival rates in the field, but without quantifying the level of uncertainty surrounding survival estimates. The main objective of **Chapter 5** was to estimate overwinter survival of different hazel dormouse populations. The results of my analysis indicate that, on average, 0.36 (0.29 - 0.44, 95% (CI) of the population survive per year. There were variations amongst the sites surveyed, and age was detected as an important factor affecting survival performance of juveniles more than adults at some of the studied populations. The outcomes of my analysis showed similarities with other studies undertaken in Britain with estimates placed between those reported by Bird et al (2012) and Trout et al (2018). Survival estimates from this study also echoed those from further afield in continental Europe where results were comparable in a similar pattern.

Low survival rates of *K*-strategists can present challenges as such species that depend heavily on yearly reproductive success to self-regulate and maintain viable populations. As indicated by Väli et al (2021), survival of individuals is one of the crucial determinants of population dynamics that needs to be monitored to understand species trends.

Implications for hazel dormouse conservation and habitat management recommendations

The hazel dormouse adaptability and versality in the use of habitat features and resources was evident in this research. This plasticity demonstrated by the species highlights the importance and potential advantages that habitat heterogeneity within their home range can offer.

Structural diversity within woodland habitats provides a range of nesting opportunities for hazel dormice, particularly during pre-hibernation period, where low growing thick scrub and mature trees with cracks, holes, crevices and climbing plants such as ivy, offer safe resting places. In young woodlands where older trees and standing deadwood are absent, creating potential nesting sites artificially by the method of tree veteranisation may be advantageous. This process mimics naturally occurring damage readily used for nesting by hazel dormice that could take years to occur, such as woodpecker holes, broken branches, stripped bark, cavities and hollows caused by fungi and lightning strikes.

Where suitable, supplementing existing woodland with the planting of native species of trees and shrubs will contribute to woodland age and structure diversity as well as increase foraging opportunities through the seasons. Similarly, the selective thinning of the woodland by felling selected trees can allow more space for remaining trees to develop. This process also opens up the canopy allowing more light to reach the woodland floor promoting the development of a diverse understorey and ground flora.

Whilst hazel dormice can use different locations to hibernate, they require sufficiently drained areas that are not prone to waterlogging. At these locations, canopy cover and a diverse ground flora, such as grasses, woodland wildflowers and ferns, will ensure adequate supplies of materials for nest building. Different species of plants will contribute for the establishment of a leaf litter layer over time, holding moisture and providing suitable hibernaculum locations. Decomposing dead wood on the ground that has either fallen down naturally or via purposely created log piles will promote suitable habitat for other small mammals, potential invertebrate prey, plants and bryophytes.

Contribution and relevance of this research

Knowledge of suitable hibernation sites of the hazel dormouse in the landscape is crucial for the welfare of the animals and protection of their habitat from human activities. Except for a brief period during the Covid-19 pandemic, the United

Kingdom has experienced a steady increase in yearly construction output of industrial, commercial, housing, and large infrastructure projects (Office for National Statistics 2022). Such activities that often involve unavoidable habitat disturbance, removal and/or fragmentation, and is only legally permitted within hazel dormouse habitat under a specific mitigation licence as both the animals and their habitat are fully protected (Natural England 2022). To comply with conditions of derogation licences, work in the winter often involve hazel dormouse hibernaculum searches to prevent animals from being injured or killed. Depending on the habitat structure and ground cover, this task can be laborious (because of low densities), costly and often inefficient.

Because of potential impact on nesting birds which are protected by law, vegetation clearance, woodland management and large-scale forestry operations are normally carried out in the autumn and winter months. Recent years have also seen outbreaks of tree pathogens such as *Phythophthora ramorum* (sudden oak death) and *Hymenoscyphus fraxineus*, resulting in an increase of Statutory Plant Health Notices served by the Forestry Commission (Forestry Research 2021) requiring landowners and managers to fell trees (often large areas) for biosecurity reasons.

Although winter is a time when impact on other species is less evident, it is a period when dormice are most vulnerable hibernating on the woodland floor. Knowledge of the best habitat patches within woodlands is vital to minimise impact on protected species.

The predictive hibernation habitat suitability model presented in **Chapter 3** can determine the way that sympathetic habitat clearance for development, woodland management or forestry operations can be carried out at landscape scale by highlighting areas where disturbance is likely to be detrimental to hibernating hazel dormouse. It can also inform timing of operations (i.e. areas to be worked on before the hibernation season) or combined with other precaution measures, such as the clearing of ground vegetation before habitat clearance takes place to discourage hazel dormice from building hibernacula within the impact zone and also facilitate systematic searches.

Further research

In a not-so-distant future, it is likely that battery powered GPS collars small enough to fit hazel dormice will become available. Such technology is likely to be less labour intensive, allowing for more individuals to be tracked constantly and simultaneously. The ability to track animals in space and time 24 hours a day will provide detailed insights of their ecology such as habitat use, location of nest sites, range, and foraging behaviour.

The use of finer resolution LiDAR derived data could potentially refine the models and improve accuracy. Already, recent LiDAR surveys over parts of Britain are being undertaken at 50cm resolution and more areas are gradually being made freely available. For smaller areas, drone LiDAR systems can currently deliver outputs at resolutions of up to 2cm. Furthermore, combining finer resolution remote sensing with GPS tracking would allow a much more detailed picture of habitat use and selection to emerge at all life-stages.

Information on survival estimates presented in this research, can also be used to model persistence of populations, particularly under a changing climate. Further research could address how winter weather/climate affects survival, and how summer/autumn resources affect the survival of subsequent cohorts. These factors will be critical for understanding how the species will respond to climate change, especially those at the margin of their range.

The methodology used to characterise hazel dormouse hibernaculum locations in **Chapter 3**, is suitable for investigations of habitat use of other species, especially those with life histories associated with microclimates or microhabitats including amphibians, butterflies, reptiles, ants as well as other mammals. The methodology could also be beneficial for forestry and agricultural purposes, matching the requirements of specific plant species or crop variety according to topography and/or microclimate conditions.

Concluding remarks

Understanding species ecology and habitat needs during different life stages is of principal importance for their conservation. And for that purpose, new methods arising from technological advances that adds to existing knowledge must be tried and validated. In this thesis, I have evaluated different search methods for the identification of hazel dormouse hibernaculum locations and provided new insights of their ecology over the hibernation period. I have investigated key environmental characteristics that make specific areas suitable for hibernation and developed a novel model capable of predicting, at landscape scale, where hibernation may take place. I have examined how hibernacula are built and the type of resources needed as well as the effort required to collect materials to build them. I have examined survival rates amongst hazel dormouse populations and how numbers are affected from year to year. The outcomes of the research presented in this thesis delivers new information on the ecology of the hazel dormouse, highlights how vulnerable to disturbance animals are in the winter and present practical measures to promote their conservation and welfare.

The steady decline in population numbers of species of priority conservation such as the hazel dormouse present serious challenges to conservation biologists. It highlights that our knowledge of species ecology, habitat requirements and conservation efforts must be greatly improved if we are to succeed reverting this current trend by creating favourable conditions to allow and promote biodiversity on Earth.

References

Abadi, F., Gimenez, O., Arlettaz, R. & Schaub, M. (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, **91**, 7.

Addicott, J. F., Aho, J. M., Antolin, M. F., Padilla, D. K., Richardson, J. S. & Soluk, D. A. (1987) Ecological neighborhoods: scaling environmental patterns. *Oikos*, **49**, 340.

Alexander, C., Korstjens A. H. & Hill R. A. (2018) Influence of micro-topography and crown characteristics on tree height estimations in tropical forests based on LiDAR canopy height models. *International journal of applied earth observation and geoinformation*, **65**, 105.

Antonelli, A., Smith, R., Fry, C., Simmonds, M. S., Kersey, P. J., Pritchard, H., Abbo, M., Acedo, C., Adams J., & Ainsworth, A. (2020) State of the World's Plants and Fungi. Royal Botanic Gardens (Kew); Sfumato Foundation.

Aplin, P. (2005) Remote sensing: ecology. *Progress in Physical Geography*, **29**, 104.

Arnett, E. B. (2006) A preliminary evaluation on the use of dogs to recover bat fatalities at wind energy facilities. *Wildlife Society Bulletin*, **34**, 1440.

Badeck, F. W., Bondeau, A., Böttcher, K., Doktor, D., Lucht, W., Schaber, J. & Sitch, S. (2004) Responses of spring phenology to climate change. New phytologist, **162**, 295.

Barnes, B. M. (1989) Freeze avoidance in a mammal: body temperatures below 0 degree C in an Arctic hibernator. *Science*, **244**, 1593.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L. & Maguire, K. C. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51.

Bartholomew, G. A. & Cade, T. J. (1957) Temperature regulation, hibernation, and aestivation in the little pocket mouse, Perognathus longimembris. *Journal of Mammalogy*, **38**, 60.

Bartholomew, G. A., Dawson W. R., & Lasiewski, R. C. (1970) Thermoregulation and heterothermy in some of the smaller flying foxes (Megachiroptera) of New Guinea. *Zeitschrift für vergleichende Physiologie*, **70**, 196.

Bartholomew, G. A. & Hudson, J. W. (1960) Aestivation in the Mohave ground squirrel Citellus mohavensis. *Bull. Mus. Comp. Zool*, **124**, 193.

Bartholomew, G. A. & MacMillen R. E. (1961) Oxygen consumption, estivation, and hibernation in the kangaroo mouse, Microdipodops pallidus. *Physiological Zoology*, **34**, 177.

Bartón, K. & Barton, M. (2020) Multi-model inference (Package MuMIn: version 1.43. 17).

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L.& Yarnell, R. W. (2020) Over-winter survival and nest site selection of the west-European hedgehog (Erinaceus europaeus) in arable dominated landscapes. *Animals*, **10**, 1449.

Beissinger, S. R. & Westphal, M. I. (1998) On the use of demographic models of population viability in endangered species management. *The Journal of wildlife management*, 821.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology letters*, **15**, 365.

Bennett, A. F. & Ruben, J. A. (1979) Endothermy and activity in vertebrates. *Science*, **206**, 649.

Bennie, J., Huntley, B., Wiltshire, A., Hill, M. O. & Baxter, R. (2008) Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological modelling*, **216**, 47.

Bennie, J., Wiltshire, A., Joyce, A., Clark, D., Lloyd, A., Adamson, J., Parr, T., Baxter, R. & Huntley, B. (2010) Characterising inter-annual variation in the spatial pattern of thermal microclimate in a UK upland using a combined empirical–physical model. *Agricultural and Forest Meteorology*, **150**, 12.

Berg, L. (1997) *Spatial distribution and habitat selection of the hazel dormouse Muscardinus avellanarius in Sweden*. Licentiate dissertation. Uppsala: Swedish University of Agricultural Sciences.

Berg, L. & Berg, A. (1998) Nest site selection by the dormouse *Muscardinus avellanarius* in two different landscapes. *Annales Zoologici Fennici*, **35**, 115.

Berg, L. & Berg, A. (1999) Abundance and survival of the hazel dormouse *Muscardinus avellanarius* in a temporary shrub habitat: a trapping study. *Annales Zoologici Fennici*, **36**, 159.

Berry, P., Sánchez-Arcilla Conejo, A., Betts, R. & Harrison, P. A. (2017) *High-end climate change in Europe: impacts, vulnerability and adaptation*. Sofia: Pensoft Publishers.

Bewley, J. D. (1997) Seed germination and dormancy. *The plant cell*, **9**, 1055.

Bieber, C., Juškaitis, R., Turbill, C. & Ruf, T. (2012) High survival during hibernation affects onset and timing of reproduction. *Oecologia*, **169**, 155.

Bird, S., Ambrose, M., Tatman, S. & Sanderson, S. (2012) A comparison of demographic statistics between two populations of *Muscardinus avellanarius*, in the north of its UK range. *Peckiana*, **8**, 215.

BlueSky International Ltd., (2020). https://www.bluesky-world.com/.

Bonan, G. B. & Doney, S. C. (2018) Climate, ecosystems, and planetary futures: The challenge to predict life in Earth system models. *Science*, **359**, 8328.

Booth, T. H. (2018) Species distribution modelling tools and databases to assist managing forests under climate change. *Forest Ecology and Management*, **430**, 196.

Botequim, B., Fernandes, P. M., Borges, J. G., González-Ferreiro, E. & Guerra-Hernández, J. (2019) Improving silvicultural practices for Mediterranean forests through fire behaviour modelling using LiDAR-derived canopy fuel characteristics. *International Journal of Wildland Fire*, **28**, 823.

Boyce, M. S., Haridas, C. V., Lee, C. T.& N. S. D. W. Group (2006) Demography in an increasingly variable world. *Trends in Ecology & Evolution*, **21**, 141.

Boyce, M. S. & McDonald, L. L. (1999) Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, **14**, 268.

Boyer, B. B. & Barnes, B. M. (1999) Molecular and metabolic aspects of mammalian hibernation: expression of the hibernation phenotype results from the coordinated regulation of multiple physiological and molecular events during preparation for and entry into torpor. *Bioscience*, **49**, 713.

Bradshaw, W. E. and Holzapfel, C. M. (2006) Evolutionary response to rapid climate change. *Science(Washington)*, **312**, 1477.

Bright, P. & Morris, P. (1990) Habitat requirements of dormice *Muscardinus avellanarius* in relation to woodland management in Southwest England. *Biological Conservation*, **54**, 307.

Bright, P. & Morris, P. (1991) Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius*, in diverse low-growing woodland. *Journal of Zoology*, **224**, 177.

Bright, P. & Morris, P. (1992) Ranging and nesting behaviour of the dormouse, *Muscardinus avellanarius* , in coppice with standards woodland. *Journal of Zoology,* **226**, 589.

Bright, P. W., (1992) Ecology and conservation of the dormouse (*Muscardinus avellanarius*). Doctoral dissertation. University of London, London, UK.

Bright, P. & Morris, P. (1993) Foraging behaviour of dormice *Muscardinus avellanarius* in 2 contrasting habitats. *Journal of Zoology*, **230**, 69.

Bright, P. & Morris, P. (1996) Why are dormice rare? A case study in conservation biology. *Mammal Review*, **26**, 157.

Bright, P., Morris, P.& Mitchell-Jones, A. J. (2006) The Dormouse Conservation Handbook. English Nature, Peterborough.

Bright, P. W., Morris, P. A. & Wiles, N. J. (1996) Effects of weather and season on the summer activity of dormice *Muscardinus avellanarius*. *Journal of Zoology*, **238**, 521.

Buckley, L. B., Hurlbert, A. H. & Jetz, W. (2012) Broad-scale ecological implications of ectothermy and endothermy in changing environments. *Global Ecology and Biogeography*, **21**, 873.

Cartledge, E. L., Baker, M., White, I., Powell, A., Gregory, B., Varley, M., Hurst J. L. & Stockley, P. (2021) Applying remotely sensed habitat descriptors to assist reintroduction programs: A case study in the hazel dormouse. *Conservation Science and Practice*, **3**, 544.

Catzeflis, F. (1984) Etude d'une population de Muscardins (*Muscardinus avellanarius*) lors du repos journalier (Mammalia, Gliridae). *Revue suisse de Zoologie*, **91**, 851.

Caughley, G. (1977) Analysis of vertebrate populations. Chichester: John Wiley and Sons.

Cavender-Bares, J., Schneider, F. D., Santos, M. J., Armstrong, A., Carnaval, A., Dahlin, K. M., Fatoyinbo, L., Hurtt, G. C., Schimel, D., Townsend, P. A., Ustin, S. L., Wang, Z.& Wilson, A. M. (2022) Integrating remote sensing with ecology and evolution to advance biodiversity conservation. *Nature Ecology & Evolution*, **6**, 506.

Cazetta, A. L. & Zenni, R. D. (2020) Pine invasion decreases density and changes native tree communities in woodland Cerrado. *Plant Ecology & Diversity*, **13**, 85.

Chanin, P. & Gubert, L. (2011) Surveying hazel dormice (*Muscardinus avellanarius*) with tubes and boxes: a comparison. *Mammal Notes*, **4**, 1.

Chanin, P. & Gubert, L. (2012) Common dormouse (*Muscardinus avellanarius*) movements in a landscape fragmented by roads. *Lutra*, **55**, 3.

Chanin, P. & Woods, M. J. (2003) *Surveying dormice using nest tubes: results and experiences from the South West Dormouse Project*. English Nature Peterborough.

Cisneros-Araujo, P., Goicolea, T., Mateo-Sánchez, M.C., García-Viñás, J.I., Marchamalo, M., Mercier, A. and Gastón, A., (2021). The role of remote sensing data in habitat suitability and connectivity modeling: Insights from the Cantabrian brown bear. *Remote Sensing*, **13**(6), 1138.

Clare, J. D., Anderson, E. M., MacFarland, D. M. & Sloss, B. L. (2015) Comparing the costs and detectability of bobcat using scat-detecting dog and remote camera surveys in central Wisconsin. *Wildlife Society Bulletin*, **39**, 210.

Clark, W. (2010) Principles of landscape ecology. *Nature Education Knowledge*, **3**, 34.

Clarke, A. & Pörtner H. O. (2010) Temperature, metabolic power and the evolution of endothermy. *Biological Reviews*, **85**, 703.

Crowley, P. H. (1992) Resampling methods for computation-intensive data analysis in ecology and evolution. *Annual Review of Ecology and Systematics*, 405.

Crutzen, P. J., (2006) The "anthropocene". In: *Earth system science in the anthropocene*: 13. Berlin: Springer.

Csorba, A. (2003) Influence of body weight on hibernation of the common dormouse (*Muscardinus avellanarius*). *Acta Zoologica Academiae Scientiarum Hungaricae*, **49**, 39.

Daams, R. & De Bruijn, H. (1995) A classification of the Gliridae (Rodentia) on the basis of dental morphology. *Hystrix-the Italian Journal of Mammalogy*, **6**, 3.

Dalagnol, R., Wagner, F. H., Galvão, L. S., Streher, A. S., Phillips, O. L., Gloor, E., Ometto J. P. & Aragão, L. E. (2021) Mind the gap: New insights on large-scale forest dynamics over Amazonian forests from airborne lidar and canopy gap data. EGU General Assembly 2021, online, 19–30 Apr 2021, EGU21-11046, https://doi.org/10.5194/egusphere-egu21-11046.

Dale, M. R. & Fortin, M-J. (2014) *Spatial analysis: a guide for ecologists*. Cambridge: Cambridge University Press.

De Bruyn, L., Gyselings, R., Kirkpatrick, L., Rachwald, A., Apoznański, G. & Kokurewicz, T. (2021) Temperature driven hibernation site use in the Western barbastelle Barbastella barbastellus (Schreber, 1774). *Scientific reports*, **11**, 1.

De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K. & Lenoir, J. (2019) Global buffering of temperatures under forest canopies. *Nature ecology & evolution*, **3**, 744.

De Jong, C. (2016) European perspectives on forest hydrology. *Forest Hydrology: Processes, Management and Assessment; Amatya, D., Williams, T., Bren, L., De Jong, C., Eds***,** Wallinford: CABI, 69.

de Vries, J. P. R., Koma, Z., WallisdeVries M. F. & Kissling, W. D. (2021) Identifying fine-scale habitat preferences of threatened butterflies using airborne laser scanning. *Diversity and Distributions*, **27**, 1251.

del Valle, J. D., Peralta, F. C. & Arjona, M. I. J. (2020) Factors affecting carcass detection at wind farms using dogs and human searchers. *Journal of Applied Ecology*, **57**, 1926.

Dematteo, K. E., Rinas, M. A., Sede, M. M., Davenport, B., Argüelles, C. F., Lovett, K. & Parker, P. G. (2009) Detection dogs: an effective technique for bush dog surveys. *The Journal of wildlife management*, **73**, 1436.

Dietz, M., Büchner, S., Hillen, J. & Schulz, B. (2018) A small mammal's map: identifying and improving the large-scale and cross-border habitat connectivity for the hazel dormouse *Muscardinus avellanarius* in a fragmented agricultural landscape. *Biodiversity and Conservation*, **27**, 1891.

Dong, P. & Chen, Q. (2017) *LiDAR remote sensing and applications*. CRC Press.

Ehlers, S. (2012) The importance of hedgerows for hazel dormice (*Muscardinus avellanarius*) in Northern Germany. *Peckiana*, **8**, 41.

Else, P. & Hulbert, A. (1981) Comparison of the" mammal machine" and the" reptile machine": energy production. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, **240**, 3.

Farmer, C. (2000) Parental care: the key to understanding endothermy and other convergent features in birds and mammals. *The American Naturalist*, **155**, 326.

Foden, W. B., Butchart, S. H., Stuart, S. N., Vié, J.-C., Akçakaya, H. R., Angulo, A., DeVantier, L. M., Gutsche, A., Turak, E. & Cao, L. (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. *PloS one*, **8**, 65427.

Forest Research, (2015) Forest cover: international comparisons.[Online] https://www.forestresearch.gov.uk/tools-and-resources/statistics/forestry-statistics/forestry-statistics-2018/international-forestry-3/forest-cover-international-comparisons/. Accessed on 16 June 2022.

Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in physical geography*, **19**, 474.

Franklin, J. (2010) *Mapping species distributions: spatial inference and prediction*. Cambridge: Cambridge University Press.

Fretwell, S. D. & Lucas, H. L. (1969) On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica*, **19**, 16.

Frohn, R. C. (2018) *Remote sensing for landscape ecology: new metric indicators for monitoring, modeling, and assessment of ecosystems*. Boca Raton: CRC Press.

Frolking, S., Palace, M. W., Clark, D., Chambers, J. Q., Shugart, H. & Hurtt, G. C. (2009) Forest disturbance and recovery: A general review in the context of spaceborne remote sensing of impacts on aboveground biomass and canopy structure. *Journal of Geophysical Research: Biogeosciences*, **114**, G00E02.

Garabedian, J. E., Moorman, C. E., Peterson, M. N. & Kilgo, J. C. (2017) Use of LiDAR to define habitat thresholds for forest bird conservation. *Forest Ecology and Management*, **399**, 24.

Geiser, F. (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.*, **66**, 239.

Getzin, S., Löns, C., Yizhaq, H., Erickson, T. E., Muñoz-Rojas, M., Huth, A. & Wiegand, K. (2022) High-resolution images and drone-based LiDAR reveal striking patterns of vegetation gaps in a wooded spinifex grassland of Western Australia. *Landscape Ecology*, **37**(3), 829.

Goldberg, A. R., Conway, C. J., Mack, D. E. & Burak, G. (2020) Winter Versus Summer Habitat Selection in a Threatened Ground Squirrel. *The Journal of Wildlife Management*, **84**(8), 1548.

Gomes, V. H., IJff, S. D., Raes, N., Amaral, I. L., Salomão, R. P., de Souza Coelho, L., de Almeida Matos, F. D., Castilho, C. V., de Andrade Lima Filho, D.& López, D. C. (2018) Species Distribution Modelling: Contrasting presence-only models with plot abundance data. *Scientific reports,* **8**, 1.

Goodwin, C. E., Hodgson, D. J., Bailey, S., Bennie, J. & McDonald, R. A. (2018) Habitat preferences of hazel dormice *Muscardinus avellanarius* and the effects of tree-felling on their movement. *Forest ecology and management*, **427**, 190.

Goodwin, C. E. D., Hodgson, D. J., Al-Fulaij, N., Bailey, S., Langton, S. & Macdonald, R. A. (2017) Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse *Muscardinus avellanarius* population. *Mammal Review*, **47**(3), 183.

Goodwin, K. M., Engel, R. E. & Weaver, D. K. (2010) Trained dogs outperform human surveyors in the detection of rare spotted knapweed (*Centaurea stoebe*). *Invasive Plant Science and Management*, **3**, 113.

Google Maps, (2021) West Devon area, Central coordinates 50.744, -3.975. [Online] Available at https://www.google.co.uk/maps. Accessed 21 February 2022. .

Goudie, A. S. (2018) *Human impact on the natural environment*. Oxford: John Wiley & Sons.

Grigg, G. C., Beard L. A. & Augee M. L. (2004) The evolution of endothermy and its diversity in mammals and birds. *Physiological and Biochemical Zoology*, **77**, 982.

Gubert, L., McDonald, R., Wilson, R., Chanin, P., Bennie, J. & Mathews, F. (2022) The elusive winter engineers: structure and materials of hazel dormouse hibernation nests. *Journal of Zoology*, **316**, 81.

Hagar, J. C., Yost, A. & Haggerty, P. K. (2020) Incorporating LiDAR metrics into a structure-based habitat model for a canopy-dwelling species. *Remote Sensing of Environment*, **236**, 111499.

Hao, T., Elith, J., Guillera-Arroita, G. & Lahoz-Monfort, J. J. (2019) A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. *Diversity and Distributions*, **25**, 839.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P. & Collins, C. D. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, **1**(2), e1500052.

Hammond, E. L. & Anthony, R. G. (2006). Mark–recapture estimates of population parameters for selected species of small mammals. Journal of Mammalogy, **87**(3), 618.

Harrison, R. L. (2006) From the field: A comparison of survey methods for detecting bobcats. *Wildlife Society Bulletin*, **34**, 548.

Hastings, A. (2013) *Population biology: concepts and models*. New York: Springer Science & Business Media.

He, K. S., Bradley, B. A., Cord, A. F., Rocchini, D., Tuanmu, M. N., Schmidtlein, S., Turner, W., Wegmann, M. & Pettorelli, N. (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, **1**, 4.

Hecker, K., Bako, B.& Csorba, G. (2003) Distribution ecology of the Hungarian dormouse species, based on the national biodiversity monitoring system. *Acta Zoologica Academiae Scientiarum Hungaricae*, **49**, 45.

Heldmaier, G., Ortmann, S. & Elvert, R. (2004) Natural hypometabolism during hibernation and daily torpor in mammals. *Respiratory physiology & neurobiology*, **141**, 317.

Hibbard, K. A., Crutzen, P. J., Lambin, E. F., Liverman, D., Mantua, N. J., McNeill, J. R., Messerli, B. & Steffen, W. (2006) Decadal interactions of humans and the environment. In: *Integrated history and future of people on earth.* (eds R. Costanza, L. Graumlich & W.Steffen), pp. 341–375. Dahlem Workshop Report 96. Boston: MIT Press.

Hinds, D. S. & MacMillen, R. E. (1985) Scaling of energy metabolism and evaporative water loss in heteromyid rodents. *Physiological Zoology*, **58**, 282.

Hock, R. J. (1951) The metabolic rates and body temperatures of bats. *The Biological Bulletin*, **101**, 289.

Hutterer, R., Kryštufek, B., Yigit, N., Mitsainas, G., Meinig, H. & Juškaitis, R. (2021) *Muscardinus avellanarius* (amended version of 2016 assessment). T*he IUCN Red List of Threatened Species* 2021: e.T13992A197519168. https://dx.doi.org/10.2305/IUCN.UK.2021-1.RLTS.T13992A197519168.en. Accessed on 13 July 2022.

Jaskierniak, D., Lucieer, A., Kuczera, G., Turner, D., Lane, P., Benyon, R. & Haydon, S. (2021) Individual tree detection and crown delineation from Unmanned Aircraft System (UAS) LiDAR in structurally complex mixed species eucalypt forests. *ISPRS Journal of Photogrammetry and Remote Sensing*, **171**, 171.

Johnson, D. H. (1980) The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**, 65.

Johnson, J. B. & Omland, K. S. (2004) Model selection in ecology and evolution. *Trends in ecology & evolution*, **19**, 101.

Jonasson, K. A. & Willis, C. K. (2012) Hibernation energetics of free-ranging little brown bats. *Journal of Experimental Biology*, **215**, 2141.

Jones, M. W., Smith, A., Betts, R., Canadell, J. G., Prentice, I. C. & Le Quéré, C. (2020) Climate change increases the risk of wildfires. *ScienceBrief Review*, **116**, 117.

Juškaitis, R. (1997) Ranging and movement of the common dormouse Muscardinus avellanarius in Lithuania. *Acta Theriologica*, **42**, 113.

Juškaitis, R. (1999) Demographic structure of two common dormouse (*Muscardinus avellanarius* L.) populations in Lithuania. *Proceedings of the Latvian Academy of Sciences Section B Natural Exact and Applied Sciences*, **53**, 107.

Juškaitis, R. (2003a) Abundance dynamics and reproduction success in the common dormouse, *Muscardinus avellanarius*, populations in Lithuania. *Folia Zoologica*, **52**, 239.

Juškaitis, R. (2003b) New data on distribution, habitats and abundance of dormice (gliridae) in Lithuania. *Acta Zoologica Academiae Scientiarum Hungaricae*, **49**, 55.

Juškaitis, R. (2007) Habitat selection in the common dormouse *Muscardinus avellanarius* (L.) in Lithuania. *Baltic Forestry*, **13**, 89.

Juškaitis, R. (1997) Ranging and movement of the common dormouse *Muscardinus avellanarius* in Lithuania. *Acta Theriologica,* **42**, 113.

Juškaitis, R. (1999) Winter mortality of the common dormouse (*Muscardinus avellanarius*) in Lithuania. *Folia Zoologica,* **48**, 11.

Juškaitis, R. (2001) Weight changes of the common dormouse (*Muscardinus avellanarius* L.) during the year in Lithuania. *Trakya Univ. J. Sci. Res. Ser. B,* **2**, 79.

Juškaitis, R. (2008) The common dormouse, *Muscardinus avellanarius*. *Ecology, population structure and dynamics. Institute of Ecology of Vilnius University Publishers, Vilnius*.

Juškaitis, R. (2014a) *The Common Dormouse "Muscardinus Avellanarius": Ecology, Population Structure and Dynamics,* 2nd edn.: Institute of Ecology of Vilnius University Publishers.

Juškaitis, R. (2014b) Summer mortality in the hazel dormouse (*Muscardinus avellanarius*) and its effect on population dynamics. *Acta Theriologica*, **59**, 311.

Juškaitis, R. & Büchner, S. (2013) *The hazel dormouse: Muscardinus avellanarius*. Westarp Wissenschaften-Verlagsgesellschaft mbH.

Juškaitis, R. & Siozinyte, V. (2008) Habitat requirements of the common dormouse (*Muscardinus avellanarius*) and the fat dormouse (Glis glis) in mature mixed forest in Lithuania. *Ekologia (Bratislava)*, **27**, 143.

Kadaster, (2021) Actueel Hoogtebestand Nederland (AHN, in Dutch). [Online] https://app.pdok.nl/ahn3-downloadpage. Accessed on 05 January 2021.

Kahmann, H. & von Frisch, O. (1950) *Zur Okologie der Haselmaus (Muscardinus avellanarius) in den Alpen*. Fischer.

Kearney, M., Shine R. & Porter W. P. (2009) The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences,* **106**, 3835.

Kelm, J., Lange, A., Schulz, B., Göttsche, M., Steffens, T. & Reck, H. (2015) How often does a strictly arboreal mammal voluntarily cross roads? New insights into the behaviour of the hazel dormouse in roadside habitats. *Folia Zoologica,* **64**, 342.

Kéry, M. & Schaub, M. (2011) *Bayesian population analysis using WinBUGS: a hierarchical perspective*. Oxford: Academic Press.

Khosravipour, A., Skidmore, A. K., Wang, T., Isenburg, M. & Khoshelham, K. (2015) Effect of slope on treetop detection using a LiDAR Canopy Height Model. *ISPRS journal of photogrammetry and remote sensing*, **104**, 44.

Koma, Z., A. Seijmonsbergen, C. & Kissling, W. D. (2021) Classifying wetland-related land cover types and habitats using fine-scale lidar metrics derived from country-wide Airborne Laser Scanning. *Remote Sensing in Ecology and Conservation*, **7**, 80.

Kooijman, B. & Kooijman, S. (2010) *Dynamic energy budget theory for metabolic organisation*. Cambridge: Cambridge university press.

Lane, J. E., Kruuk, L. E., Charmantier, A., Murie, J. O. & Dobson, F. S. (2012) Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature, **489**, 554.

Leadley, P., Pereira, H. M., Alkemade, R., Fernandez-Manjarrés, J. F., Proença, V., Scharlemann, J. P., Walpole, M. J. (2010) Biodiversity scenarios: projections of 21st century change in biodiversity, and associated ecosystem services. Secretariat of thre Convention on Biological Diversity. Montreal. Technical Series no. 50, 132 pages.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological monographs*, **62**, 67.

Leitão, P. J. & Santos, M. J. (2019) Improving models of species ecological niches: a remote sensing overview. *Frontiers in Ecology and Evolution*, **7**, 9.

Lembrechts, J. J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider S., Pellissier, L., Pauchard, A., Ratier Backes, A. & Dimarco, R. D. (2019a) Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography*, **28**, 1578.

Lembrechts, J. J., Nijs, I. & Lenoir, J. (2019b) Incorporating microclimate into species distribution models. *Ecography*, **42**, 1267.

Lemmers, P., van der Putten, T., Vonk, L., Krekels, R., Müskens, G., Bekker, D.L., La Haye, M., & Foppen, R.P.B. (2022) Zenderonderzoek hazelmuis 2018-2019. Onderzoek naar najaarsactiviteit en winterverblijfplaatsen. Natuurbalans - Limes Divergens BV / Zoogdiervereniging, Nijmegen (in Dutch).

Lennon, J. T. & Jones, S. E. (2011) Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nature reviews microbiology*, **9**, 119.

Levin, S. A., Grenfell, B., Hastings, A.& Perelson, A. S. (1997) Mathematical and computational challenges in population biology and ecosystems science. *Science*, **275**, 334.

Lewis, S. L. & Maslin, M. A. (2015) Defining the anthropocene. *Nature*, **519**, 171.

Lichstein, J. W., Dushoff, J., Ogle, K., Chen, A., Purves, D. W., Caspersen J. P., & Pacala, S. W. (2010) Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. *Ecological Applications*, **20**, 684.

Likhachev, G. (1966) Population structure of the common dormouse (*Muscardinus avellanarius*). *Bull. Mosk. Obsc. Ispyt. Prir. Biologie*, **71**, 18.

Linnaeus, C. (1758) *Systema naturae*. Stockholm Holmiae (Laurentii Salvii).

Liu, H., Shen, X., Cao, L., Yun, T., Zhang, Z., Fu, X., Chen, X. & Liu, F. (2020) Deep learning in forest structural parameters estimation using airborne LiDAR data. *IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing*, **14**, 1603.

Long, R. A., Donovan, T. M., Mackay, P., Zielinski, W. J. & Buzas, J. S. (2007) Effectiveness of scat detection dogs for detecting forest carnivores. *The Journal of Wildlife Management*, **71**, 2007.

Lyman, C. P. (2013) *Hibernation and torpor in mammals and birds*. London: Elsevier.

Maclean, I. M., Mosedale, J. R. & Bennie, J. J. (2019) Microclima: An r package for modelling meso-and microclimate. *Methods in Ecology and Evolution*, **10**, 280.

Malcolm, J. R., Liu, C., Neilson, R. P., Hansen, L. & Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation biology*, **20**, 538.

Mallet, C. & Bretar, F. (2009) Full-waveform topographic lidar: State-of-the-art. *ISPRS Journal of photogrammetry and remote sensing*, **64**, 1.

Manly, B., McDonald, L., Thomas, D. L., McDonald, T. L. & Erickson, W. P. (2007) *Resource selection by animals: statistical design and analysis for field studies*. London: Springer Science & Business Media.

Massimino, D., Beale, C. M., Suggitt, A. J., Crick, H. Q., Macgregor, N. A., Carroll, M. J., Maclean ,I. M. & Pearce-Higgins, J. W. (2020) Can microclimate offer refuge to an upland bird species under climate change? *Landscape Ecology*, **35**, 1907.

Mataveli, G. A., Chaves, M. E., Brunsell, N. A. & Aragão, L. E. (2021) The emergence of a new deforestation hotspot in Amazonia. *Perspectives in Ecology and Conservation*, **19**, 33.

Mathews, F., Swindells, M., Goodhead, R., August, T. A., Hardman, P., Linton, D. M. & Hosken, D. J. (2013) Effectiveness of search dogs compared with human observers in locating bat carcasses at wind-turbine sites: A blinded randomized trial. *Wildlife Society Bulletin,* **37**, 34.

Mayor, S. J., Schneider, D. C., Schaefer, J. A. & Mahoney, S. P. (2009) Habitat selection at multiple scales. *Ecoscience*, **16**, 238.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C. & Cushman, S. A. (2016) Multi-scale habitat selection modeling: a review and outlook. *Landscape Ecology*, **31**, 1161.

McIntosh, R. P. (1986) *The background of ecology: concept and theory*. Cambridge: Cambridge University Press.

Merritt, J. F., Lima, M. & Bozinovic, F. (2001) Seasonal regulation in fluctuating small mammal populations: feedback structure and climate. *Oikos*, **94**, 505.

Miller-Rushing, A. J., Høye, T. T., Inouye, D. W. & Post, E. (2010) The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 3177.

Mills, C. A. (2012a) Conservation and ecology of the hazel dormouse, *Muscardinus avellanarius*. Doctoral dissertation. University of Exeter, Exeter, UK.

Mills, L. S. (2012b) *Conservation of wildlife populations: demography, genetics, and management*. Chichester: John Wiley & Sons.

Morin, X. & Thuiller, W. (2009) Comparing niche-and process-based models to reduce prediction uncertainty in species range shifts under climate change. *Ecology*, **90,** 1301.

Morris, D. W. (1988). Habitat-dependent population regulation and community structure. *Evolutionary Ecology*, **2**(3), 253.

Morris, D. W. (2003). Toward an ecological synthesis: a case forhabitat selection. *Oecologia*, **136**, 1.

Morris, P. A. (1999) *Muscardinus avellanarius* . In: A. J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralík, and J. Zima (eds), *The Atlas of European Mammals*. London: Academic Press.

Morris, P. A. (2003) A review of research on British dormice (Gliridae) and the effect of increasing public and scientific awareness of these animals. *Acta Zoologica Academiae Scientiarum Hungaricae*, **49**, 125.

Morris, P. A. (2004) Dormice. British natural history series. Linton: Cromwell Press.

Næsset, E. & Økland, T. (2002) Estimating tree height and tree crown properties using airborne scanning laser in a boreal nature reserve. *Remote Sensing of Environment*, **79**, 105.

Nagendra, H. (2001) Using remote sensing to assess biodiversity. *International journal of remote sensing*, **22**, 2377.

Naveh, Z. & Lieberman, A. S. (2013) *Landscape ecology: theory and application*. New York: Springer Science & Business Media.

Neal, D. (2018) *Introduction to population biology*. Cambridge: Cambridge University Press.

Nichols, J. D. (2016) And the first one now will later be last: time-reversal in Cormack–Jolly–Seber models. *Statistical Science*, **31**, 175.

Oli, M. K. & Dobson, F. S. (2003) The relative importance of life-history variables to population growth rate in mammals: Cole's prediction revisited. *The American Naturalist*, **161**, 422.

Olsoy, P. J., Shipley, L. A., Rachlow, J. L., Forbey, J. S., Glenn, N. F., Burgess, M. A. & Thornton, D. H. (2018) Unmanned aerial systems measure structural habitat features for wildlife across multiple scales. *Methods in Ecology and Evolution*, **9**, 594.

Panchetti, F., Sorace, A., Amori, G. & Carpaneto, G. M. (2007) Nest site preference of common dormouse (*Muscardinus avellanarius*) in two different habitat types of Central Italy. *Italian Journal of Zoology*, **74**, 363.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, **37**, 637.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37.

Passalacqua, P., Belmont, P., Staley, D. M., Simley, J. D., Arrowsmith, J. R., Bode, C. A., Crosby, C., DeLong, S. B., Glenn, N. F. & Kelly, S. A. (2015) Analyzing high resolution topography for advancing the understanding of mass and energy transfer through landscapes: A review. *Earth-Science Reviews*, **148**, 174.

Pauli, J. N., Zuckerberg, B., Whiteman, J. P. & Porter, W. (2013) The subnivium: a deteriorating seasonal refugium. *Frontiers in Ecology and the Environment*, **11**, 260.

Penczykowski, R. M., Connolly, B. M. & Barton, B. T. (2017) Winter is changing: trophic interactions under altered snow regimes. *Food Webs*, **13**, 80.

Pettorelli, N., Safi, K. & Turner, W. (2014) Satellite remote sensing, biodiversity research and conservation of the future. *Philosophical Transactions of the Royal Society B*, **369**, 20130190.

Pianka, E. R. (1970) On r-and K-selection. *The american naturalist*, **104**, 592.

Pretzlaff, I., Radchuk, V., Turner, J. M. & Dausmann, K. H. (2021) Flexibility in thermal physiology and behaviour allows body mass maintenance in hibernating hazel dormice. *Journal of Zoology*, **314**, 1.

QGIS Development Team, (2020) QGIS Geographic Information System. QGIS Development Team (Ed.). QGIS Association.

R Core Team (2017) R: A language and environment for statistical computing. *PBC. https://www.R-project.org/*.

R Studio Team, (2020) R Studio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Randin, C. F., Ashcroft, M. B., Bolliger, J., Cavender-Bares, J., Coops, N. C., Dullinger, S., Dirnböck, T., Eckert, S., Ellis, E. & Fernández, N. (2020) Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote sensing of environment*, **239**, 111626.

Reiners, T., Nöding, J.& Encarnação, J. (2012) Habitat suitability model for the common dormouse (*Muscardinus avellanarius*) based on high-resolution climatic, landscape and forest inventory data. *Peckiana*, **8**, 87.

Rhodes, M. W., Bennie, J. J., Spalding, A., ffrench-Constant, R. H. & Maclean, I. M. (2022) Recent advances in the remote sensing of insects. *Biological Reviews*, **97**, 343.

Richards, C., White, A., Hurrell, E. & Price, F. (1984) The food of the common dormouse, *Muscardinus avellanarius*, in south Devon. *Mammal Review*, **14**, 19.

Risser, P. G. (1987) Landscape ecology: state of the art. *Landscape heterogeneity and disturbance*. New York: Springer-Verlag.

Rödel, H. G., Bora, A., Kaetzke, P., Khaschei, M., Hutzelmeyer, H. & Von Holst, D. (2004) Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. *Oecologia*, **140**, 566.

Rosa, M. F. & Stow, D. A. (2014) Mapping fuels at the wildland-urban interface using colour ortho-images and LiDAR data. *Geocarto International*, **29**, 570.

Rose, R. A., Byler, D., Eastman, J. R., Fleishman, E., Geller, G., Goetz, S., Guild, L., Hamilton, H., Hansen M. & Headley, R. (2015) Ten ways remote sensing can contribute to conservation. *Conservation Biology*, **29**, 350.

Rosenzweig, M. L. (1981) A theory of habitat selection. *Ecology,* **62**, 327.

Rossolimo, O. L., Potapova, E. G., Pavlinov, I. Y., Kruskop, S. V. & Voltzit, O. V., (2001) Soni (Myoxidae) mirovoi fauny [Dormice (Myoxidae) of the World]. Moskva: Izdatel’stvo Moskovskogo universiteta (in Russian).

Roughgarden, J., Running, S. W. & Matson, P. A. (1991) What does remote sensing do for ecology? *Ecology*, **72**, 1918.

Ruf, T. & Geiser, F. (2015) Daily torpor and hibernation in birds and mammals. *Biological Reviews*, **90**, 891.

Sánchez-Díaz, B. & Mata-Zayas, E. E. (2019) Remote sensing as indispensable technology in ecology to support the protection of biodiversity: A review. *International Journal of Conservation Science*, **10**, 811.

Sandercock, B. K. (2020) Mark-recapture models for estimation of demographic parameters. *In: Murray, D. L. and Sandercock, B. K. (eds), Population ecology in practice*. Chichester: John Wiley & Sons.

Sara, M., Casamento, G. & Spınnato, A. (2001) Density and breeding of *Muscardinus avellanarius* L., 1758 in woodlands of Sicily. *Trakya Üniversitesi Fen Bilimleri Dergisi*.

Schaub, M. & Abadi, F. (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, **152**, 227.

Schmidt-Nielsen, K. (1997) *Animal physiology: adaptation and environment*. Cambridge: Cambridge University Press.

Schulz, B., Ehlers, S., Lang, J., & Büchner, S. (2012) Hazel dormice in roadside habitats. *Peckiana*, **8**, 39.

Sendor, T. & Simon, M. (2003) Population dynamics of the pipistrelle bat: effects of sex, age and winter weather on seasonal survival. *Journal of Animal Ecology*, **72**, 308.

Shang, G.-Z., Zhu, Y.-H., Wu, Y., Cao, Y.-F. & Bian, J.-H. (2019) Synergistic effects of predation and parasites on the overwinter survival of root voles. *Oecologia*, **191**, 83.

Shaw, W. T. (1921) Moisture and altitude as factors in determining the seasonal activities of the Townsend ground squirrel in Washington. *Ecology*, **2**, 189.

Shaw, W. T. (1925) Duration of the aestivation and hibernation of the Columbian ground squirrel (Citellus columbianus) and sex relation to the same. *Ecology*, **6**, 75.

Silvertown, J. & Charlesworth, D. (2009) *Introduction to plant population biology*. Oxford: John Wiley & Sons.

Slastionenko, J. B., (1990) Data on maternal behavior and postnatal development of the dormouse (*Muscardinus avellanarius* L.). In: Salmanov A. V. & Darevsky I. S. (eds.) Issledovaniya po zoologii pozvonochnykh. Trudy Zoologicheskogo instituta AN SSSR (Investigations on Vertebrates Zoology. Proceedings of the Zoological Institute Academy of Sciences USSR), **213**, 143 (in Russian with English summary).

Solonen, T., (2006) Overwinter population change of small mammals in southern Finland. In: *Annales Zoologici Fennici*: 295*.* Finnish Zoological and Botanical Publishing Board.

Southwood, T. R. (1977) Habitat, the templet for ecological strategies? *Journal of animal ecology*, **46**, 337.

Spanhove, T., Borre, J. V., Delalieux, S., Haest, B. & Paelinckx, D. (2012) Can remote sensing estimate fine-scale quality indicators of natural habitats? *Ecological Indicators*, **18**, 403.

Spitzenberger, F. & Bauer, K. (2001) *Die Säugetierfauna Österreichs*. Bundesministerium für Land-und Forstwirtschaft, Umwelt und Wasserwirtschaft.

Stanhope, K., (2015) Ecological Monitoring using Wildlife Detection Dogs: Bat Carcass Searches at the Wanlip Wind Turbine. *Practice – Bulletin of the Chartered Institute of Ecology and Environmental Management,* **88**, 29.

Stark, J. R. & Fridley, J. D. (2022) Microclimate-based species distribution models in complex forested terrain indicate widespread cryptic refugia under climate change. *Global Ecology and Biogeography*, **31**(3), 562.

Steffen, W., Crutzen, P. J. & McNeill, J. R. (2007) The Anthropocene: are humans now overwhelming the great forces of nature. *AMBIO: A Journal of the Human Environment*, **36**, 614.

Steffen, W., Sanderson, R. A., Tyson, P. D., Jäger, J., Matson, P. A., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H.-J. & Turner, B. L. (2006) *Global change and the earth system: a planet under pressure*. Berlin: Springer Science & Business Media.

Stommel, H. (1963) Varieties of oceanographic experience. *Science*, **139**, 572.

Thieme, H. R. (2018) *Mathematics in population biology*. Woodstock: Princeton University Press.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F., De Siqueira, M. F., Grainger, A.& Hannah, L. (2004) Extinction risk from climate change. *Nature*, **427**, 145.

Thuiller, W., Albert, C., Araujo, M. B., Berry, P. M., Cabeza, M., Guisan, A., Hickler, T., Midgley, G. F., Paterson, J. & Schurr, F. M. (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in plant ecology, evolution and systematics*, **9**, 137.

Tilman, D., Clark, M., Williams, D. R., Kimmel, K., Polasky, S. & Packer, C. (2017) Future threats to biodiversity and pathways to their prevention. *Nature*, **546**, 73.

Title, P. O. & Bemmels, J. B. (2018) ENVIREM: an expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*, **41**, 291.

Trexler, A. (2015) *Anthropocene fictions: the novel in a time of climate change*. University of Virginia Press.

Trout, R., Brooks, S.& Rudlin, P. (2012a) Hazel dormice in British conifer forests and their ecology in a pine plantation during restoration to broadleaf. *Peckiana*, **8**, 31.

Trout, R. C., Brooks, S., Combe, F. J. & Rudlin, P. (2018) The different effects of periodic experimental tree removal patterns on the population demography of the hazel dormice (*Muscardinus avellanarius*) in a conifer plantation. *Folia Zoologica*, **67**, 110.

Trout, R. C., Brooks, S. E., Rudlin, P. & Neil, J. (2012b) The effects of restoring a conifer Plantation on an Ancient Woodland Site (PAWS) in the UK on the habitat and local population of the Hazel Dormouse (*Muscardinus avellanarius*). *European Journal of Wildlife Research*, **58**, 635.

Turner, M. G. (1989) Landscape ecology: the effect of pattern on process. *Annual review of ecology and systematics*, 171.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E. & Steininger, M. (2003) Remote sensing for biodiversity science and conservation. *Trends in ecology & evolution*, **18**, 306.

Urban, M. C. (2015) Accelerating extinction risk from climate change. *Science*, **348**, 571.

Väli, Ü., Kalvāns, A. & Tuvi, J. (2021) Apparent survival and dispersal in a recovered Osprey population: effects of age, sex and social status. *Journal of Ornithology*, **162**, 1025.

Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*, 893.

Ver Hoef, J. M. & Boveng, P. L. (2007) Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology*, **88**, 2766.

Verbeylen, G. (2006) Status and conservation of the common dormouse (*Muscardinus avellanarius*) in the Province of Limburg (Flanders, Belgium). *Lutra*, **49**, 75.

Verbeylen, G., Andre, A., Desmet, A., Manzanares, L., Mels, B., Pulles, R., Swinnen, K., Vanseuningen, I., Vermeiren, M. & students (2017) *Nest site selection and use of other habitats by the hazel dormouse Muscardinus avellanarius in Voeren (Flanders)*. Report Natuur.studie 2017/3, Natuurpunt Research Department (Mammal Working Group), Mechelen, Belgium.

Viejou, R., Avgar, T., Brown, G. S., Patterson, B. R., Reid, D. E., Rodgers, A. R., Shuter, J., Thompson, I. D. & Fryxell, J. M. (2018) Woodland caribou habitat selection patterns in relation to predation risk and forage abundance depend on reproductive state. *Ecology and evolution*, **8**, 5863.

Vierling, K. T., Vierling, L. A., Gould, W. A., Martinuzzi, S. & Clawges, R. M. (2008) Lidar: shedding new light on habitat characterization and modeling. *Frontiers in Ecology and the Environment*, **6**, 90.

Vihervaara, P., Auvinen, A.-P., Mononen, L., Törmä, M., Ahlroth, P., Anttila, S., Böttcher, K., Forsius, M., Heino J. & Heliölä, J. (2017) How essential biodiversity variables and remote sensing can help national biodiversity monitoring. *Global Ecology and Conservation*, **10**, 43.

Vilhelmsen, H. (1996) The distribution, habitat requirements and nestsites of the common dormouse in Denmark. *schläfer und Bilche. tagungsbericht*, **1**, 49.

Visser, M. E. (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 649.

Vogel, P. & Frey, H. (1995) The hibernation of the common dormouse *Muscardinus avellanarius* (Gliridae, Rodentia) in nature: nest, frequency of arousal and body temperature. *Bulletin de la Societe Vaudoise des Sciences Naturelles*, **83**, 217.

Walhovd, H. (1976) Partial arousals from hibernation in a pair of common dormice, *Muscardinus avellanarius* (Rodentia, Gliridae), in their natural hibernaculum. *Oecologia*, **25**, 321.

Walhovd, H. & Jensen, J. V. (1976) Some aspects of the metabolism of hibernating and recently aroused common dormouse *Muscardinus avellanarius* L.(Rodentia, Gliridae). *Oecologia*, **22**, 425.

Wang, C., Morgan, G. & Hodgson, M. E. (2021) SUAS for 3D tree surveying: Comparative experiments on a closed-canopy earthen dam. *Forests*, **12**, 659.

Wang, L. C. (1978) Energetic and field aspects of mammalian torpor: the Richardson's ground squirrel. In: *Strategies in cold*: *Natural torpidity and thermogenesis* (eds L.C.H. Wang & J.W. Hudson), page 109. New York: Academic Press.

Warren, R., VanDerWal, J., Price, J., Welbergen, J. A., Atkinson, I., Ramirez-Villegas, J., Osborn, T. J., Jarvis, A., Shoo, L. P., Williams S. E. & Lowe, J. (2013) Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change*, **3**, 678.

Wasser, S. K., Davenport, B., Ramage, E. R., Hunt, K. E., Parker, M., Clarke, C. & Stenhouse, G. (2004) Scat detection dogs in wildlife research and management: application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. *Canadian Journal of Zoology*, **82**, 475.

Węgrzyn, E. (2013) Resource allocation between growth and endothermy allows rapid nestling development at low feeding rates in a species under high nest predation. *Journal of avian biology*, **44**, 383.

Weldy, M. J., Lesmeister, D. B. & Epps, C. W. (2022) Emigration effects on estimates of age-and sex-specific survival of two sciurids. *Ecology and Evolution*, **12**, e8833.

Werner, J., Sfakianakis, N., Rendall, A. D. & Griebeler, E. M. (2018) Energy intake functions and energy budgets of ectotherms and endotherms derived from their ontogenetic growth in body mass and timing of sexual maturation. *Journal of theoretical biology*, **444**, 83.

White, C. R., Phillips, N. F. & Seymour, R. S. (2005) The scaling and temperature dependence of vertebrate metabolism. *Biology Letters*, **2**, 125.

White, G. C. & Burnham, K. P. (1999) Program MARK: survival estimation from populations of marked animals. *Bird study*, **46**, S120.

White, G. C., Burnham, K. P. & Anderson, D. R. (2001) Advanced features of program MARK. In: *Wildlife, land, and people: priorities for the 21st century. Proceedings of the second international wildlife management congress.* The Wildlife Society, Bethesda, Maryland, USA: 368.

Wiens, J. A. (1989) Spatial scaling in ecology. *Functional ecology*, **3**, 385.

Williams, C. M., Henry, H. A. & Sinclair, B. J. (2015) Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biological Reviews*, **90**, 214.

Wilz, M. (1999) *Hibernation, Aestivation und taeglicher Torpor beim Siebenschlaefer (Glis glis, L.)*. Doctorate dissertation. Phillips University, Marburg, Germany.

Wilz, M. & Heldmaier, G. (2000) Comparison of hibernation, estivation and daily torpor in the edible dormouse, Glis glis. *Journal of Comparative Physiology B*, **170**, 511.

Wolton, R. (2009) Hazel dormouse *Muscardinus avellanarius* (L.) nest site selection in hedgerows. *Mammalia*, **73**, 7.

Wu, J. & Loucks, O. L. (1995) From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *The Quarterly review of biology*, **70**, 439.

Wuttke, N., Büchner, S., Roth, M. & Böhme, W. (2012) Habitat factors influencing the distribution of the hazel dormouse (*Muscardinus avellanarius*) in the Ore Mountains, Saxony, Germany. *Peckiana*, **8**, 21.

Zellweger, F., De Frenne, P., Lenoir, J., Rocchini, D. & Coomes, D. (2019) Advances in microclimate ecology arising from remote sensing. *Trends in Ecology & Evolution*, **34**, 327.